Journal of Nematology 26(3):286–295. 1994.

Competition between the Plant-parasitic Nematodes *Pratylenchus neglectus* and *Meloidogyne chitwoodi*

KODIRA C. UMESH, HOWARD FERRIS,[1] AND DAVID E. BAYER[2]

Abstract: In experiments on competition between *Pratylenchus neglectus* and *Meloidogyne chitwoodi* in barley, the species that parasitized the roots first inhibited penetration by the latter species. Prior presence of *P. neglectus* impeded the development of *M. chitwoodi*. *Pratylenchus neglectus* reduced egg production, final population levels, and reproductive index of *M. chitwoodi*. The reduction was linearly related to initial population densities of *P. neglectus*. Initial population densities of *M. chitwoodi* had no effect on final population levels of *P. neglectus*. Carbon assimilation by barley plants was reduced when either nematode species was present alone, but not when both were present together. Both nematode species assimilated lower amounts of carbon when present together than when present alone. A split-root experiment demonstrated that translocatable chemicals were not involved in the competition between the two species.

Key words: competition, interaction, lesion nematode, *Meloidogyne chitwoodi*, nematode, *Pratylenchus neglectus*, root-knot nematode.

Interspecific competition is common between plant-parasitic nematodes (7). For example, root penetration and final population levels of *Pratylenchus neglectus* (Rensch) Filipjev and Schuurmans Stekhoven and *Meloidogyne chitwoodi* Golden, O'Bannon, Santo, and Finley were lower when both species were present together than when either was present alone (23).

Three of the six categories of competition proposed by Schoener (19), preemptive competition, chemical competition, and consumptive competition, are useful for summarizing competitive interactions among plant-parasitic nematodes. Preemptive competition occurs when a unit of space is occupied by one species, thereby preventing another species from entering that space. Nematode species may inhibit other nematode species through competition for feeding sites (5,6). Chemical competition occurs when a species produces a toxin or allelochemical that suppresses another species. For example, a nematode-induced change in host physiology may render the host unsuitable for a competing species (8,9,13,15). Consumptive competition occurs when some essential resource, usually food, is consumed by one species, reducing or depleting the quantity available to the competing species. Inhibition of root growth and disruption of root tissues in a host plant may be indications of consumptive competition (20,21). However, these categories are not mutually exclusive.

The objectives of this study were to determine the nature of competition between *P. neglectus* and *M. chitwoodi*, the effect of competition on fecundity of *M. chitwoodi*, and the extent to which the effects are density dependent.

Materials and Methods

Soil from potato fields near Tulelake, northern California, (sand 48%, silt 37%, clay 15%, organic matter 11.5%, pH 7.2, cation exchange capacity 41.5 c mol Kg^{-1} and electrical conductivity 2.71 dS m^{-1}), or white silica sand (Corona Industrial Sand Co., Corona, CA), were autoclaved and aerated for 1 week before use. Cultures of *P. neglectus* and *M. chitwoodi* were maintained in the greenhouse on barley and tomato, respectively. Inoculum of *P. neglectus* was obtained by placing infected roots in a mist chamber, and inoculum of *M. chitwoodi* was obtained by shaking infected roots in 0.05% NaOCl for 4 minutes and allowing the eggs to hatch in a mist

Received for publication 11 March 1993.

[1] Former Graduate Student and Professor, Department of Nematology, University of California, Davis, CA 95616.

Current address of senior author: Department of Plant Pathology, University of California, Davis, CA 95616.

[2] Professor, Department of Botany, University of California, Davis, CA 95616.

The authors thank Drs. B. A. Jaffee, E. P. Caswell-Chen, and J. M. Duniway for reviewing this manuscript.

chamber (12,13). All experiments were conducted at least twice. Except as indicated, data from the different trials were pooled and subjected to statistical analyses by blocking for trial effects.

Preemptive competition: Barley seedlings were established in 150-cm^3 plastic cups containing white silica sand and placed in a constant-temperature water bath at 20 ± 2 C. About 800 each of *P. neglectus* mixed life stages or *M. chitwoodi* second-stage juveniles (J2) were added to each cup in different treatment combinations. The treatments were *P. neglectus, M. chitwoodi, P. neglectus* + *M. chitwoodi* added simultaneously, *P. neglectus* added 5 days before *M. chitwoodi,* and *M. chitwoodi* added 5 days before *P. neglectus.* The first inoculations were made when seedlings were 10 days old. The treatments were replicated eight times in a completely randomized design. The plants were watered lightly after adding the nematodes and fertilized twice weekly with half-strength Hoaglands nutrient solution. Deionized water was added on other days. Seven days after the second inoculation, roots were stained with acid fuchsin (4) and the number of each nematode species in the roots was determined with a dissecting microscope.

The trial was repeated in a similar manner, except that seedlings were 12 days old at the first inoculation. For the treatments receiving either nematode species earlier than the other, ca. 900 *P. neglectus* or 750 *M. chitwoodi* were added per cup. Seven days later ca. 800 *P. neglectus* or 350 *M. chitwoodi* were added to each cup. Treatments were replicated five times in a completely randomized design. Data from the two trials were pooled and were subjected to analysis of variance and Duncan's multiple-range test.

In a third trial, the treatment schedule was the same as for the first trial, but inoculum levels were 1,200 *P. neglectus* or 800 *M. chitwoodi.* Twenty replicate plants of each treatment were maintained in a growth chamber at 20 C. Five plants were destructively sampled 7, 14, 21, and 30 days after adding the nematodes. The roots were stained with acid fuchsin, and the numbers of *M. chitwoodi* and their developmental stages were determined. Data on the number of different stages of *M. chitwoodi* at each sampling time were analyzed by a nonparametric one-way procedure and Kruskall-Wallis test. Differences among the developmental stages of each nematode in roots were tested by a pairwise Mann-Whitney test (18).

