Supplement to the Journal of Nematology 30(4S):632–638. 1998.

Fungi Parasitic on Juveniles and Egg Masses of *Meloidogyne hapla* in Organic Soils from New York

NICOLE M. VIAENE AND GEORGE S. ABAWI[1]

Abstract: Fungi associated with egg masses and juveniles of *Meloidogyne hapla* were isolated from organic soil samples obtained from five fields planted to lettuce or onion in New York. The soil samples were placed in sterilized clay pots, infested with *M. hapla*, and planted to lettuce. After 4 months, egg masses and juveniles were surface-disinfested, plated on water agar, and examined for fungal infection. Depending on the soil sample, fungal isolates were recovered from 13% to 30%, and from 5% to 24% of the egg masses and juveniles, respectively. A total of 24 and 16 isolates collected from egg masses and juveniles, respectively, were selected for further characterization. Fifteen of the isolates were considered as egg-mass pathogens as they were able to infect healthy assay egg masses and could be succesfully reisolated. These fungi included species of *Fusarium, Alternaria,* and *Verticillium psalliotae.* Six of the egg-mass-parasitizing fungi could not be identified. Nine fungal isolates were found to be pathogenic to juveniles of *M. hapla;* six were identified as *Monacrosporium* sp., two as *Arthrobotrys* sp., and one as *Hirsutella rhossiliensis.* The remaining 16 fungal isolates were unable to infect egg masses or juveniles, and thus were considered nonparasitic to *M. hapla.*

Key words: Alternaria, antagonist, *Arthrobotrys,* biological control, *Fusarium, Hirsutella, Meloidogyne hapla, Monacrosporium,* nematode, nematophagous fungus, northern root-knot nematode, *Verticillium.*

Meloidogyne hapla Chitwood, the northern root-knot nematode, is an important pathogen of lettuce (*Lactuca sativa* L.), onion (*Allium cepa* L.), carrot (*Daucus carota* L.), and other vegetables grown on organic soils in New York (Gaskin and Crittenden, 1956). Commercially acceptable lettuce, onion, and carrot cultivars with resistance to *M. hapla* are not available (Abawi and Laird, 1994; Abawi and Robinson, 1991; Abawi et al., 1997). Control of *M. hapla* is currently limited to the use of soil nematicides. However, high application costs, dependence of nematicide action on weather and soil conditions, and concern for the environment and human health have increased the interest in alternative control measures (Noling and Becker, 1994). Some of the tactics that can be used in an integrated management program include host resistance, crop rotation, sanitation, and incorporation of cover crops and other organic materials. There is increasing interest in expanding information on the antagonists of nematodes such that future use of these organisms may provide an additional tool for the management of plant-parasitic nematodes (Kerry and Jaffee, 1997).

The infective second-stage juvenile is the only migratory stage in the life cycle of *M. hapla.* This stage can be brief, especially if the juvenile hatches close to the root and invades the root tissues within minutes. In a field study on the development of *M. hapla* on lettuce in organic soil, newly hatched juveniles were found about 28 days after the first eggs were laid (Bélair, 1989). Female root-knot nematodes are well protected from antagonists because they are imbedded in the galls they induce on plant roots. Their egg masses, however, are usually exposed on the root surface for longer periods of time. Most egg masses of *M. hapla* are exposed to antagonists for months in soil in the absence of host crops. Thus, eggs can be considered the most vulnerable stage in the life cycle of *Meloidogyne* spp. Nematophagous fungi that destroy eggs can reduce damage to the subsequent crop by reducing the initial nematode inoculum, whereas fungi that eliminate invading second-stage juveniles are able to decrease damage on the current crop. The latter may result in lower population densities of *M. hapla* because fewer nematodes will develop into egg-laying females.

Only two surveys on nematophagous

Received for publication 19 December 1997.

[1] Former Graduate Research Assistant and Professor, Department of Plant Pathology, New York State Agricultural Experiment Station, Cornell University, Geneva, NY 14456.

The authors thank Linda Hanson and Kathie Hodge for their help in the identification of *Fusarium* species and nematode-trapping fungi.

