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# Antagonists of Plant-parasitic Nematodes in Florida Citrus[1]

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*Abstract:* In a survey of antagonists of nematodes in 27 citrus groves, each with a history of *Tylenchulus semipenetrans* infestation, and 17 noncitrus habitats in Florida, approximately 24 species of microbial antagonists capable of attacking vermiform stages of *Radopholus citrophilus* were recovered. Eleven of these microbes and a species of *Pasteuria* also were observed attacking vermiform stages of *T. semipenetrans. Verticillium chlamydosporium, Paecilomyces lilacinus, P. marquandii, Streptomyces* sp., *Arthrobotrys oligospora*, and *Dactylella ellipsospora* were found infecting *T. semipenetrans* egg masses. Two species of nematophagous amoebae, five species of predatory nematodes, and 29 species of nematophagous arthropods also were detected. Nematode-trapping fungi and nematophagous arthropods were common inhabitants of citrus groves with a history of citrus nematode infestation; however, obligate parasites of nematodes were rare.
*Key words:* biological control, burrowing nematode, citrus nematode, nematophagous arthropod, nematophagous fungus, *Pasteuria, Streptomyces.*

Nematode control in citrus has relied heavily upon nematicides that are highly water soluble, toxic to vertebrates, and persistent (13). In addition to nematicides, resistant rootstocks have been used to limit losses associated with citrus (*Tylenchulus semipenetrans* Cobb) and burrowing (*Radopholus citrophilus* Huettel et al.) nematodes. These rootstocks are not always horticulturally acceptable, however, and some have limited tolerance to cold and disease. Furthermore, occurrence of resistance-breaking nematode populations in the field and variability in citrus rootstock germplasm suggest that existing rootstocks require improvement before they can be relied upon to limit nematode-related yield losses (13,16).

Improved understanding of the identity and function of antagonists will be necessary if they are to be used as management tools of plant-parasitic nematodes (14,24). This paper reports the results of a survey of citrus groves and other habitats in Florida for the presence of antagonists to plant-parasitic nematodes.

## MATERIALS AND METHODS

*Sampling:* Randomly selected 10 × 10 tree blocks in 27 citrus groves, each with a history of citrus nematode infestation, in Marion, Lake, Seminole, Orange, Brevard, Polk, Hardee, Highlands, St. Lucie, and Dade counties in Florida were sampled. The presence of citrus nematode was confirmed in 25 of the groves surveyed. Nine groves were sampled by bulking cores from three to five trees. In each of 18 groves, five individual trees older than 10 years were sampled. Each sample consisted of three cores (7 cm d, 15–30 cm deep) of citrus fibrous roots exposed by removing surface soil at equidistant locations midway between the trunk and dripline of each tree. Tools were disinfected with 0.5% NaOCl between samples. Samples were placed in polyethylene bags in ice chests and processed the same or the next day.

Seventeen noncitrus habitats in Orange, Seminole, Lake, and Brevard counties also were sampled, including soil and litter from a composted garden, rotted horse manure, beach wrack, a rotted palm tree, a carrot field muck soil, and rhizosphere soil from stands of live oak, pine, palmetto, banana, broomsedge, anthurium, and impatiens. Samples of citrus leaf litter (normally not

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included in samples) from two sites (Ona and Apopka, FL) also were evaluated for the presence of nematode antagonists.

*Isolation of nematophagous microbes:* Citrus roots from each tree or bulked sample were gently rolled to dislodge rhizosphere soil, root fragments, and citrus nematode egg masses. The dislodged material was passed through a 1-mm-pore sieve and collected on a 0.25-mm-pore sieve. The screens were then tapped to remove very fine sand grains that interfered with observation. The screened rhizosphere material (0.25 g) was divided into equal subsamples and sprinkled on two 9-cm petri dishes, each containing 4 ml solidified 1.0% water agar (WA). Between samples, sieves were washed in soapy water, disinfected with 1.0% NaOCl, rinsed with tap water, and dried with compressed air. Soil, litter, and root fragments from the noncitrus samples and two citrus litter samples were plated on four replicate WA plates. Because these samples were not comparable in composition and moisture content to the citrus samples, material was added to each plate to cover a surface area similar (by visual estimation) to that obtained with citrus root samples. Each dish was inoculated with 5,000 *Radopholus citrophilus* (sometimes supplemented with *R. similis*) in 0.5 ml water and then incubated at 25 ± 1 C. Bait nematodes were obtained from monoxenic carrot disk cultures extracted enzymatically (15). At five sites the efficacy of burrowing nematode as a bait organism was evaluated by baiting one of each pair of plates with 5,000 burrowing nematodes, and the other plate in the pair with 5,000 *Rhabditis* sp., which had been isolated from citrus roots, cultured on pea soup agar, and extracted by Baermann funnel (2).