Chemical competition: The root systems of 10-day-old barley seedlings were separated into halves. Each half of the root system was placed in one of two adjacent square plastic pots (150 cm^3) containing Tulelake soil. One week later nematodes were added to each pot. Each half root system received 5 ml of suspension containing either ca. 1,700 *P. neglectus* (Pn), 800 *M. chitwoodi* (Mc), or tap water without nematodes (uninoculated control, UC). Nematode treatment combinations for each half root system were as follows: UC|UC, Pn|UC, Mc|UC, Pn|Mc, Pn|Pn, and Mc|Mc. The nematodes were pipetted into four holes 4 cm deep in the soil and the holes were covered with soil. Each pot was watered lightly. The treatments were replicated seven times and were completely randomized. The plants were placed in a growth chamber at 22 ± 1 C, with alternating cycles of 12 hours light and darkness. The plants received only deionized water to avoid potential interference by nutrient solutions. Nematodes in each treatment were extracted 72 days after inoculation by soil elutriation and centrifugal flotation (3), and root extraction by misting for 7 days (22). Nematodes were counted with a dissecting microscope. Weights of fresh root and shoot also were recorded. The nematode numbers were log transformed, and the data were subjected to analysis of variance and Duncan's multiple-range test. Data on the numbers of *M. chitwoodi* were analyzed separately for each trial because of a significant treatment by trial interaction.

Consumptive competition: Barley seedlings were established in 150-cm^3 polystyrene cups with white silica sand. Ten-day-old

seedlings were inoculated with 5 ml suspension of either ca. 1,500 *P. neglectus,* 850 *M. chitwoodi,* both nematodes, or uninoculated. The treatments were replicated six times. Thirty days later, plants were enclosed in plastic bags (each bag contained one plant from each of the four treatments) and placed in a chemical fume hood with a cool ray floodlight giving a photon flux density of ca. 1,600 μmol m^{-2} s^{-1}. A supply of $^{14}CO_2$ was liberated by treating aqueous ^{14}C sodium bicarbonate (1 mCi/ml) with an excess of lactic acid. An aliquot (80 μCi $^{14}CO_2$/bag) was then injected into each plastic bag. The plants were exposed to $^{14}CO_2$ and alternating periods of 12 hours light and 12 hours darkness for 4 days. They were then harvested and roots were separated into halves. One half of each root system and the entire shoot were dried in an oven and used for determining ^{14}C activity. A known quantity of the root and shoot from each treatment was combusted in a Packard model 306 tri-carb sample oxydizer, and the ^{14}C-assimilate in the samples was quantified by liquid scintillation spectrometry (24). Nematodes were extracted from the other half of each root system. Ten swollen females of *M. chitwoodi* were hand-picked and placed in a scintillation vial. *Pratylenchus neglectus* was extracted by placing the roots in a cheesecloth bag and suspending the bag in a 50-ml beaker with water for 16 hours. The numbers of *P. neglectus* in each replicate were counted, and the suspension was concentrated to 0.5 ml and then transferred to scintillation vials. About 10 ml of toluene-based scintillation fluid was added to the vials, and the ^{14}C activity was determined by liquid scintillation spectrometry assuming counting efficiencies were the same as for ^{14}C from plant tissue.

Roots from four other plants with similar nematode treatments, but not exposed to $^{14}C_2$, were stained with acid fuchsin and the total numbers of adult *M. chitwoodi* in the roots determined with a dissecting microscope. The number of *P. neglectus* recovered after 16 hours was considered equivalent to the total number in the roots.

The experiment was conducted twice. In the second trial, four replications were maintained, and a higher concentration of ^{14}C (200 μCi/bag) was injected into the bags. Data on the radioactivity (^{14}C disintegrations per minute) in the nematodes were compared by *t*-tests, and data on the radioactivity in each plant root and shoot were subjected to analysis of variance and Duncan's multiple-range test. Data from the two trials were analyzed separately because of the varying ^{14}C concentrations used. Results from both trials were similar; data from the first trial were less variable and are presented.

Fecundity of M. chitwoodi: Barley seedlings were grown in 150 cm^3 polystyrene cups containing white silica sand. Five ml of nematode suspension containing ca. 250 *M. chitwoodi* or ca. 900 *P. neglectus* were added per cup when the seedlings were 10 days old. The treatments, which were replicated five times, were *M. chitwoodi* alone or *M. chitwoodi* plus *P. neglectus*. The plants were watered lightly after adding the nematodes. Half-strength Hoaglands nutrient solution was added to the cups every other day, alternating with deionized water. The sand was washed from the roots 45 days later, and the roots were dipped in 0.01% erioglaucine solution for 15 minutes to stain the egg-masses (16). Five egg-masses of similar size were removed from each replicate root system and placed in a counting dish. About 3–5 ml of 0.1% NaOCl was added to dissolve the gelatinous matrix surrounding the eggs, and the number of eggs per egg-mass was counted. The experiment was repeated with ca. 300 *M. chitwoodi* and 900 *P. neglectus*/cup, and the number of eggs per egg mass was determined 40 days after inoculating the plants. Data were subjected to analysis of variance.