E-mail: n.viaene@clo.fgov.be

fungi associated with *M. hapla* have been conducted (Ma, 1991; Roccuzzo et al., 1993). Isolated fungi reported in these surveys included species of *Arthrobotrys, Monacrosporium, Catenaria, Verticillium, Acremonium, Cylindrocarpon,* and *Fusarium.* Several fungi isolated from other nematode species were also able to parasitize *M. hapla.* They included *Drechmeria coniospora* (Drechsler) Gams & Jansson (Townshend et al., 1989), *Arthrobotrys* spp. (Den Belder and Jansen, 1994; Townshend et al., 1989), *Monacrosporium cionopagum* (Drechsler) Subram., *Duddingtonia flagrans* (Duddington) Cooke (Den Belder and Jansen, 1994), *Hirsutella rhossiliensis* Minter & Brady (Viaene, 1996), and *Verticillium chlamydosporium* Goddard (de Leij et al., 1993; Viaene, 1996). The objective of this study was to isolate and characterize potential fungal antagonists of *M. hapla* from organic soils in New York. A summary of the results was published previously (Viaene and Abawi, 1995).

Materials and Methods

Samples of organic soils were collected in September from four commercial onion fields near Oswego and Batavia, New York. The fields were selected because they had a long history of onion and lettuce production, but *M. hapla* had not caused major problems to date in these fields. Soil samples also were taken from experimental microplots filled with organic soil taken from a commercial lettuce fields near Oswego, New York. Soil in half of the microplots was treated with methyl bromide prior to infestation of both soils with *M. hapla* and planting to onions. Galling of onion roots in the unfumigated soil was less severe than that observed in the methyl bromide-treated soil at the same infestation densities, suggesting that antagonists of *M. hapla* might be present in the soil.

Three clay pots (500 cm^3) were filled with the soils from each field, and two seeds of lettuce cv. Montello were planted in each pot. Two weeks after planting, an aqueous suspension containing 2,000 eggs of *M. hapla* was pipetted on top of the soil in each pot to stimulate the activity and growth of potential parasites. Nematode eggs were obtained from roots of tomato (*Lycopersicon esculentum* Mill. cv. Rutgers) using the sodium-hypochlorite method (Hussey and Barker, 1973). The lettuce plants were maintained in the greenhouse at a temperature varying between 21 °C and 24 °C, watered twice a day, and fertilized weekly (NPK, 16-32-16). Foliar insects were controlled as needed. Pots were replanted with lettuce 9 weeks after the first planting. The pots were maintained for a total of 4 months.

Lettuce roots were carefully washed free of soil, and egg masses were picked from the six root systems of each soil sample (30 to 112 egg masses/soil sample). Egg masses were surface-disinfested for 1 minute in a 0.5% NaOCl solution and rinsed twice in sterile, distilled water. They were then placed on 1.5% water agar (WA) in 9-cm-diam. petri dishes (10 egg masses per dish) and incubated at 22 °C. Egg masses were examined regularly for fungal growth over a period of 1 month using a dissecting microscope. Hyphae growing from egg masses were transferred to quarter-strength corn meal agar (1/4 CMA) and incubated at 22 °C for at least 10 days. Subcultures of the isolated fungi were made on WA and 1/4 CMA until pure cultures were obtained. In order to test the capability of the isolated fungi to colonize egg masses, surface-disinfested egg masses were added to the cultures of the selected fungi on WA, incubated for at least 14 days, and examined for fungal colonization. It was assumed that fungi had to be able to colonize the egg mass before they could infect eggs. Therefore, no separate eggs were spread on the colonized agar plates, but eggs still contained within the gelatinous matrix were used instead. To verify that the assay egg masses were not previously parasitized, 10 of them were added to a plate with WA only (control) each time a new batch was used. Cultures of the fungi growing out of the assay egg masses were compared with the cultures isolated from the egg masses obtained from the soil samples. Some egg masses were squashed, and their eggs were observed at

×400 magnification to verify whether fungal mycelia were present inside the eggs.