After removal of rhizosphere material for the sprinkle-bait plates, citrus roots from 18 groves (five samples per grove) were incubated in jars at 25 C (28) for 5–7 days. Subsequently, the roots were rinsed in tap water and the nematode suspension was centrifuged at 175 *g* for 5 minutes. All but 1 ml supernatant was aspirated, and the pellet was dispersed and pipetted onto 1% WA in 9-cm petri dishes that were incubated at 25 C. Roots from bulked samples and noncitrus habitats were not processed.

Bait and root incubation plates were examined with a compound inverted light microscope at 100–400 magnification at 1–3-day intervals for up to 6 weeks. Fungi were identified using keys (1,5,11,17,18, 20,23) and original descriptions. Spores or infected nematodes were transferred with a flamed wire to an appropriate medium. Most Eumycota were cultured on corn meal, yeast malt agar, or potato dextrose agar. Streptomycetes were cultured on tryptic soy agar. Chytridiomycetes were cultured on YpSs agar (9). Most other endoparasites could be maintained in burrowing or rhabditid nematodes on 1% WA plates at 25 C. Nematode cadavers infected with microbes that could not be identified were transferred with a flamed wire to 1% WA plates with fresh burrowing nematodes from monoxenic cultures to determine if further infection occurred.

*Isolation of predators:* Ten citrus groves were surveyed for nematophagous arthropods. Five citrus groves and six noncitrus sites were surveyed for predatory nematodes. Nematophagous arthropods were extracted from 100–200 $cm^3$ soil in standard Tullgren funnels over 70% ethanol. Predatory nematodes were obtained from 180 $cm^3$ soil in Baermann funnels. Other predatory animals including amoebae, nematodes, and arthropods were obtained from bait plates and root incubations. Live arthropods were tested for predation on *R. citrophilus* in small arenas (27).

## Results

*Microbial antagonists:* Approximately 24 microbial species antagonistic to vermiform stages of burrowing nematode were isolated from bait plates, and 12 microbial species were observed attacking citrus nematodes from root incubations (Table 1). In addition, *Paecilomyces lilacinus* (Thom.) (Samson), *P. marquandii* (Massee) (Hughes), and *Verticillium chlamydosporium* Goddard (also isolated from vermiform

TABLE 1. Microbial antagonists of vermiform stages of phytonematodes recovered from the rhizospheres of 27 citrus groves and from 19 samples of soil and litter from other habitats in Florida.

