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Influence of Temperature and Host Plant on the Interaction Between *Pratylenchus neglectus* and *Meloidogyne chitwoodi*

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Abstract: The interaction between *Pratylenchus neglectus* (Pn) and *Meloidogyne chitwoodi* (Mc) was investigated at soil temperatures of 15, 20, and 25 C on barley and potato. Maximum numbers of Pn and Mc penetrated barley roots at 20 C, whereas a minimum number penetrated at 15 C. *Pratylenchus neglectus* restricted root penetration by Mc over time and vice-versa. Population densities of each species increased with increasing temperature. Concomitant inoculation of the two species resulted in lower numbers of Pn at 15 and 25 C in both barley and potato, whereas the numbers of Mc were lower at 15 C in barley and at 25 C in potato. Root weights of potato and barley at 15 and 20 C, respectively, were lowered by the presence of both nematodes singly or concomitantly. At 25 C, barley plants inoculated with Mc alone had lower shoot weight than uninoculated controls, but the damage was restricted when Pn also was present. The two species interact competitively, and the outcome varies with soil temperature and host plant. Pn has the potential to suppress Mc population levels and reduce the damage it causes to potato and barley.

Key words: barley, competition, *Hordeum vulgare,* interaction, *Meloidogyne chitwoodi,* nematode, penetration, population change, potato, *Pratylenchus neglectus, Solanum tuberosum,* temperature.

Populations of *Meloidogyne chitwoodi* Golden, O'Bannon, Santo, and Finley, and *Pratylenchus neglectus* (Rensch) Filipjev and Schuurmans Stekhoven occur in fields used for potato (*Solanum tuberosum*) and barley (*Hordeum vulgare*) production in northern California and parts of the northwest United States (20,29,34). *Meloidogyne chitwoodi* is a pathogen of potatoes, causing blemishes on tubers and reducing their yield and quality (12,22). The ability of *P. neglectus* to suppress potato yields varies with soil types (21,28), but the nematode does not cause blemishes on tubers. *Pratylenchus neglectus* did not damage wheat and barley under experimental conditions (19,32). The interaction between *P. neglectus* and *M. chitwoodi* and their combined effect on host plants have not been studied.

Abiotic and biotic factors that can affect the outcome of nematode–nematode interactions include soil temperature (4,16, 33) and host suitability (14,15). Temperature may affect plant-parasitic nematodes either directly or indirectly through the host plant.

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Among the different types of interactions that occur between organisms, interspecific competition is considered to be of major ecological importance in structuring natural communities (24,26). Although some ecologists disagree on its importance (3,35), many kinds of organisms at different trophic levels exhibit interspecific competition in the field (27). Competitive interactions between plant-parasitic nematode species, wherein the population of one or both of the species is suppressed (7) and plant damage is reduced, are apparently common (6,8,18,23).

We hypothesized that competition by *P. neglectus* would suppress the population density of *M. chitwoodi* and thus result in reduced potato tuber damage. Our objectives were to quantify the influence of soil temperature and host suitability on the population changes of *P. neglectus* and *M. chitwoodi* interactions, and to determine the effect of concomitant populations of these nematodes on yields of barley and potato.

MATERIALS AND METHODS

Soil from potato fields near Tulelake, 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), was autoclaved for 30 minutes at ca. 115 C and 20 psi, then aerated for 1 week and used in experiments. Cultures of *P. neglectus* and *M. chitwoodi* were maintained in a greenhouse on barley cv. Steptoe and tomato (*Lycopersicon esculentum*) cv. Columbia, respectively. *Pratylenchus neglectus* inoculum was obtained by placing infected roots in a mist chamber (30). *Meloidogyne chitwoodi* inoculum was obtained by shaking the roots in 0.05% NaOCl for 4 minutes (13), collecting the eggs, and placing them in a mist chamber (30). The experiments were conducted on barley cv. Steptoe and potato cv. Russet Burbank in controlled-temperature water baths in a greenhouse.

Interaction in barley: Two barley seedlings were grown in 1-liter polystyrene cups filled with autoclaved soil. Two cups were embedded in each of 5-liter plastic buckets filled with steam-sterilized sand. When the seedlings were 10 days old, the plastic buckets containing the cups were placed in water baths at 15, 20, and 25 ± 2 C. Three days later, nematodes were added to the cups by pipetting 2.5 ml of a nematode suspension into each of four holes about 5 cm deep between the seedlings. The holes were covered with soil, and the cups were lightly watered. The nematode treatments were 1,500 *P. neglectus*, 500 *M. chitwoodi*, 1,500 *P. neglectus* + 500 *M. chitwoodi*, and a nematode-free control treatment that received 10 ml of tap water. Six water baths were maintained, two at each of the three temperatures. There were two replications in each water bath, four per nematode treatment. The treatments were randomized within each water bath. Soil temperature was monitored by a probe placed ca. 10 cm deep in the center of the cup and was recorded at hourly intervals by a computer. The plants were supplied with half-strength Hoaglands nutrient solution twice a week and deionized water on other days.