The following method, based on a dilution plating procedure (Jaffee et al., 1988), was used to detect fungal parasites of *M. hapla* juveniles. Four 120-cm^3 plastic cups were each filled with 100 cm^3 of organic soil obtained from the previously described pots containing the five different soil samples. Cups were incubated at 22 °C for 10 days before 3,000 or 5,000 assay juveniles of *M. hapla* were added. Freshly hatched assay nematodes were collected from Baermann funnels on top of which eggs of *M. hapla* had been pipetted on autoclaved sand, or from petri dishes containing disinfested mature egg masses placed on WA. After 5 to 7 days of incubation, nematodes were extracted from the organic soil in each cup using a centrifugal-flotation method (Jenkins, 1964). Extracted juveniles were rinsed in 10% NaOCl for 30 seconds, rinsed, and resuspended in sterile, distilled water. A 1-ml suspension of juveniles obtained from each cup was spread onto three petri dishes with WA (0.33 ml per petri dish). Plates were incubated at 22 °C for 7 days before they were examined for parasitized nematodes. Infected juveniles were transferred to 1/4 CMA and incubated until fungal colonies developed. Colonies were subcultured on WA and 1/4 CMA and purified when necessary. Freshly hatched assay juveniles were added to most of the fungal cultures obtained to verify the pathogenicity of the isolated fungi. Fungi reisolated from the infected assay juveniles were compared with the original test isolate. Rhabditoid nematodes were sometimes added to plates with isolated fungi to investigate the parasitizing potential of the fungus or to enhance formation of trapping structures. Populations of rhabditoid nematodes were grown on *Enterobacter cloacae* on half-strength nutrient agar and were provided by P. Mullin (Department of Plant Pathology, Cornell University, Ithaca, NY).

All fungal isolates were grown on WA, 1/4 CMA, and potato dextrose agar (PDA) or malt agar (MA). Colony color, texture, and growth rate, as well as the description and measurements of reproductive structures, were recorded for identification. Measurements and observations were made with dissecting and compound microscopes, either from prepared microscope slides or directly from the cultures on the petri plate. Fungal structures on microscope slides were prepared in lactophenol blue, lactophenol, or water. Several references were used in the identification of the fungi (Barron, 1968, 1977; Cooke and Godfrey, 1964; Gams, 1971; Liu and Zhang, 1994; Minter and Brady, 1980; Nelson et al., 1983; van Oorschot, 1985).

Results

A total of 311 egg masses and 1,026 juveniles of *M. hapla* were examined for fungal infection. Depending on the soil sample, between 13% and 30% of the egg masses exhibited fungal growth, and between 5% and 24% of the juveniles were found to be infected with fungi (Table 1). Twenty-four and 16 representative fungal isolates from infected egg masses and juveniles, respectively, were selected for characterization (Table 1). Four of the isolates that colonized egg masses belonged to the genus *Fusarium,* three were identified as *Alternaria,* and two were identified as *Verticillium psalliotae* Treschow. Six other fungal isolates that colonized egg masses could not be identified, primarily because they did not sporulate (Table 2). Three of these unidentified isolates caused egg masses to turn pink, and their mycelia were observed inside the eggs. All 15 of the above-mentioned isolates were able to colonize assay egg masses and were reisolated from them. Mycelia were observed inside the eggs of squashed colonized egg masses taken at random from each of the fungal cultures, but egg parasitism was not quantified. In addition, it was assumed that the mycelia inside the eggs belonged to the fungus colonizing the egg mass. Nine of the fungal cultures isolated from egg masses did not re-infect the assay egg masses. They included common soil fungi such as *Penicillium* sp. and *Chaetomium* sp. All assay egg masses and juveniles of *M. hapla* that were

TABLE 1. Percentage of egg masses and juveniles (J2) of *Meloidogyne hapla* with fungal growth in organic soils from New York, and the numbers of fungal isolates selected for characterization.

	Number of egg masses and J2 examined		Egg masses and J2 with fungi (%)		Number of fungal isolates selected	
Soil sample[a]	Egg masses	J2	Egg masses	J2	Egg masses	J2
A	112	316	21	5	4	5
B	60	393	15	9	5	2
C	30	228	13	15	2	4
D	60	33	30	24	4	1
E	49	56	29	11	9	4
Total	311	1,026			24	16

[a] Soil samples were obtained from five locations in New York: A) Ferlito farm, Oswego; B) Sheldon farm, Oswego; C) Elba muck, Elba; D) Jacobson farm, Oswego; E) experimental microplots, Geneva (filled with organic soil from another field from Ferlito farm, Oswego).

put on plates with water agar (control) were uninfected, as all attempts made for fungal recovery were negative.

Several species of *Arthrobotrys* and *Monacrosporium* were found to parasitize juveniles of *M. hapla* in the various soils sampled (Table 2). Two isolates of *M. ellipsosporum* (Preuss) Cooke & Dickinson were obtained from the same soil, but the morphology of their conidia differed. Conidia of one isolate were larger and wider and had a more bulbous middle cell than the conidia of the

TABLE 2. Fungi found in association with egg masses and juveniles of *Meloidogyne hapla* in samples of organic soil collected from various production areas in New York.