| Species | Mode of infection | Infection† *Radopholus citrophilus* | Infection† *Tylenchulus semipenetrans* | Number of positive sites‡ Citrus | Number of positive sites‡ Other | Frequency§ (Mean ± SE) |
|---|---|---|---|---|---|---|
| *Arthrobotrys dactyloides* Drechsler | Constricting ring | + | + | 20 | 3 | 0.44 ± 0.06 |
| *Catenaria anguillulae* Sorokine | Zoospore | + | + | 19 | 10 | 0.68 ± 0.08 |
| *Arthrobotrys oligospora* Fresenius | Adhesive network | + | + | 19 | 3 | 0.59 ± 0.07 |
| *Streptomyces* sp. | ?Spore | + | + | 19 | 3 | 0.35 ± 0.08 |
| *Dactylella ellipsospora* Grove | Adhesive knob | + | + | 18 | 11 | 0.41 ± 0.10 |
| *Dactylella cionapaga* Drechsler | Adhesive hyphae | + | + | 18 | 4 | 0.57 ± 0.08 |
| *Rhizophidium* sp. | Zoospore | + | + | 12 | 7 | 0.37 ± 0.08 |
| *Arthrobotrys musiformis* Drechsler | Adhesive network | + | + | 12 | 1 | 0.32 ± 0.08 |
| *Dactylaria eudermata* Drechsler | Adhesive network | + | − | 9 | 6 | 0.10 ± 0.05 |
| *Myzocytium* spp. | Zoospore | + | + | 5 | 4 | 0.14 ± 0.06 |
| Unidentified lagenidioid | Zoospore | + | − | 5 | 3 | 0.13 ± 0.06 |
| *Dactylaria* nr. *candida* (Nees) Sacc. | Adhesive knob & nonconstricting ring | + | + | 4 | 0 | 0.02 ± 0.02 |
| *Dactylaria haptospora* Drechsler | Adhesive knob & spore | + | − | 1 | 1 | 0.01 ± 0.01 |
| *Haptoglossa heterospora* Drechsler | Spore | + | − | 1 | 1 | 0.01 ± 0.01 |
| *Pasteuria* (Thorne) Sayre & Starr | Spore | − | + | 1 | 0 | 0.06 ± 0.17 |
| *Dactylaria sclerohypha* Drechsler | Adhesive knob | + | − | 1 | 0 | 0.01 ± 0.01 |
| *Verticillium* spp. | Spore | + | − | 0 | 4 | |
| *Gonimochaete horridula* Drechsler | Adhesive spore | + | − | 0 | 2 | |
| *Gonimochaete latitubus* Newell, Cefalu & Fell | Adhesive spore | + | − | 0 | 1 | |
| *Dactylella phymatopaga* Drechsler | Adhesive knob | + | − | 0 | 1 | |
| *Dactylella bembicoides* Drechsler | Constricting ring | + | − | 0 | 4 | |
| *Dactylaria brochopaga* Drechsler | Constricting ring | + | − | 0 | 2 | |

† Host response: + = infections observed; − = infections not observed.
‡ For all 27 citrus groves and 19 other samples irrespective of sampling effort.
§ Mean proportion citrus rhizospheres positive for antagonist, based on combined bait plate and root incubation data from 18 groves from which five replicate samples were taken.

burrowing nematodes) were observed growing from citrus nematode egg masses that included hypha-filled eggs. *Streptomyces* sp., *Arthrobotrys oligospora* Fresenius, and *Dactylella ellipsospora* Grove also were observed growing from citrus nematode egg masses, but only vermiform stages within the egg masses appeared to be attacked. *Harposporium anguilullae* Lohde, *H. helicoides* Drechsler, and *Nematoctonus leptosporus* Drechsler were isolated from rhabditid nematodes, but never from burrowing nematodes. Mean number of species of microbial antagonists detected on plates baited with burrowing nematodes (3.0 ± 0.3) was greater than on plates baited with *Rhabditis* sp. (1.6 ± 0.3) ($P < 0.05$, Wilcoxon signed ranks test).

Nematode-destroying fungi were common in the citrus rhizosphere, but only 17 species were collected from 27 citrus sites as opposed to 26 species from 19 noncitrus rhizosphere sites (including two samples of citrus litter). Within-site diversity (based on sprinkle-bait plates only) averaged 5.8 ± 0.4 species/site in the citrus rhizosphere, but only 4.1 ± 0.4 species/site in other habitats ($P < 0.01$, Mann-Whitney test). Plots of cumulative species number against cumulative sample number (species area curve) indicated that the isolation of new species reached an asymptote in the citrus groves, but not in the noncitrus habitats.