Initial nematode density: Barley seedlings were established in 1,000-cm^3 polystyrene cups containing sterilized Tulelake soil. Two seedlings were maintained per cup, and nematodes were added 12 days after germination. Treatments included all possible combinations of five densities (0, 400,

800, 1,200, and 2,400) of *P. neglectus* and *M. chitwoodi*. The 25 treatments were replicated 10 times and arranged randomly on a greenhouse bench at 20 C. Five replicates of all treatments were sampled 45 days after inoculation, and the remaining treatments were sampled 87 days after inoculation. Nematode numbers and fresh root and shoot weight of the plants were recorded. Nematodes were extracted from soil by elutriation and centrifugal flotation and from roots by incubation in a mist chamber for 7 days; they were counted with a dissecting microscope. The reproductive index was calculated as the ratio of final population and initial population (Pf/Pi). Multiple linear regression models were fitted to the means of the final populations (Pf) versus initial densities (Pi) of the two nematodes.

The experiment was repeated with all combinations of three levels (400, 800, 2,400) of initial population density for *M. chitwoodi* and five levels for *P. neglectus*. The treatments were replicated five times. The final population densities of the nematodes and plant root and shoot weights were recorded 70 days after inoculation. Due to differences in treatment levels between the two trials, data were not pooled for analysis. However, results in both trials were similar, and data from the first trial are presented.

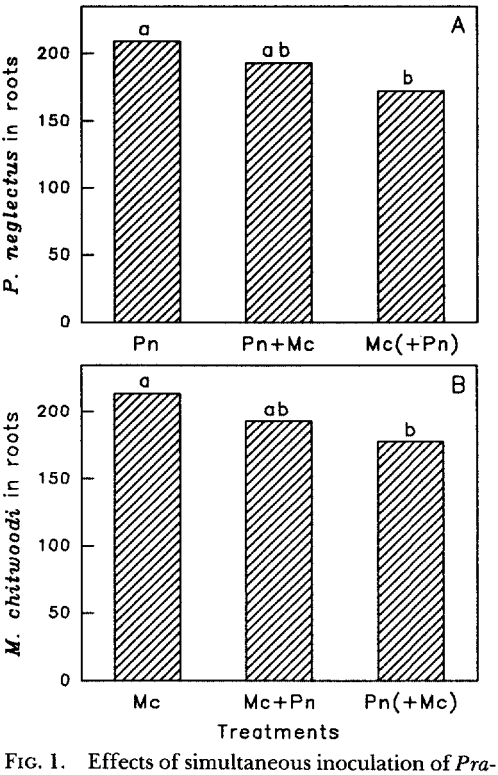

FIG. 1. Effects of simultaneous inoculation of *Pratylenchus neglectus* and *Meloidogyne chitwoodi* and 5 days prior inoculation of one species on root penetration of the other in greenhouse experiments at 20 C. A) numbers of *Pratylenchus neglectus* in roots and B) numbers of *Meloidogyne chitwoodi* in roots. The treatments are indicated as follows: Pn = *P. neglectus* alone, Pn + Mc = *P. neglectus* + *M. chitwoodi* inoculated simultaneously, Mc(+Pn) = *M. chitwoodi* inoculated 5 days before *P. neglectus*, Mc = *M. chitwoodi* alone, Mc + Pn = *M. chitwoodi* + *P. neglectus* inoculated simultaneously, and Pn(+Mc) = *P. neglectus* inoculated 5 days before *M. chitwoodi*. The values are means of 13 replicates. Bars with same letters do not differ significantly ($P \leq 0.05$) according to Duncan's multiple-range test.

RESULTS

Preemptive competition: When *M. chitwoodi* was added to roots 5 days before *P. neglectus*, the numbers of *P. neglectus* penetrating the root was slightly ($P \leq 0.05$) reduced (Fig. 1A). Similarly, the prior presence of *P. neglectus* inhibited root penetration by *M. chitwoodi* (Fig. 1B). Development of *M. chitwoodi* was hindered by *P. neglectus* (Table 1). On day 21, there were more mature *M. chitwoodi* when present alone than in either of the treatments with *P. neglectus*. There was no difference in development of *M. chitwoodi* between the two treatments with *P. neglectus* (Table 1). Addition of *P. neglectus* simultaneously with *M. chitwoodi* did not delay the development of *M. chitwoodi* at 30 days, but addition of *P. neglectus* 5 days before *M. chitwoodi* delayed ($P \leq 0.05$) the development of *M. chitwoodi* compared to the other two treatments (Table 1).

Chemical competition: Population levels of either *P. neglectus* or *M. chitwoodi* on one half of the root system were not influenced by the presence or absence of the other species on the opposite half of the root system (Fig. 2A,B). Fresh weights of uninoculated control (UC|UC) split root systems did not differ from those inoculated with

TABLE 1. Effect of *Pratylenchus neglectus* on root penetration and development of *Meloidogyne chitwoodi* when added simultaneously to, or five days before, *M. chitwoodi*.

Day	Treatment†	Development stage				Pairwise comparisons‡		
		J2	J3	J4	Adult	A	B	C
7	Mc	267§	5	—	—	NS	NS	NS
	Mc + Pn	257	4	—	—			
	Pn(+Mc)	216	4	—	—			
14	Mc	50	160	—	—	NS	NS	NS
	Mc + Pn	51	150	—	—			
	Pn(+Mc)	44	137	—	—			
21	Mc	5	64	103	8	S	S	NS
	Mc + Pn	7	66	94	5			
	Pn(+Mc)	7	65	88	3			
30	Mc	—	24	71	82	NS	S	S
	Mc + Pn	—	25	64	81			
	Pn(+Mc)	—	30	59	70			

† Mc = *M. chitwoodi* alone, Mc + Pn = *M. chitwoodi* and *P. neglectus* added simultaneously, and Pn(+Mc) = *P. neglectus* added 5 days before *M. chitwoodi*.