After 62 days, nematodes were extracted from roots in a mist chamber for 7 days and from 100 cm^3 soil by sieving (140, 75, and 37-μm pore-size sieves) and centrifugal flotation (30), and quantified with the aid of a dissecting microscope. The effect of single and combined nematode treatments on the plants at different temperatures was assessed by comparing fresh root and shoot weights of plants grown in the presence and absence of nematodes. The effects of nematode treatments were analyzed separately for each temperature by analysis of variance and Duncan's multiple-range test. The experiment was repeated, but the second trial was terminated after 74 rather than 62 days. Data from the two trials were pooled and analyzed by blocking for trial effects.

Interaction in potato: Potato plants were established from 2.5 cm^3 tuber pieces with eye-buds. One plant was established per 1,500 cm^3 pot. Soil temperature, nematode treatments, data analyses, and all experimental procedures were as described for barley.

Root penetration: Barley seedlings were grown in 150-cm^3 polystyrene cups filled with white silica sand. The cups were placed in constant-temperature water baths at 15, 20, and 25 ± 2 C, as described. Each cup received ca. 900 *P. neglectus*, 330 *M. chitwoodi*, or 900 *P. neglectus* + 330 *M. chitwoodi*, in 5 ml of suspension. The cups were watered lightly after inoculation. Four replications were destructively sampled 2, 4, 8, and 15 days after inoculation. Plant roots were stained with acid fuchsin (2), and the number of individuals of each species in the root was determined with the aid of a dissecting microscope. The experiment was repeated; the treatments in the second trial consisted of ca. 800 *P. neglectus*, 260 *M. chitwoodi*, or 800 *P. neglectus* + 260 *M. chitwoodi*, in 4 ml of suspension per cup. Data from the two trials were pooled, and an exponential growth model, $Y = a(1 - e^{-bx})$, where Y = the number of nematodes of a species in the root, a = the maximum Y, b = the rate at which Y is approached, and x = time (days after inoculation), was fitted to the means across sampling dates at each temperature. The lines fitted to means of single- and two-species treatments were compared by F-test ratio (5).

RESULTS

Interaction in barley: Numbers of *P. neglectus* in roots and soil increased with increasing soil temperature when *M. chitwoodi* was absent, but the presence of *M. chitwoodi* reduced ($P \leq 0.05$) the numbers of *P. neglectus* at 15 and 25 C (Fig. 1A). Similarly, numbers of *M. chitwoodi* increased with soil temperature, but the presence of *P. neglectus* reduced ($P \leq 0.05$) the numbers of *M. chitwoodi;* only at 15 C (Fig. 1B).

At 15 C, fresh shoot, root, and head weights of barley did not differ among any of the treatments (Table 1). At 20 C, barley inoculated with nematodes had lower ($P \leq 0.05$) fresh root weight than did the uninoculated controls, but the reduction was similar among the different nematode treatments (Table 1). Shoot and head weights were not affected. At 25 C, fresh shoot, root, and head weights of the plants inoculated with both species together, or with *P. neglectus* alone, did not differ from those of the uninoculated control. However, plants inoculated with *M. chitwoodi* alone had lower ($P \leq 0.05$) shoot weight than the controls (Table 1).

Interaction in potato: The influence of temperature on numbers of *P. neglectus* and *M. chitwoodi* in potato was similar to that in barley. Nematode numbers were greater at higher soil temperature (Fig. 1C,D). *Meloidogyne chitwoodi* reduced ($P \leq 0.05$) *P. neglectus* numbers at 15 C and 25 C