Twelve species of nematode-trapping fungi, representing all major trap types, were isolated during this study. Every cit-

TABLE 2. Predators of nematodes recovered from citrus rhizosphere soil in Florida citrus groves.

| | Fed on nematodes in vitro | Congeners or closely related species reported to be nematophagous (22,26,27) | Nematodes in gut contents |
|---|---|---|---|
| Mesostigmata | | | |
| Parasitidae | | | |
| *Gamasiphis* (two species) | X | | |
| Rhodacaridae | | | |
| *Afrodacarellus* sp. | | X | |
| *Afrogamasellus citri* Loots | | X | |
| *Rhodacarus denticulatus* Berlese | X | | |
| Ascidae | | | |
| *Protogamasellus mica* (Athias) | X | | |
| *Protogamasellus* nr. *brevicornis* Genis, Loots, & Ryke | X | | |
| *Protogamasellus* n. sp. | X | | |
| *Protogamasellus* nr. *massula* (Athias) | X | | |
| *Protogamasellopsis* nr. *corticalis* Evans & Purvis | X | | |
| *Asca duosetosa* (Fox) | | X | |
| *Cheiroseius* nr. *browningi* (Evans & Hyatt) | | X | |
| *Gamasellodes vermivorax* Walter | | X | |
| *Gamasellodes rectiventris* Lindquist | | X | |
| *Lasioseius dentatus* Fox | X | | |
| Laelapidae | | | |
| *Cosmolaelaps* nr. *weeversi* Oudemans | X | | |
| *Cosmolaelaps* nr. *vacua* (Michael) | X | | |
| *Cosmolaelaps* nr. *carvalhoi* (van Aswegen & Loots) | | X | |
| *Euandrolaelaps* sp. | | X | |
| *Geolaelaps* nr. *aculeifer* Can. | X | | |
| *Geolaelaps* nr. *angusta* (Karg) | X | | |
| *Hypoaspis* nr. *similiseta* Karg | | X | |
| *Hypoaspis* (2 species) | X | | |
| Macrochelidae | | | |
| *Holostaspella bifoliata* (Trag.) | X | | |
| Pachylaelapidae | | | |
| *Zygoseius furciger* Berlese | X | | |
| Astigmata | | | |
| Acaridae | | | |
| *Schwiebia rocketti* Woodring | X | | |
| Prostigmata | | | |
| Alicorhagiidae | | | |
| *Alicorhagia* sp. | | X | |
| Symphyla | | | |
| Scutigerellidae | | | |
| *Symphylellopsis arvernorum* Ribaut | | | X |
| Sarcodina | | | |
| *Theratromyxa weberi* Zwillenberg | X | | |
| *Thecamoeba* sp. | X | | |
| Nematoda | | | |
| Mononchida | | | |
| *Mononchus* sp. | | X | |

TABLE 2. Continued.

| | Fed on nematodes in vitro | Congeners or closely related species reported to be nematophagous (22,26,27) | Nematodes in gut contents |
|---|---|---|---|
| Dorylaimida | | | |
| *Dorylaimus* sp. | X | | |
| *Discolaimus* sp. | | X | |
| *Labronema* sp. | | X | |
| Diplogasteridae | | | |
| *Fictor* sp. | X | | |

rus grove sampled had 1–6 species of trapping fungi, and 174 of the 187 individual samples (93%) from citrus roots contained at least one trapping fungus. Two Chytridiomycetes, *Catenaria anguilullae* Sorokin and a species of *Rhizophidium*, were among the most frequently collected antagonists in citrus samples (Table 1). Other zoosporic and related fungi were relatively rare and difficult to identify with certainty. Several forms of *Myzocytium*-like oomycetes have been combined in Table 1. An unidentified fungus that appeared similar to *Nematophthora gynophila* Kerry & Crump, but which produced oospores within the sporangia rather than laterally, also was recovered.

Spores similar to those of *Pasteuria penetrans* (Thorne) Sayre & Starr were observed only on citrus nematode juveniles and males from Ona. Several juveniles from this grove were filled with *Pasteuria* spores. No females with clear indications of infection by *Pasteuria* could be found.

An actinomycete, *Streptomyces* sp., was recovered from dead burrowing nematodes and from citrus nematode egg masses. Nematode bodies were filled with a fine mycelium, and numerous spiral conidiophores that divided basipetally into small round conidia were produced from the cadavers.

