Biological Control of Root-Knot Nematodes (*Meloidogyne* spp.) on Peach

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Portion of a thesis submitted by the senior author in partial fulfillment of the requirements for the Ph.D. degree.
Supported in part by a grant from the California Fresh Peach Advisory Board.
The senior author acknowledges the financial support of a CSIRO postgraduate studentship.
Accepted for publication 9 February 1979.

ABSTRACT

STIRLING, G. R., M. V. McKENRY, and R. MANKAU. 1979. Biological control of root-knot nematodes (*Meloidogyne* spp.) on peach. Phytopathology 69: 806-809.

Meloidogyne spp. appeared to be under natural biological control in some peach orchards on Lovell rootstock in the San Joaquin Valley, CA. The many species of nematode-trapping fungi occurring in these orchards played only a minor role in regulating *Meloidogyne* populations. Distribution of nematode-trapping fungi was related to factors other than root-knot nematodes. Trapped *Meloidogyne* larvae were not extracted from soil around Lovell peach, and predation was not stimulated by adding larvae to soil. The fungus *Dactylella oviparasitica* was a more successful biological control agent against *Meloidogyne* spp. and occurred in close association with the nematode. Although *Meloidogyne* eggs were an important food source, the fungus was able to survive without the nematode. *D. oviparasitica* parasitized most of the eggs in the relatively small egg masses (300–400 eggs) produced by *Meloidogyne* spp. females on Lovell peach. The fungus was less effective on tomato and grape, rarely parasitizing more than half the eggs in the larger egg masses (1,000–1,500 eggs) produced by the nematode on these crops.

Additional key words: Acremonium, Arthrobotrys, Monacrosporium, Prunus persica.

Root-knot nematodes (*Meloidogyne* spp.) reduce the longevity and productivity of peach (*Prunus persica* (L.) Batsch) trees on Lovell and other rootstocks (11,16,19). Most peach growers in the San Joaquin Valley, CA, use the *Meloidogyne*-resistant Nemaguard rootstock. A recent survey of orchards on Lovell rootstock showed that *Meloidogyne* populations were unexpectedly low (10). Physical factors and climatic conditions were suitable for the nematode because populations were high in adjacent grape (*Vitis vinifera* 'Thompson seedless') vineyards, and it was suggested that areas where Lovell rootstock remained were biologically unsuited to *Meloidogyne* spp. (10).

The possibility that root-knot nematodes were under natural biological control prompted a search for likely antagonists. Low numbers of predacious mites and predacious nematodes were found in most orchards, but they did not appear to significantly reduce *Meloidogyne* spp. populations (20). *Dactylella oviparasitica* Stirling and Mankau, a parasite of *Meloidogyne* eggs, and several species of nematode-trapping fungi also occurred (18,23), and the objective of this research was to determine their role in the natural biological control of *Meloidogyne* spp. on Lovell peach.

MATERIALS AND METHODS

The occurrence of root-knot nematodes, nematode-trapping fungi, and *D. oviparasitica* was studied in 14 peach orchards (seven on Lovell and seven on Nemaguard rootstock) and in seven grape (*Vitis vinifera* 'Thompson seedless') vineyards. The soils in the fields were of similar texture (sandy loam), and adjacent orchards and vineyards were chosen when possible. Soil samples were collected in September when population densities of *Meloidogyne* were at a maximum (9,10). Cores were taken 1–3 m from the trunk of at least 40 peach trees and from the berm area of at least 40 grapevines. The samples were collected with a 2-cm diameter Oakfield tube at depths of 10–45 cm. Roots were collected from six trees or vines at each site.

Occurrence of root-knot nematodes. Two 500-g subsamples of soil were processed using a Fenwick can (8). The overflow was collected on a 38-μm screen and placed on a Baermann funnel to extract the nematodes.

Occurrence of nematode-trapping fungi. Nematode-trapping fungi were isolated by incubating two 1-g root samples on one-quarter-strength corn meal agar (CMA/4) or by processing five 10-g subsamples of soil using the method of Mankau (17). A quantitative estimate of their abundance was obtained using a most probable number technique modified from that of Eren and Pramer (7). Soil (50 g) was shaken vigorously in 50 ml of water, a 10-ml subsample was removed, and a twofold dilution series was prepared with water blanks. Five replicate 0.1-ml portions of each of eight dilutions were added to CMA/4. After the suspension was absorbed into the agar, a drop of a suspension of *Caenorhabditis elegans*, a bacterial feeding nematode cultured with mixed bacteria on peanut butter agar (15 g peanut butter, 16 g agar, 1 L water) was added to each plate.

Occurrence of *D. oviparasitica*. *D. oviparasitica* either was isolated directly from *Meloidogyne* egg masses collected in the field or from egg masses on tomato seedlings grown in field soil in the greenhouse or was observed on roots incubated on agar (22).