‡ Pairwise comparisons for differences in age structure between the treatments. A = Mc versus Mc + Pn; B = Mc versus Pn(+Mc); C = Mc + Pn versus Pn(+Mc). NS = not significantly different, and S = significantly different ($P \leq 0.05$) at each sampling time, according to pairwise Mann-Whitney test.

§ Values are means of five replications.

P. neglectus or *M. chitwoodi* in one half (UC|Pn or UC|Mc). Plants with *P. neglectus* and *M. chitwoodi* in opposite halves of the root system (Pn|Mc), or with *P. neglectus* in both halves (Pn|Pn), had lower ($P \leq 0.05$) root weights than the uninoculated control. Fresh shoot weights of plants with *P. neglectus* on both halves of the root system were lower ($P \leq 0.05$) than the uninoculated control plants or plants with either species in one half of the root system. Shoot weights of plants with *P. neglectus* or *M. chitwoodi* on both halves of the root system did not differ from each other.

Consumptive competition: The quantity of ^{14}C per individual *P. neglectus* or *M. chitwoodi* did not differ between single and combined species treatments (Fig. 3A,B). The amount of ^{14}C in the total numbers of *P. neglectus* was lower ($P \leq 0.05$) when *M. chitwoodi* was present (Fig. 3C). The quantity of ^{14}C in *M. chitwoodi* had a lower mean but was not significantly reduced when *P. neglectus* was present (Fig. 3D).

Since the quantity of ^{14}C in nematodes is influenced by the quantity of ^{14}C in plants, the ^{14}C in nematodes as a proportion of that in the plant was considered. The ratios of ^{14}C-activity in *P. neglectus* or *M. chitwoodi* to the total radioactivity in the roots were not significantly lower when both the species were together than when they were present alone (Fig. 4A,B). However, the ratios of ^{14}C-activity in *P. neglectus* or *M. chitwoodi* to that in the whole plant were different ($P \leq 0.05$) between single species and two species treatments (Fig. 4C,D).

The amount of ^{14}C assimilates in the roots was higher ($P \leq 0.05$) in the nematode-free control plants than in the plants inoculated with nematodes (Fig. 5A). The plants with nematodes had similar amounts of ^{14}C in the roots. The quantity of ^{14}C in the shoots was similar in all the treatments (Fig. 5B). The plants inoculated with either species alone had lower ($P \leq 0.05$) amounts of ^{14}C assimilates than did the nematode-free control plants, whereas ^{14}C assimilates in plants inoculated with both species did not differ from the nematode-free controls (Fig. 5C).

The amount of ^{14}C in the roots was probably influenced by the dry root weights. The plants inoculated with nematodes had lower ($P \leq 0.05$) dry root weights than the uninoculated control (Fig. 6A). The dry root weights did not differ among the nematode treatments.

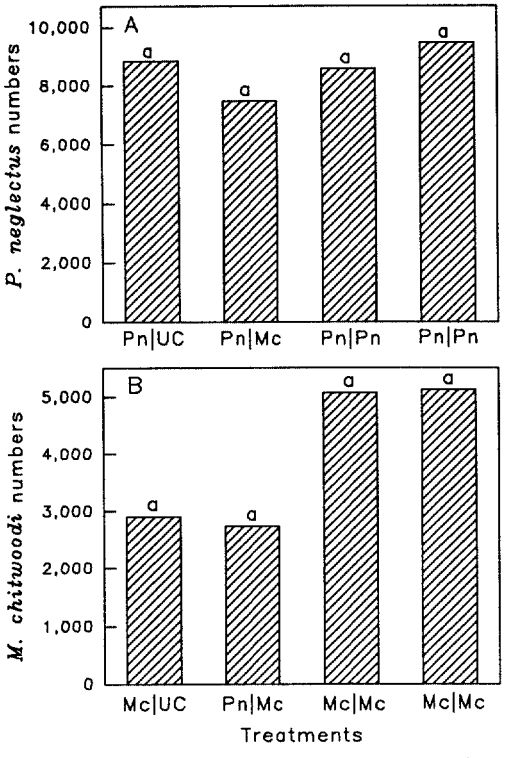

FIG. 2. Effects of nematode-induced translocatable factors on the population levels of each species in a split-root experiment. A) Total numbers of *Pratylenchus neglectus* and B) total numbers of *Meloidogyne chitwoodi*, 72 days after inoculating the plants. The treatments for either half of a root system are indicated as follows: Pn|UC = *P. neglectus* on one half and no nematodes on the opposite half, Pn|Mc = *P. neglectus* and *M. chitwoodi* on opposite halves, Pn|Pn = *P. neglectus* on both halves, and Mc|Mc = *M. chitwoodi* on both halves. The values for numbers of *P. neglectus* are means of 13 replicates pooled from two trials, and the values for numbers of *M. chitwoodi* are means of seven replicates from the first trial. Bars with same letters do not differ significantly ($P \leq 0.05$) according to Duncan's multiple-range test.