*Predators:* Thirty-six species of predators that fed on nematodes were collected (Table 2). Dorylaimida (including species of *Labronema, Discolaimus, Dorylaimus,* and *Mononchus*) were the most frequently observed predatory nematodes. The vampyrellid *Theratromyxa weberi* Zwillenberg, a commonly isolated amoeba, was observed feeding on small rhabditid nematodes. Another amoeba, resembling a species of *Thecamoeba* that is known to prey on nematodes in Florida (6), also was observed engulfing small rhabditid nematodes.

Nematophagous arthropods were present in all of the citrus groves sampled. Mesostigmatic mites (Acari: Mesostigmata) were the most diverse (26 species) and abundant. Mean densities were estimated at three groves and ranged from 0.5 to 11.8 Mesostigmata/100 $cm^3$ soil. Sixteen of the mite species were obtained alive, and they readily fed on burrowing nematodes in small laboratory arenas. The gut contents of a symphylan, *Symphylellopsis arvernorum* Ribaut (Scolopendrellidae), collected from six citrus groves, included dorylaims with large odontostyles. A springtail, *Onychiurus* sp., and an oribatid mite, *Galumna* sp., fed on burrowing nematodes in the laboratory, but no systematic attempt was made to determine the prevalence of nematophagy in other mycophagous soil arthropods from citrus groves.

## DISCUSSION

All surveys are highly dependent on the techniques used to recover antagonists. We sampled citrus roots or rhizosphere soil from groves with a history of citrus nematode infestation and used plant-parasitic nematodes as bait. In this way we hoped to isolate antagonists with a high potential for use as biological control agents. Every grove and almost every sample from the citrus rhizosphere contained one or more microbial antagonists of plant-parasitic nematodes. Nematode-trapping fungi and endoparasites such as *C. anguillulae,* which obtain nutrition from both detritus and nematodes, were the most common antagonists in the citrus rhizosphere. More than 20 species of antagonists to plant-parasitic nematodes, mostly generalist trapping fungi and predators, have been reported from citrus groves in California (10,12,19,24).

In our survey, specialized nematode parasites were rare. For example, species of *Pasteuria* are thought to be species-specific, or even strain-specific, parasites of nematodes (21). The *Pasteuria* sp. we found infecting citrus nematode was very abundant (present in 19 of 20 samples) at one site but was not recovered at any of the 26 other sites. Fattah et al. (8) also reported a strain of *P. penetrans* from Iraq that sporulates within the juvenile. Obligate parasites might have been detected more frequently in this study if techniques that emphasize recovery of moribund or dead hosts had been used more extensively (B. Jaffee, pers. comm.).

Without extensive study, it is often difficult to determine if a microbial organism is in fact a nematode antagonist. Procaryotes are not often reported as nematode antagonists, but 70% of the citrus groves we sampled contained a *Streptomyces* sp. that appears to be a parasite of both burrowing and citrus nematode. A species of *Streptomyces* has been reported to attack tylenchid and aphelenchid nematodes by means of sticky spores (21). Isolates of the citrus *Streptomyces* sp. have been sent to R. Charudatan (University of Florida, Gainesville) for further evaluation.

Generalist predators of nematodes have not been studied extensively, but at least nine species of predatory nematodes have been reported to feed on citrus nematode and at least three species feed on burrowing nematode (3,4,7,22). Predatory nematodes, however, appeared to be relatively rare in the groves sampled. Nematophagous arthropods, especially mesostigmatic mites, were common and occasionally abundant in citrus rhizospheres. Many mesostigmatic mites have rapid generation times and high reproductive outputs, and they feed voraciously on nematodes, indicating that they may have potential as biological control agents (26,27).

Noncitrus habitats in Florida also contain organisms that can attack burrowing nematodes, yet several of these antagonists were not detected in adjacent citrus groves. The manner in which nematode predators and parasites become dispersed is unknown, but our results indicate that citrus groves have relatively predictable antagonist fauna and flora dominated by generalist predators (Mesostigmata, Dorylaimida) and fungi (nematode-trapping fungi and chytrids). Factors contributing to the formation of this assemblage of generalists, and limiting the establishment of more specialized antagonists, require investigation.

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