Fungal species	Soil sample[a]	Number of isolates	Accession number[b]
	Egg masses		
Parasitic			
Fusarium sp.	A	2	4956, 4962
F. oxysporum	B,C	2	4963, 4964
Verticillium psalliotae	C,D	2	4960, 4965
Alternaria sp.	B,D	3	
not identified	A,D	6	
Total		15	
Nonparasitic			
Penicillium sp.	E	1	
Chaetomium sp.	E	1	
not identified	B,E	7	
Total		9	
	Juveniles		
Parasitic			
Arthrobotrys dactyloides	A	1	4955
A. oligospora	E	1	4967
Monacrosporium sp.	C,E	2	4961
M. cionopagum	E	1	4966
M. ellipsosporum	B,C	3	4957–4959
Hirsutella rhossiliensis	E	1	
Total		9	
Nonparasitic			
Harposporium anguillulae	A	1	4954
Penicillium sp.	A,B	2	
not identified	A,C,D	4	
Total		7	

[a] Soil samples were obtained from five locations in New York: A) Ferlito farm, Oswego; B) Sheldon farm, Oswego; C) Elba muck, Elba; D) Jacobson farm, Oswego; E) experimental microplots, Geneva (filled with organic soil from another field from Ferlito farm, Oswego).

[b] USDA ARS Collection of Entomopathogenic Fungal Cultures (ARSEF).

other isolate. *Hirsutella rhossiliensis* was found in one of the nematodes retrieved from the soil of the field microplots. Seven of the 16 fungal isolates, obtained through the modified dilution-plating procedure, were unable to infect assay juveniles of *M. hapla* that were added to petri dishes with the fungal cultures. One of them, *Harposporium anguillulae* Lohde, parasitized the rhabditoid assay nematodes. In culture, the fungus produced a synanamorph attributable to the genus *Hirsutella,* which contains several entomopathogenic and nematophagous species (Jaffee et al., 1988; Minter and Brady, 1980). However, the *Hirsutella* conidia obtained in the isolate found in this study were not observed to infect juveniles of *M. hapla* in petri-dish assays (Hodge et al., 1997). Cultures of several of the isolated fungi have been deposited in the USDA ARS Collection of Entomopathogenic Fungal Cultures (ARSEF: Plant Protection Research Unit, U.S. Plant, Soil, and Nutrition Laboratory, Tower Road, Ithaca, NY 14853). Their accession numbers are included in Table 2.

Discussion

Some of the fungi found in association with *M. hapla* in the present study have been reported previously as parasites of different species of root-knot nematodes and of the soybean cyst nematode (Carris and Glawe, 1989; Chen et al., 1994; Hidalgo et al., 1997; Ma, 1991; Roccuzzo et al., 1993). *Fusarium oxysporum* Schlecht. also was reported as a parasite of *M. hapla* eggs (Ma, 1991). Mycelium of the two *F. oxysporum* isolates found in the present study was clearly seen inside the eggs of the assay egg masses. Some of the egg masses infested with the fungus showed a bright pink color. It was suggested by Chen et al. (1996) that *F. oxysporum* is a good soil and cyst colonizer and that it should be regarded as a potential biological control agent of the soybean cyst nematode. Three of the six unidentified fungal isolates also colored the egg masses pink. Although observation of the cultures showed that two of the six isolates did not belong to the genus *Fusarium,* because atypical chlamydospores for this genus were observed, it is possible that the other four isolates belong to the genus. Further study on the unidentified fungi and *Fusarium* spp. isolated from egg masses in this study is warranted as potential biocontrol agents could be discovered. It is possible that some of the cultures of *M. hapla* maintained in the greenhouse on tomato were infected with one or more of these isolates and that not enough assay egg masses were tested in the control plates to detect this infestation. It is not unusual that pot cultures of plant-parasitic nematodes in the greenhouse become contaminated with nematode antagonists (Chen et al., 1996; Walter et al., 1993).

Verticillium psalliotae has been reported as a mycoparasite and was isolated from cysts of *Globodera rostochiensis* (Barron, 1968; Gams, 1971, 1988). Its ability to parasitize eggs of *Meloidogyne* spp. has been reported only recently (Hidalgo et al., 1997). In the present study, *V. psalliotae* was isolated from soils of two different counties, suggesting that several isolates are present in the organic soils of New York. Further study of this species of *Verticillium* is warranted as it might have similar properties as *V. chlamydosporium,* a biocontrol agent of root-knot and cyst nematodes that has been studied thoroughly (Kerry and Jaffee, 1997).