Predation of *Meloidogyne* larvae in field soil. Two experiments were designed to quantify the amount of parasitism and predation of second-stage *Meloidogyne* larvae in soil from peach orchards. In the first experiment, soil was collected in September from two peach orchards on Lovell rootstock near Parlier, CA. Cores were removed from the root zone of 30 trees in each orchard with a 2-cm diameter Oakfield tube at depths of 10–40 cm. Each sample was mixed thoroughly, and a portion of the soil was sterilized by autoclaving for 1 hr. Sixteen 30-ml vials were partially filled with 30 g of autoclaved soil, and field soil was added to another 32 vials. Samples of a suspension containing a known number of recently hatched *M. incognita* second-stage larvae were pipetted into all the vials containing autoclaved soil and into half the vials containing field soil. Thus, 16 replicate vials contained either field soil, field soil plus larvae, or autoclaved soil plus larvae. The soil moisture content was adjusted to 7.5%, and vials were lightly capped to prevent desiccation but allow gaseous exchange and kept in the laboratory at about 24 C. Nematodes were extracted from eight vials in each treatment 4 and 8 days later. The soil was added to about 500 ml of water in a flask; the mixture was shaken vigorously, allowed to

00031-949X/79/000146$03.00/0
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settle for 15 sec, and then decanted through two 38-μm sieves. The material retained on the sieves was centrifuged in a sugar solution (484 g sucrose/L water) at 1,200 rpm (about 250 *g*) for 20 sec, and the nematodes were collected from the supernatant on a 25-μm sieve. The number of *Meloidogyne* larvae was counted, and larvae were observed for parasitism.

The experiment was repeated using soil collected in December from one additional orchard, except that only 15 g of soil was used and it was adjusted to a moisture content of 9% and placed in 5-cm diameter petri dishes instead of vials. In both experiments, parasites and predators in the soil were identified by processing five 10-g samples by the method of Mankau (17). Antagonists associated with the *Meloidogyne* larval inoculum were identified by adding nematode suspensions to CMA/4 plates.

Parasitism of *Meloidogyne* eggs by *D. oviparasitica*. Estimates of the number of *Meloidogyne* eggs parasitized by *D. oviparasitica* were obtained from three peach orchards on Lovell rootstock. In each orchard, roots were collected at approximately monthly intervals for 12 mo from five trees known to be moderately or heavily infested with root-knot nematodes. Eggs were liberated from about 30 egg masses, and parasitized and unparasitized eggs were counted.

A greenhouse test (22) was used to determine whether *D. oviparasitica* was sufficiently active in the rhizosphere of peach to parasitize *Meloidogyne* eggs. Roots and adherent soil were collected from 20 trees in three peach orchards. The roots were cut into small pieces and combined with the soil; the resulting mixture was termed rhizosphere soil. Soil without roots also was collected. Rhizosphere or nonrhizosphere soil was mixed with autoclaved soil to produce a dilution series containing field soil and autoclaved soil in ratios of 1:0, 1:1, 1:3, 1:7, and 0:1. Four replicate samples of each dilution of each soil were added to 350-ml pots. Tomato seedlings were planted in the pots and inoculated 4 days later with 100 *M. incognita* larvae. After 44 days in a plant growth chamber at 26 C, 20 egg masses from each plant were examined for parasitized eggs.

The effects of incorporating mycelium of *D. oviparasitica* into soil on populations of *M. incognita* on peach were also studied. Mycelium of *D. oviparasitica* (isolates C, K, and S) was grown in YPSS shake culture (23). Each isolate was incorporated into autoclaved soil from the peach orchard from which it had been originally isolated (23) at rates equivalent to 0.28, 0.23, and 0.21 mg of dry mycelium per gram of dry soil, respectively. Pots (6 L) were filled either with autoclaved soil from each orchard or with soil containing *D. oviparasitica;* 10 g of sand containing hyphae, vesicles, arbuscles, and chlamydospores of the mycorrhizal fungus *Glomus fasiculatus* was then incorporated into the soil. A Lovell peach seedling was planted in each pot, and the pots were transferred to a lathhouse and embedded in wood shavings to reduce soil temperature fluctuations, as described by Lownsbery et al (15). Soil moisture conditions in peach orchards were simulated by watering plants when the soil moisture potential approached −500 millibars, as measured by tensiometers. One month after being tranferred to pots, seedlings were inoculated with 2,000 *M. incognita* larvae.

After growing for 5 mo during summer and autumn, the plants were harvested and fresh weights of tops and roots were recorded. The number of galls on each root system was counted, and some egg masses were checked for parasitized eggs. Nematodes were extracted from a 500-g soil sample from each pot using a Fenwick can (8), and the overflow was collected on a 38-μm sieve and placed on a Baermann funnel. Soil from each pot was also assayed for *D. oviparasitica* by means of a greenhouse test (22).