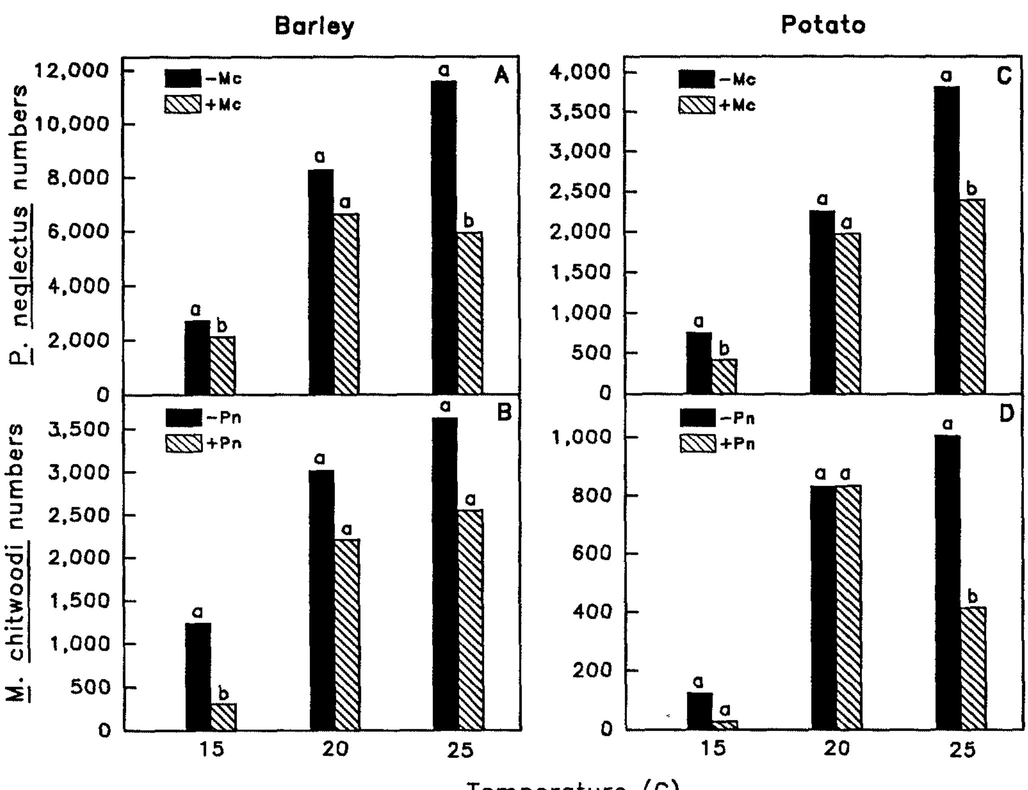

FIG. 1. Effects of temperature on nematode population levels in pots in greenhouse. A) *Pratylenchus neglectus* (Pn) on barley, B) *Meloidogyne chitwoodi* (Mc) on barley, C) *P. neglectus* on potato, and D) *M. chitwoodi* on potato. The number of nematodes per 1,000 cm^3 soil and roots were determined at crop maturity. The treatments were as follows: −Mc = *P. neglectus* alone; +Mc = *P. neglectus* and *M. chitwoodi* inoculated concomitantly; −Pn = *M. chitwoodi* alone; +Pn = *M. chitwoodi* and *P. neglectus* inoculated concomitantly. The values are means of eight replicates from two trials. Statistical comparisons were made at each temperature level between single and concomitant inoculations; bars with same letters are not significantly different according to Duncan's multiple-range tests ($P \leq 0.05$).

TABLE 1. Effects of single and mixed populations of *Pratylenchus neglectus* and *Meloidogyne chitwoodi* on weights of barley and potato at three soil temperatures in a greenhouse.

	Barley			Potato		
Treatment†	Shoot (g)	Root (g)	Head (g)	Shoot (g)	Root (g)	Tuber (g)
			15 C			
UC	42.3 a	16.4 a	17.4 a	71.4 a	42.5 a	145.9 a
Pn	39.0 a	14.9 a	19.4 a	71.5 a	34.0 b	142.0 a
Mc	36.3 a	14.0 a	20.4 a	74.3 a	32.1 b	143.3 a
Pn + Mc	39.9 a	14.0 a	20.0 a	68.3 a	34.4 b	141.4 a
			20 C			
UC	44.4 a	16.3 a	20.5 a	72.9 a	26.6 a	134.5 b
Pn	38.4 a	12.5 b	21.0 a	71.8 a	24.5 a	153.6 a
Mc	38.0 a	12.3 b	19.4 a	71.6 a	24.0 a	135.0 b
Pn + Mc	37.1 a	12.6 b	18.8 a	68.6 a	25.3 a	132.3 b
			25 C			
UC	42.6 a	13.4 a	16.9 a	80.1 a	29.4 a	123.1 a
Pn	37.5 ab	10.8 a	17.3 a	71.4 a	26.1 a	119.4 a
Mc	32.0 b	10.8 a	15.4 a	74.8 a	26.5 a	119.5 a
Pn + Mc	37.4 ab	12.3 a	17.5 a	69.6 a	27.5 a	135.1 a

Values are means of eight replicates from two trials. Means followed by the same letters at a temperature within a column are not significantly different according to Duncan's multiple-range test ($P \leq 0.05$).