Arthrobotrys dactyloides Drechsler and *A. oligospora* Fresenius were found to parasitize juveniles of *M. hapla* in kiwi fields (Roccuzzo et al., 1993), and *A. oligospora* was isolated from *M. hapla* in peanut field soil (Ma, 1991). The isolates of *A. dactyloides* and *A. oligosporum* found in this study, as well as the isolates of the other nematode-trapping fungi, *M. cionopagum, M. ellipsosporum,* and *Monacrosporium* sp., should be investigated further, as some of them were able to capture and destroy almost all of the assay juveniles added to petri-dish cultures. In addition, application of sodium alginate pellets or wheat bran colonized by the isolate of *A. oligospora* to organic soil resulted in a significant reduction in penetration of juveniles of *M. hapla* into lettuce seedlings in studies conducted in the growth chamber (Abawi et al., unpublished data).

Hirsutella rhossiliensis has been studied intensively as a parasite of root-knot and cyst nematodes in soil microcosms, in the greenhouse, in field microplots, and in the field (Kerry and Jaffee, 1997). The isolate of *H. rhossiliensis* from the soil in the experimental field microplots might be a new isolate, or it could also be the isolate that was used in adjacent microplots where the fungus was tested as a biocontrol agent. Study of the variation in pathogenicity of the two isolates will demonstrate whether the newly identified isolate is suitable for managing *M. hapla* in organic soil.

With the isolation of fungal antagonists of *M. hapla* from organic soils, a first step is set in the search for biological control agents that are well adapted to the conditions prevailing in commercial lettuce and onion fields in New York. It is assumed that these isolates will be more efficient in suppressing the populations of *M. hapla* in organic soils in New York than isolates retrieved from other areas with different soil types. Generally, local isolates will better tolerate extremes of temperature and moisture, disperse more rapidly in the soil, compete more efficiently in the rhizosphere, and be better adapted to the surrounding soil organisms (Stirling, 1991). Fungi that are parasitic to *M. hapla* were isolated from each soil sample. A next step in the search for effective biological control agents could be the study of the capability of the isolated fungi to suppress the nematode population in pots or in the field. Naturally occurring antagonists of *Meloidogyne sp.* on grapes and kiwi fruit were not able to suppress the nematode population below the damage threshold density (Mertens and Stirling, 1993; Roccuzzo et al., 1993). Fungi that are effective in parasitizing different stages in the life cycle of *M. hapla* could be combined for adequate suppression of the nematode population. However, long-term protection of a host crop against *M. hapla* will be achieved more effectively when other management strategies, in addition to the application of antagonists, are applied as part of an integrated pest management program.

Literature Cited

Abawi, G. S., and P. Laird. 1994. Increasing occurrence and damage of the northern root-knot nematode on onions in New York. Phytopathology 84:1370 (Abstr.).

Abawi, G. S., J. W. Ludwig, and L. Fusco. 1997. Symptoms and damage of the northern root-knot nematode on carrots in New York. Phytopathology 87 (Suppl.):1 (Abstr.).

Abawi, G. S., and R. W. Robinson. 1991. Reaction of selected lettuce germplasm to artificial inoculation by *Meloidogyne hapla* in the greenhouse. Journal of Nematology 23:519 (Abstr.).

Barron, G. L. 1968. The genera of Hyphomycetes from soil. Malabar, FL: Robert E. Krieger Publishing.

Barron, G. L. 1977. The nematode-destroying fungi. Guelph, Ontario: Canadian Biological Publications.

Bélair, G. 1989. A note on the development of *Meloidogyne hapla* on lettuce in organic soil in Québec. Phytoprotection 70:133–136.

Carris, L. M., and D. A. Glawe. 1989. Fungi colonizing cysts of *Heterodera glycines*. USDA Bulletin 786. University of Illinois, Urbana-Champaign, IL.

Chen, S., D. W. Dickson, J. W. Kimbrough, R. McSorley, and D. J. Mitchell. 1994. Fungi associated with females and cysts of *Heterodera glycines* in a Florida soybean field. Journal of Nematology 26:296–303.

Chen, S. Y., D. W. Dickson, and D. J. Mitchell. 1996. Pathogenicity of fungi to eggs of *Heterodera glycines*. Journal of Nematology 28:148–158.

Cooke, R. C., and B. E. S. Godfrey. 1964. A key to the nematode-destroying fungi. Transactions of the British Mycological Society 47:61–74.

de Leij, F. A. A. M., B. R. Kerry, and J. A. Dennehy. 1993. *Verticillium chlamydosporium* as a biological control agent for *Meloidogyne incognita* and *M. hapla* in pot and micro-plot tests. Nematologica 39:115–126.