Host effect. Since *Meloidogyne* egg masses from Lovell peach consistently contained fewer eggs than those from Thompson seedless grape, the ability of the nematode to reproduce on these hosts was tested. Tomato was included for comparison because it is a standard host of *Meloidogyne*. Lovell peach, Thompson seedless grape, and Pearson tomato seedlings were grown in sterilized sand and inoculated with 100 *M. incognita* larvae. Two days after inoculation, the roots were washed and the plants were transplanted to new sand and incubated in a plant growth chamber at 27 C. Three plants of each species were removed 25, 30, 35, 40, and 45 days after inoculation. Eggs were liberated from at least 10 egg masses by treatment with 1% NaOCl and counted.

Parasitism of *M. incognita* eggs by *D. oviparasitica* was also compared on different hosts. Six Lovell peach and Pearson tomato seedlings inoculated 2 days previously with 100 *M. incognita* larvae were planted in autoclaved Hanford sandy loam soil containing the equivalent of 1.34 mg of dry mycelium of *D. oviparasitica* (isolate S) per gram of dry soil. Plants were grown for 38 days in a plant growth chamber at 27 C, and then egg masses containing *D. oviparasitica* were selected as previously described (21) and parasitized and unparasitized eggs were counted.

RESULTS

Occurrence of root-knot nematodes. The average *Meloidogyne* population on Lovell peach was smaller than that on Thompson seedless grape (Table 1). The average for Lovell peach, however, was increased by a high count in one orchard, whereas in the other Lovell orchards the average was 13 times lower than that in vineyards. Root-knot nematodes did not occur on Nemaguard rootstock.

Occurrence of nematode-trapping fungi. Similar species of nematode-trapping fungi occurred on Lovell peach, Nemaguard peach, and Thompson seedless grape (Table 1). *Arthrobotrys dactyloides* and *Monacrosporium ellipsosporum*, two of the most common species in all three situations, usually occurred at levels of 5–50 propagules per gram, but other species usually were present at levels of less than 5 propagules per gram.

Occurrence of *D. oviparasitica*. *Meloidogyne* egg masses from Lovell peach orchards contained an average of 154 eggs, and in all orchards some of the eggs contained *D. oviparasitica.* Egg masses from vineyards contained an average of 1,126 eggs, and *D. oviparasitica* parasitized eggs in three of the seven vineyards sampled. An unidentified fungus was parasitic or saprobic in a few eggs in two vineyards. Results of greenhouse tests confirmed that *D. oviparasitica* was active in fields where it had been observed in egg masses. When roots were incubated on agar, conidia of *D. oviparasitica* were observed on roots from all vineyards and from some of the Lovell peach orchards. The presence of conidia, however, did not always correlate with the presence of parasitized eggs in the field or in the greenhouse test. Similarly, conidia of *D. oviparasitica* occurred on roots from two Nemaguard peach orchards, although root-knot nematodes were absent and parasitized eggs were not observed in greenhouse tests.

Predation of *Meloidogyne* larvae in field soil. Soil from Lovell peach orchards to which *M. incognita* larvae were added contained between 0 and 1.3 root-knot nematodes per gram. Numbers of *Meloidogyne* larvae extracted from field soil to which nematodes had been added were corrected by subtracting these "background" counts. There were no significant differences between these

TABLE 1. *Meloidogyne* populations and occurrence of nematode-trapping fungi in seven fields each of Lovell peach, Nemaguard peach, and Thompson seedless grape

	Lovell peach	Nemaguard peach	Thompson seedless grape
Nematodes[a]			
Meloidogyne spp.	187	0	970
Nematode-trapping fungi[b]			
Arthrobotrys arthrobotryoides	3	0	1
A. conoides	6	6	0
A. dactyloides	6	4	3
Dactylaria sp.	1	1	2
Monacrosporium ellipsosporum	5	5	6
M. gephyrophagum	0	1	0
Monacrosporium (undescribed species)	6	5	7
Nematoctonus sp.	1	2	2
Stylopage hadra	3	0	2

[a]Larval numbers per 500 g of soil. Means of two samples from each of seven sites.
[b]Number of occurrences in seven fields.

corrected larval counts and the number of larvae recovered from autoclaved soil after 4 or 8 days (Table 2), despite the range of nematode-trapping fungi and other antagonists of nematodes in field soil from peach orchards. Larvae were not trapped in soil from any of the fields. In one field, ring traps of *A. dactyloides* sometimes occurred in suspensions of nematodes extracted from the soil, but trapped nematodes were not observed. *Acremonium* sp., which produces infective spores that adhere to nematodes, consistently parasitized *Meloidogyne* larvae in one field, but no more than 0.5% was ever infected. An unidentified fungus with a thallus that filled the carcass of the larva in a manner similar to *Haptoglossa* sp. was also observed occasionally. Although the nematode-trapping fungi *A. dactyloides, M. ellipsosporum,* and *M. gephyrophagum* were sometimes associated with the *Meloidogyne* larvae used as inoculum, they were not observed trapping nematodes in autoclaved or field soil.