† UC = Uninoculated control; Pn = *Pratylenchus neglectus* alone; Mc = *Meloidogyne chitwoodi* alone; Pn + Mc = *Pratylenchus neglectus* and *Meloidogyne chitwoodi* inoculated concomitantly.

but not at 20 C (Fig. 1C). The presence of *P. neglectus* reduced ($P \leq 0.05$) the numbers of *M. chitwoodi* at 25 C but not at 15 and 20 C (Fig. 1D).

The influence of temperature on fresh weights of potato was generally similar to that on barley (Table 1). The nematode treatments reduced ($P \leq 0.05$) root weight only at 15 C. At 20 C, treatment with *P. neglectus* alone had greater ($P \leq 0.05$) tuber weight than other treatments. Shoot weights were not affected by the nematodes.

Root penetration: The numbers of both *P. neglectus* and *M. chitwoodi* penetrating the root increased up to 15 days at all temperatures (Fig. 2). Most *M. chitwoodi* were at the root tip and the zone of root elongation, whereas most *P. neglectus* were in the zone of lateral root emergence. Root penetration by the two species was fitted to an exponential model, $Y = a(1 - e^{-bx})$. The model accounted for 98% of the variability among means. Temperature affected root penetration by the nematodes; highest and lowest numbers of both species penetrated the roots at 20 C and 15 C, respectively. The numbers and (or) rate of penetration of *P. neglectus* into roots did not differ at any temperature ($P \leq 0.05$), regardless of the nematode treatment (Fig. 2). However, at 15 and 20 C, the numbers and (or) rate of penetration of *M. chitwoodi* into roots were lower ($P \leq 0.05$) in the presence of *P. neglectus* than in their absence (Fig. 2).

Discussion

The competitive interaction between *P. neglectus* and *M. chitwoodi* on barley and potato was affected by soil temperature and host plant. Competition was greatest at extremes of the temperature range tested. The negative effect of *M. chitwoodi* on *P. neglectus* was greatest at 25 C on barley and potato, whereas the negative effect of *P. neglectus* on *M. chitwoodi* was greatest at 15 C in barley and at 25 C in potato. Competition between *Heterodera glycines* and *Pratylenchus scribneri* in soybean was also affected by soil temperature (16). In other organisms, the intensity of competitive interactions varies with the abiotic and biotic environment (27). Our results substantiate the significance of environment on competition.