Den Belder, E., and E. Jansen. 1994. The influence of temperature, nutrition, light, and the growth time of the mycelium on capture and infection of *Meloidogyne hapla* and *Arthrobotrys oligospora*. Fundamental and Applied Nematology 17:57–66.

Gams, W. 1971. *Cephalosporium*-artige Schimmelpilze (Hyphomycetes). Stuttgart: Gustav Fischer Verlag.

Gams, W. 1988. A contribution to the knowledge of nematophagous species of *Verticillium*. Netherland Journal of Plant Pathology 94:123–148.

Gaskin, T. A., and H. W. Crittenden. 1956. Studies of the host range of *Meloidogyne hapla*. Plant Disease Reporter 40:265–270.

Hidalgo, L., J. M. Bourne, and B. R. Kerry. 1997. Characterization of nematophagous species of *Verticillium* from Cuban coffee plantations. P. 48 *in* Third International Scientific Seminar of Plant Protection - Abstracts.

Hodge, K. T., N. M. Viaene, and W. Gams. 1997. Two *Harposporium* species with *Hirsutella* synanamorphs. Mycological Research 101:1377–1382.

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.

Jaffee, B. A., J. T. Gaspard, H. Ferris, and A. E. Mul-

doon. 1988. Quantification of parasitism of the soilborne nematode *Criconemella xenoplax* by the nematophagous fungus *Hirsutella rhossiliensis*. Soil Biology and Biochemistry 20:631–636.

Jenkins, W. R. 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Disease Reporter 48:692.

Kerry, B. R., and B. A. Jaffee. 1997. Fungi as biological control agents for plant-parasitic nematodes. Pp. 203–218 *in* D. T. Wicklow and B. Söderström, eds. The Mycota IV. Environmental and microbial relationships. Berlin: Springer-Verlag.

Liu, X. Z., and K. Q. Zhang. 1994. Nematode-trapping species of *Monacrosporium* with special reference to two new species. Mycological Research 98:862–868.

Ma, C. Z. 1991. Investigation on the fungi parasites of *Meloidogyne hapla* in peanut field soil. Disinsectional Microorganism 3:202–207. (In Chinese; English summary.)

Mertens, M. C. A., and G. R. Stirling. 1993. Parasitism of *Meloidogyne* spp. on grape and kiwifruit by the fungal egg parasites *Paecilomyces lilacinus* and *Verticillium chlamydosporium*. Nematologica 39:400–410.

Minter, D. W., and B. L. Brady. 1980. Mononematous species of *Hirsutella*. Transactions of the British Mycological Society 74:271–282.

Nelson, P. E., T. A. Tousson, and W. F. O. Marasas. 1983. *Fusarium* species: An illustrated manual for identification. University Park, PA: Pennsylvania State University Press.

Noling, J. W., and J. O. Becker. 1994. The challenge of research and extension to define and implement alternatives to methyl bromide. Supplement to the Journal of Nematology 26:573–586.

Roccuzzo, G., A. Ciancio, and R. Bonsignore. 1993. Population density and soil antagonists of *Meloidogyne hapla* infecting kiwi in southern Italy. Fundamental and Applied Nematology 16:151–154.

Stirling, G. R. 1991. Biological control of plant-parasitic nematodes: Progress, problems, and prospects. Wallingford, UK: CAB International.

Townshend, J. L., M. Meskine, and G. L. Barron. 1989. Biological control of *Meloidogyne hapla* on alfalfa and tomato with the fungus *Meria coniospora*. Journal of Nematology 21:179–183.

van Oorschot, C. A. N. 1985. Taxonomy of the *Dactylaria* complex, V. A review of *Arthrobotrys* and allied genera. Studies in Mycology 26:61–96.

Viaene, N. M. 1996. Damage threshold and biological control of the northern root-knot nematode (*Meloidogyne hapla* Chitwood) infecting lettuce (*Lactuca sativa* L.) in organic soil. Ph.D. thesis, Cornell University, Ithaca, NY.

Viaene, N. M., and G. S. Abawi. 1995. Nematophagous fungi associated with *Meloidogyne hapla* in organic soils in New York. Phytopathology 85:1561 (Abstr.)

Walter, D. E., D. T. Kaplan, and E. L. Davis. 1993. Colonization of greenhouse nematode cultures by nematophagous mites and fungi. Supplement to the Journal of Nematology 25:789–794.