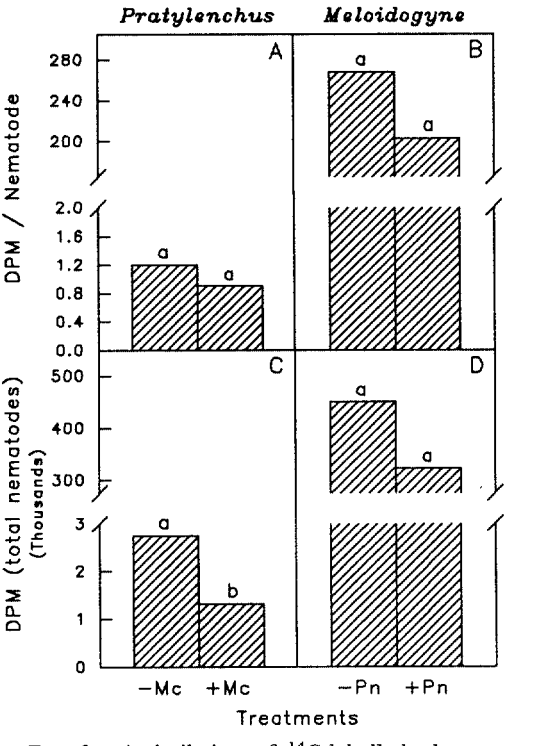

FIG. 3. Assimilation of ^{14}C-labelled photosynthates by *Pratylenchus neglectus* and *Meloidogyne chitwoodi*, as indicated by the amount of ^{14}C activity (disintegrations per minute) quantified by liquid scintillation spectrometry. A,B) ^{14}C per *P. neglectus* and *M. chitwoodi*, respectively. C,D) ^{14}C in total numbers of *P. neglectus* and *M. chitwoodi*, respectively. The treatments − and + refer to the absence or presence of the species, Pn = *P. neglectus*, and Mc = *M. chitwoodi*. The values are means of six replicate treatments. Bars with same letters do not differ significantly ($P \leq 0.05$) according to *t*-test.

The dry shoot weight of plants inoculated with *P. neglectus* alone was lower than that of the uninoculated control, but did not differ from that of the other nematode treatments (Fig. 6B). The shoot weight of plants inoculated with both nematode species or *M. chitwoodi* alone did not differ from that of the uninoculated control.

Fecundity of M. chitwoodi: The numbers of eggs per egg mass of *M. chitwoodi* were lower ($P \leq 0.05$) when *P. neglectus* was present. The egg masses of *M. chitwoodi* contained 139 eggs in the absence of *P. neglectus* as compared to 120 eggs in the presence of *P. neglectus*. The numbers are pooled from two trials.

Initial nematode density: At 45 days, numbers of either nematode species and weights of plant root and shoot were not correlated with initial densities of *P. neglectus* or *M. chitwoodi* (data not presented). At 87 days, numbers of *M. chitwoodi* were positively correlated with initial densities of that species, but were negatively correlated with the initial densities of *P. neglectus* ($P \leq 0.05$) (Fig. 7A). The multiple linear model $Y = 2704 + 10.68\ Pi_{Mc} - 0.00295\ (Pi_{Mc} \times Pi_{Pn})$, where Pi_{Mc} is the initial density of *M. chitwoodi* and Pi_{Pn} is the initial density of *P. neglectus*, explains about 80% of the varia-

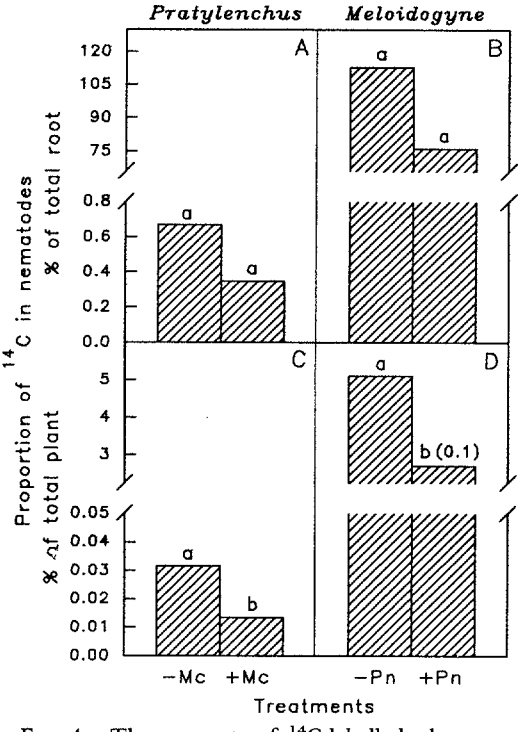

FIG. 4. The amounts of ^{14}C-labelled photosynthates assimilated by *Pratylenchus neglectus* and *Meloidogyne chitwoodi* relative to that in plants. A,B) ^{14}C activity in *P. neglectus* and *M. chitwoodi*, respectively, as a proportion of ^{14}C in barley roots. C,D) ^{14}C activity in *P. neglectus* and *M. chitwoodi*, respectively, as a proportion of ^{14}C in the whole plant. The treatments − and + refer to the absence or presence of the species, Pn = *P. neglectus*, and Mc = *M. chitwoodi*. The values are means of six replicate treatments. Bars with same letters do not differ significantly ($P \leq 0.05$) according to *t*-test.