The impact of soil temperature on nematode population levels may be a di-

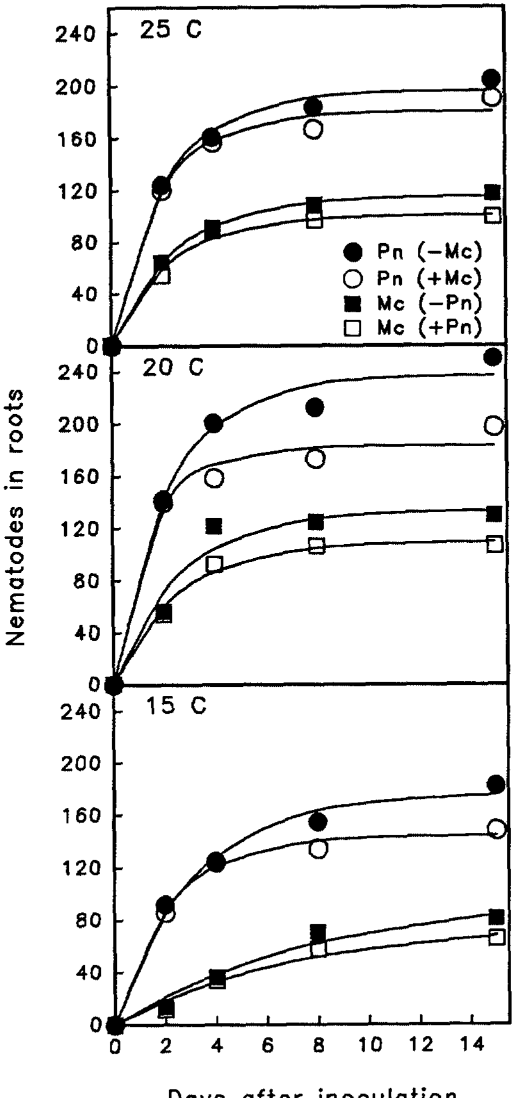

FIG. 2. Numbers of *Pratylenchus neglectus* (Pn) and *Meloidogyne chitwoodi* (Mc) invading barley roots, as affected by soil temperature and days after inoculation. The symbols are the observed values (means of eight replicates from two trials). The lines are the values predicted by the model, $Y = a(1 - e^{-bx})$, where Y = the number of nematodes of a species in the root, a = the maximum Y, b = the rate at which Y is approached, and x = time (days after inoculation). The parameter values according to the model are: at 25 C, a = 196.5, b = 0.47 for Pn alone, and a = 180, b = 0.53 for Pn when present with Mc; a = 115.7, b = 0.4 for Mc alone and a = 100.7, b = 0.44 for Mc when present with Pn; at 20 C, a = 236.7, b = 0.45 for Pn alone, and a = 182.9, b = 0.65 for Pn when present with Mc; a = 133.7, b = 0.38 for Mc alone and a = 109.8, b = 0.39 for Mc when present with Pn; and at 15 C, a = 176.4, b = 0.33 for Pn alone, and a = 144, b = 0.46 for Pn when present with Mc; a = 100.4, b = 0.12 for Mc alone and a = 77.8, b = 0.14 for Mc when present with Pn.

rect effect on the nematode or an indirect effect mediated through the physiology of the host root. It is difficult to differentiate between the two effects, but the effect of temperature on competition in the two host plants suggests that altered root physiology may be more important. Although photosynthates are known to be translocated to different plant organs (sinks), the process of partitioning of assimilates is not clearly understood. It is believed to depend on competition between sinks (11). Plant-parasitic nematodes, especially *Meloidogyne* spp., are considered to function as additional sinks (1,17). Competition for photosynthates probably occurs between plant tissues, between nematode species, and between plant and nematodes. This competition is further complicated by temperature, which influences the partitioning of photosynthates to the various sinks (36). It is probable that barley and potato have different thermal optima, and their photosynthate partitioning is likely to vary with temperature.

The F-test to determine if the lines fitted to the data on root penetration for each nematode species were significantly different did not allow us to determine whether the total numbers in the roots or the rate of penetration were different. The lines fitted to numbers of *M. chitwoodi* in roots differed significantly between the treatments, indicating that *P. neglectus* progressively restricted penetration by *M. chitwoodi.* Although the lines fitted to numbers of *P. neglectus* in roots did not differ because of within-treatment variations, they had a lower asymptote in the presence of *M. chitwoodi.* This suggests that *P. neglectus* and *M. chitwoodi* interfered with each other in root penetration, in spite of selecting different root zones for feeding. Possibly, each nematode species alters root physiology or damages the root surface while probing, thus depleting the feeding sites for the other. Similar results were obtained by Estores and Chen (9), wherein root penetration by *Pratylenchus penetrans* was inhibited by *Meloidogyne incognita* 36 hours after inoculation when both species were present on the same root segment, but not before 7 days when the species were in opposite halves of a split-root system. In other studies on different crops, root penetration by *Meloidogyne* sp. was suppressed by *Pratylenchus* sp. (10,31).

Plant damage induced by a single nematode species may be increased or decreased by the presence of another species, depending on the nematode species and host plant (7). *Pratylenchus neglectus* suppressed yields of potato in sandy soils (21) but not in clay soils (28). It did not appear to be a serious pathogen of barley in our earlier experiments (32) or in the present studies. In previous studies, *M. chitwoodi* reduced root and tuber weight of potato at 15, 20, and 25 C (25). In our study, tuber weight was not affected by *M. chitwoodi,* while root weights of potato and barley were lower in the presence of the nematode at 15 and 20 C, respectively. *Meloidogyne chitwoodi* reduced shoot weight of barley at 25 C when present alone but not when present with *P. neglectus,* substantiating the belief that competition between these nematodes can offset plant damage. Tuber quality could not be assessed in these studies because of the small size of tubers in pots and lack of obvious symptoms. However, tuber damage is correlated with final nematode population levels (25). Therefore, reduction in *M. chitwoodi* population levels should result in reduced tuber damage. Although the results are encouraging, more experiments are needed before we can exploit competitive interactions between plant-parasitic nematodes to reduce plant damage.

Literature Cited

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

2. 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.

3. Connell, J. H. 1980. Diversity and coevolution of competitors, or the ghost of competition past. Oikos 35:131–138.

4. Dickerson, O. J. 1979. The effects of temperature on *Pratylenchus scribneri* and *P. alleni* populations on soybeans and tomatoes. Journal of Nematology 11:23–26.

5. Draper, N. R., and H. Smith. 1986. Applied regression analysis. New York: Wiley.

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. Gay, C. M., and G. W. Bird. 1973. Influence of concomitant *Pratylenchus brachyurus* and *Meloidogyne* spp. on root penetration and population dynamics. Journal of Nematology 5:212–217.

11. Gifford, R. M., and L. T. Evans. 1981. Photosynthesis, carbon partitioning and yield. Annual Review of Plant Physiology 32:485–509.

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

13. 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.

14. Johnson, A. W. 1970. Pathogenicity and interaction of three nematode species on six bermuda grasses. Journal of Nematology 2:36–41.

15. Johnson, A. W., and C. J. Nusbaum. 1970. Interactions between *Meloidogyne incognita, M. hapla* and *Pratylenchus brachyurus* in tobacco. Journal of Nematology 2:234–240.

16. Lawn, D. A., and G. R. Noel. 1990. Effects of temperature on competition between *Heterodera glycines* and *Pratylenchus scribneri* on soybean. Nematropica 20:57–69.

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

18. Mishara, S. D., and H. S. Gaur. 1981. Effect of individual and concomitant inoculation with *Meloidogyne incognita* and *Rotylenchulus reniformis* on the growth of black gram, *Vigna mungo.* Indian Journal of Nematology 11:25–28.

19. Mojtahedi, H., and G. S. Santo. 1992. *Pratylenchus neglectus* on dryland wheat in Washington. Plant Disease 76:323.

20. Nyczepir, A. P., J. H. O'Bannon, G. S. Santo, and A. M. Finley. 1982. Incidence and distribution of *Meloidogyne chitwoodi* and *M. hapla* in potato from the northwestern United States. Journal of Nematology 14:347–353.

21. Olthof, Th. H. A. 1990. Reproduction and parasitism of *Pratylenchus neglectus* on potato. Journal of Nematology 22:303–308.

22. Pinkerton, N. J., and G. S. Santo. 1986. Control of *Meloidogyne chitwoodi* in commercially grown Russet Burbank potatoes. Plant Disease 70:860–863.

23. Rao, K. T., and A. R. Seshadri. 1981. Studies on interaction between *Meloidogyne incognita* and *Rotylenchulus reniformis* on grape vine seedlings. Indian Journal of Nematology 11:101–102.

24. Rhode, K. 1991. Intra- and interspecific interactions in low density populations in resource-rich habitats. Oikos 60:91–104.

25. 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.

26. Schoener, T. W. 1982. The controversy over interspecific competition. American Scientist 70:586–595.

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

28. Scholte, K., and J. J. s'Jacob. 1989. Synergistic interaction between *Rhizoctonia solani* Kuhn, *Verticillium dahliae* Kleb., *Meloidogyne* spp. and *Pratylenchus neglectus* (Rensch) Chitwoodi & Oteifa, in potato. Potato Research 32:387–395.

29. Siddiqui, I. A., S. A. Sher, and A. M. French. 1973. Distribution of plant-parasitic nematodes in California. California Department of Food and Agriculture, Division of Plant Industry, Sacramento, California.

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

31. Turner, D. R., and R. A. Chapman. 1972. Infection of seedlings of alfalfa and red clover by concomitant populations of *Meloidogyne incognita* and *Pratylenchus penetrans*. Journal of Nematology 4:280–286.

32. Umesh, K. C., and H. Ferris. 1992. Effects of temperature on *Pratylenchus neglectus* and on its pathogenicity to barley. Journal of Nematology 24: 504–511.

33. Wallace, H. R. 1983. Interactions between nematodes and other factors on plants. Journal of Nematology 15:221–227.

34. Westerdahl, B. B., H. L. Carlson, J. Grant, J. D. Radewald, N. Welch, C. A. Anderson, J. Darso, D. Kirby, and F. Shibuya. 1992. Management of plant-parasitic nematodes with a chitin–urea soil amendment and other materials. Supplement to the Journal of Nematology 24:669–680.

35. Wiens, J. A. 1977. On competition and variable environments. American Scientist 65:590–597.

36. Wolf, S., A. Marani, and J. Rudich. 1991. Effect of temperature on carbohydrate metabolism in potato plants. Journal of Experimental Botany 42: 619–625.