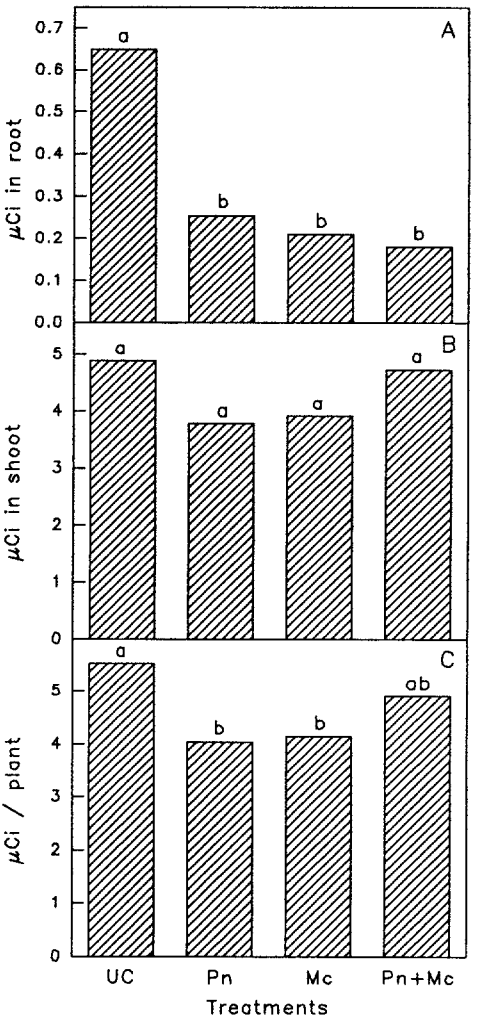

FIG. 5. The effect of *Pratylenchus neglectus* and *Meloidogyne chitwoodi* on photosynthate assimilation by barley in A) root, B) shoot, and C) the whole plant. The treatments are indicated as follows: UC = uninoculated control, Pn = *P. neglectus* alone, Mc = *M. chitwoodi* alone, and Pn + Mc = *P. neglectus* + *M. chitwoodi* inoculated together. The values are means of six replicate treatments. Bars with same letters do not differ significantly ($P \leq 0.05$) according to Duncan's multiple-range test.

tion in *M. chitwoodi* population means. The numbers of *P. neglectus* were positively correlated ($P \leq 0.05$) with initial densities of *P. neglectus*, but were not affected by *M. chitwoodi* (Fig. 7B). About 90% of the variation in numbers of *P. neglectus* is explained by the model $Y = 4337 + 7.02\ Pi_{Pn} + 0.00053\ (Pi_{Pn} \times Pi_{Mc})$.

The reproductive index (Pf/Pi) of *M. chitwoodi* was not influenced significantly by its initial densities (Pi), but was negatively correlated ($P \leq 0.05$) with the $Pi_{Mc} \times Pi_{Pn}$ interaction term. The relationship is explained by the model $Y = 12.9 + 0.00008\ Pi_{Mc} - 0.000002\ (Pi_{Mc} \times Pi_{Pn})$, $R^2 = 0.48$ (Fig. 8A). Reproductive index of *P. neglectus* was negatively correlated with its initial densities but was not affected by the presence of *M. chitwoodi*. The relationship is explained by the model $Y = 16.4 - 0.0033\ Pi_{Pn} + 0.0000002\ (Pi_{Pn} \times Pi_{Mc})$, $R^2 = 0.73$ (Fig. 8B).

The fresh root and shoot weights of barley were not significantly reduced by either nematode in the density-range tested (data not presented).

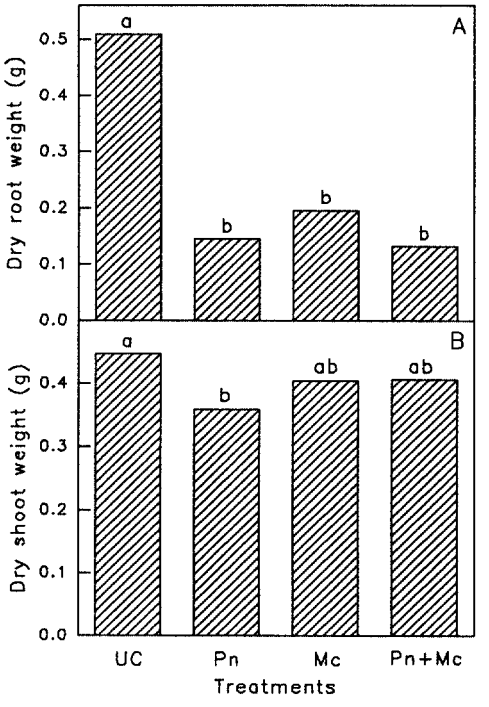

FIG. 6. The effect of *Pratylenchus neglectus* and *Meloidogyne chitwoodi* on dry weights of A) barley root and B) barley shoot, at 34 days after inoculation. The treatments are indicated as follows: UC = uninoculated control, Pn = *P. neglectus* alone, Mc = *M. chitwoodi* alone, and Pn + Mc = *P. neglectus* + *M. chitwoodi* inoculated together. The values are means of six replicate treatments. Bars with same letters do not differ significantly ($P \leq 0.05$) according to Duncan's multiple-range test.

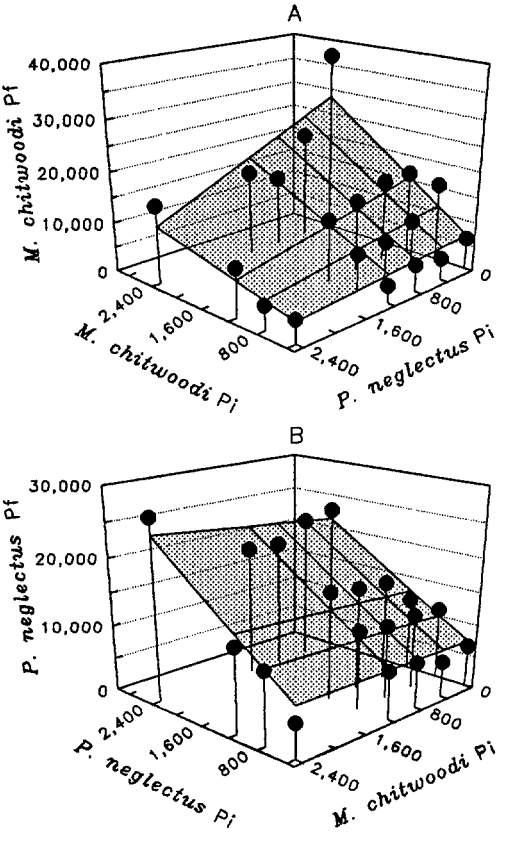

FIG. 7. The influence of initial population densities (Pi) of *Pratylenchus neglectus* and *Meloidogyne chitwoodi* on the final population levels (Pf) of A) *M. chitwoodi* and B) *P. neglectus* in barley, 87 days after inoculation, in greenhouse experiments. The symbols (closed circles) represent the means of five observed values, and the response surface represents the predicted values according to a linear multiple regression model. The models for final population levels of *M. chitwoodi* and *P. neglectus* are, respectively, $Y = 2704 + 10.68\ Pi_{Mc} - 0.00295(Pi_{Mc} \times Pi_{Pn})$, $R^2 = 0.79$, and $Y = 4337 + 7.02\ Pi_{Pn} + 0.000525(Pi_{Pn} \times Pi_{Mc})$, $R^2 = 0.90$, where Y = the final population level, Pi_{Mc} = initial population density of *M. chitwoodi*, and Pi_{Pn} = initial population density of *P. neglectus*.

DISCUSSION

Pratylenchus neglectus and *M. chitwoodi* exhibited preemptive competition in barley. The species of nematode that parasitized the roots first inhibited root penetration by the latter species. Also, the development of *M. chitwoodi* was restricted due to the prior presence of *P. neglectus*. Root sizes appeared similar following invasion of either species, but there may have been fewer preferred sites. Root weights were not different between single and combined species treatments in other experiments (23).

The split-root experiments did not support the hypothesis that competition was mediated by translocatable chemicals. It is possible, however, that nematode secretions may inhibit the competing species locally.

Tests for consumptive competition suggest reduced availability of nutrients to *M. chitwoodi*, which may be due to root damage caused by the feeding and migration of *P. neglectus*. Based on the ^{14}C assay, the amount of carbon assimilated per individual of *P. neglectus* or *M. chitwoodi* was not statistically different between the single and combined species treatments. However, both species had consistently lower means of ^{14}C levels in the combined spe-

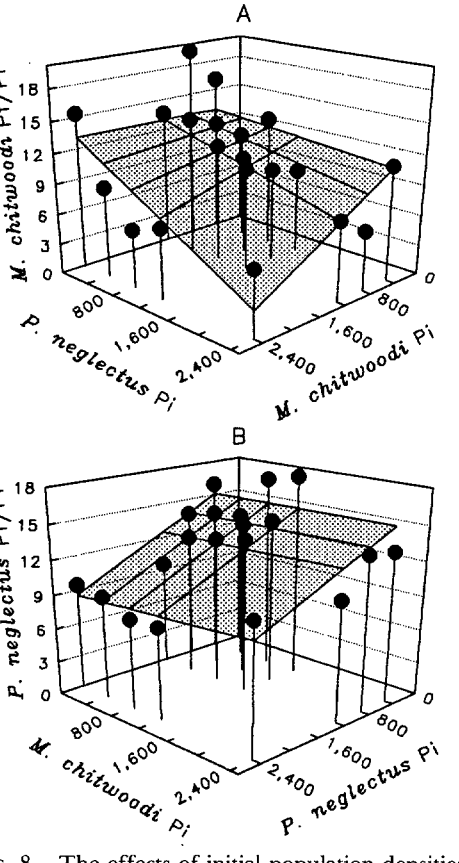

FIG. 8. The effects of initial population densities (Pi) of *Pratylenchus neglectus* and *Meloidogyne chitwoodi* on the reproductive index (Pf/Pi) of A) *M. chitwoodi* and B) *P. neglectus*, in barley, 87 days after inoculation, in greenhouse experiments. The symbols (closed circles) represent the means of five observed values, and the response surface represents the predicted values according to linear multiple regression models. The reproductive indexes of *M. chitwoodi* and *P. neglectus* are explained by the models, respectively, $Y = 12.9 + 0.00008\ Pi_{Mc} - 0.000002(Pi_{Mc} \times Pi_{Pn})$, $R^2 = 0.48$, and $Y = 16.41 - 0.0033\ Pi_{Pn} + 0.0000002(Pi_{Pn} \times Pi_{Mc})$, $R^2 = 0.73$, where Y = reproductive index, Pi_{Mc} = initial population density of *M. chitwoodi*, and Pi_{Pn} = initial population density of *P. neglectus*.

cies treatments than in the single species treatments. Furthermore, carbon assimilation was lower in the plants inoculated with either species alone than in the nematode-free plants, whereas carbon assimilation was not reduced in the plants inoculated with both nematode species.

Bird and Loveys (2) demonstrated that *Meloidogyne javanica* functions as a metabolic sink and that at least some of the nutrients required by these nematodes originate from photosynthates. McClure (14) confirmed and extended the results of Bird and Loveys (2) by demonstrating that the majority of ^{14}C-labelled photosynthate was accumulated in swollen *M. incognita* females and associated egg masses. Our studies demonstrate that ^{14}C-labelled photosynthates are assimilated by both *M. chitwoodi* and *P. neglectus*. *Meloidogyne chitwoodi* withdrew a much greater proportion of photosynthate, however, than did *P. neglectus*, and both species accumulated lower amounts of photosynthate when present concomitantly than when present alone.

Reduced nutrition probably is the cause of delayed development and reduced egg production by *M. chitwoodi*. Final population levels of *M. chitwoodi* decreased linearly with higher initial population densities of *P. neglectus*, thus demonstrating the density-dependent nature of competition (1). The reproductive index of *M. chitwoodi* was not influenced by its initial population density, which implies that resources were not limited. In the presence of *P. neglectus*, the reproductive index of *M. chitwoodi* decreased, probably due to depletion of nutrients. However, *P. neglectus* population size was not affected by *M. chitwoodi* initial densities. The reproductive index of *P. neglectus* decreased with increase in levels of *P. neglectus* initial population density but was not influenced by the initial population densities of *M. chitwoodi*, in the range tested. The lack of negative effects on *P. neglectus* population levels in these experiments is unclear. In other experiments, *M. chitwoodi* and *P. neglectus* were mutually suppressive, depending on soil temperature and host plant (23).

Our studies demonstrate that *P. neglectus* competes with and has the potential to restrict population levels of *M. chitwoodi*. Data from field plots (10) and earlier studies (11,17) indicate a close correlation between final population levels of *M. chitwoodi* and blemish ratings of potato tubers. Therefore, reduced number or delayed development of *M. chitwoodi* is likely to result in fewer blemishes on tubers. More

than one mechanism of competition appears to be involved in the interaction between these nematodes. The different mechanisms of competition probably complement each other in suppressing concomitant species. Field experiments to manage and maximize the effects of competition are necessary before we can exploit competitive interactions as a method of suppressing *M. chitwoodi* and reducing blemishes on potato tubers.

Literature Cited

1. Begon, M., and M. Mortimer. 1986. Population ecology, a unified study of animals and plants. Cambridge, MA: Blackwell Scientific Publications.

2. Bird, A. F., and B. R. Loveys. 1975. The incorporation of photosynthates by *Meloidogyne javanica*. Journal of Nematology 7:111–113.

3. Byrd, D. W., Jr., K. R. Barker, H. Ferris, C. J. Nusbaum, W. E. Griffin, R. H. Small, and C. A. Stone. 1976. Two semiautomatic elutriators for extracting nematodes and certain fungi from soil. Journal of Nematology 8:206–212.

4. Byrd, D. W., Jr., T. Kirkpatrick, and K. R. Barker. 1983. An improved technique for clearing and staining plant tissue for detection of nematodes. Journal of Nematology 15:142–143.

5. Duncan, L., and H. Ferris. 1982. Interactions between phytophagous nematodes. Pp. 29–51 *in* D. Freckman, ed. Nematodes in soil ecosystems. Austin, TX: University of Texas Press.

6. Duncan, L. W., and H. Ferris. 1983. Validation of a model for prediction of host damage by two nematode species. Journal of Nematology 15:227–234.

7. Eisenback, J. D. 1985. Interactions among concomitant populations of nematodes. Pp. 193–213 *in* J. N. Sasser and C. C. Carter, eds. An advanced treatise on *Meloidogyne*, Vol. 1, Biology and control. Raleigh, NC: North Carolina State University Graphics.

8. Estores, R. A., and T. A. Chen. 1970. Interaction of *Pratylenchus penetrans* and *Meloidogyne incognita acrita* as cohabitants on tomatoes. Phytopathology 60: 1291 (Abstr.).

9. Estores, R. A., and T. A. Chen. 1972. Interactions of *Pratylenchus penetrans* and *Meloidogyne incognita* as coinhabitants in tomato. Journal of Nematology 4:170–174.

10. Ferris, H., H. L. Carlson, and B. B. Westerdahl. 1994. Crop rotation effects on population levels of *Meloidogyne chitwoodi* and *Pratylenchus neglectus*, and consequences for potato crops. Agronomy Journal 86:340–348.

11. Griffin, G. D. 1985. Host–parasite relationship of *Meloidogyne chitwoodi* on potato. Journal of Nematology 17:395–399.

12. Hussey, R. S., and K. R. Barker. 1973. A comparison of methods of collecting inocula of *Meloidogyne* spp., including a new technique. Plant Disease Reporter 57:1025–1028.

13. Kraus-Schmidt, H., and S. A. Lewis. 1981. Dynamics of concomitant populations of *Hoplolaimus columbus, Scutellonema brachyurum* and *Meloidogyne incognita* on cotton. Journal of Nematology 13:41–48.

14. McClure, M. A. 1977. *Meloidogyne incognita:* A metabolic sink. Journal of Nematology 9:88–90.

15. Norton, D. C. 1969. *Meloidogyne hapla* as a factor in alfalfa decline in Iowa. Phytopathology 59: 1824–1828.

16. Omwega, C. O., and I. J. Thomason. 1988. A nondestructive technique for screening bean germ plasm for resistance to *Meloidogyne incognita*. Plant Disease 72:970–972.

17. Santo, G. S., and J. H. O'Bannon. 1981. Effect of soil temperature on the pathogenicity and reproduction of *Meloidogyne chitwoodi* and *M. hapla* on Russet Burbank potato. Journal of Nematology 13:483–486.

18. SAS Institute. 1988. SAS/STAT users guide, Release 6.03 edition. Cary, NC: SAS Institute.

19. Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122: 240–285.

20. Sikora, R. A., D. P. Taylor, R. B. Malek, and D. J. Edwards. 1972. Interaction of *Meloidogyne naasi, Pratylenchus penetrans* and *Tylenchorhynchus agri* on creeping bentgrass. Journal of Nematology 4:162–165.

21. Sikora, R. A., R. B. Malek, D. P. Taylor, and D. J. Edwards. 1979. Reduction of *Meloidogyne naasi* infection of creeping bentgrass by *Tylenhorhynchus agri* and *Paratrichodorus minor*. Nematologica 25:179–183.

22. Southey, J. F. 1986. Laboratory methods for work with plant and soil nematodes. Technical bulletin 2. London: Her Majesty's Stationery Office.

23. Umesh, K. C., and H. Ferris. 1994. Influence of temperature and host plant on the interaction between *Pratylenchus neglectus* and *Meloidogyne chitwoodi*. Journal of Nematology 26:65–71.

24. Wang, C. H., and D. L. Willis. 1965. Radiotracer methodology in biological science. Englewood, NJ: Prentice Hall.