Parasitism of *Meloidogyne* eggs by *D. oviparasitica*. Parasitized eggs were found throughout the year in orchards on Lovell peach. Although between 20 and 60% of the eggs always were parasitized, the total level of parasitism was probably much higher. *D. oviparasitica* destroyed eggs in less than 9 days at 27 C (21), and some parasitized eggs probably disappeared before being counted.

D. oviparasitica was closely associated with peach roots; the number of egg masses containing parasitized eggs was considerably higher in rhizosphere than in nonrhizosphere soil. In rhizosphere soil from three orchards, 85, 70, and 30% of egg masses contained parasitized eggs, and although parasitism decreased as the soil was diluted with autoclaved soil, parasitized eggs were still observed at the highest dilution of field soil (Table 3).

Peach seedlings grown in the presence of *D. oviparasitica* were about the same size as those grown in autoclaved soil but had fewer galls on their roots and fewer *Meloidogyne* larvae in the surrounding soil (Table 4). Larval numbers were not reduced significantly in soil containing *D. oviparasitica* isolate S, suggesting that this isolate was a slightly less virulent parasite of *M. incognita* eggs than isolates C and K. All isolates of the fungus were active 5 mo after being added to soil, since 60–70% of the eggs in the egg masses examined were parasitized at the end of the experiment. Parasitized eggs were found in 76 and 9% of the egg masses from tomato plants grown in soil originally infested with *D. oviparasitica* isolates S and K but not in soil infested with isolate C.

Host effect. The number of eggs in egg masses of *M. incognita* from grape and tomato increased to about 1,000 30 days after inoculation and remained at that level or increased over the next 15 days (Table 5). Females were still producing eggs 45 days after inoculation. On Lovell peach, egg production began at about the same time as on grape and tomato but ceased earlier, and egg masses generally contained a maximum of 300–400 eggs (Table 5). Nematodes that entered grape or tomato roots almost always matured, but nematode development was more variable on peach. Nematodes entered the roots and initiated galls, but different numbers reached maturity on different plants, possibly because Lovell peach seedlings were genetically variable.

D. oviparasitica parasitized eggs of *M. incognita* on both peach and tomato, but differences in egg production on the hosts led to differences in the proportion of eggs parasitized. Forty days after inoculation of the nematode, *D. oviparasitica* had parasitized about 96% of the 121 eggs in egg masses on peach but only 57% of the 937 eggs in egg masses on tomato. At this stage, egg production by the nematode was almost complete on peach but was continuing on tomato. Few female nematodes were parasitized by *D. oviparasitica*, but more were parasitized on peach than on tomato.

TABLE 2. Corrected numbers of *Meloidogyne incognita* larvae extracted from field or autoclaved soil after being added 4 and 8 days previously[a]

	Experiment 1		Experiment 2		
	Soil 1	Soil 2	Soil 1	Soil 2	Soil 3
4 days					
Field soil	833	908	951	1,091	929
Autoclaved soil	627	920	702	1,129	1,103
8 days					
Field soil	636	669	1,135	1,274	1,407
Autoclaved soil	574	885	1,324	1,215	1,348
Overall means (all soils × all times)					
Field soil	761		1,131		
Autoclaved soil	752		1,137		

[a]Numbers are the means of eight replicates, except that overall means are from 32 replicates (Experiment 1) or 48 replicates (Experiment 2). Analysis of variance showed no significant differences ($P = 0.05$) in any paired comparison between autoclaved and field soil.

DISCUSSION

Our results confirm those of Ferris et al (10), that many orchards on Lovell rootstock in the San Joaquin Valley support relatively low root-knot nematode populations. Only a small proportion of the trees had high *Meloidogyne* populations and heavily galled roots, the reaction normally expected of Lovell peach in sandy loam soils. Eleven times fewer *Meloidogyne* eggs and larvae were observed in a Lovell peach orchard than in a nearby vineyard (10), and we found similar differences when comparing larval counts at seven other sites (Table 1). Differences in such factors as root distribution and in the ability of the two hosts to support reproduction of the nematode may have accounted for some of the variations. Natural biological control, however, may also have been occurring on Lovell peach, since individual Lovell peach trees could support *Meloidogyne* populations as high as or higher than those on grape.

There was no evidence that nematode-trapping fungi played more than a minor role in regulating *Meloidogyne* populations in peach orchards. Similar species and numbers of nematode-trapping fungi occurred in Lovell and Nemaguard peach orchards and in vineyards, despite large differences in the *Meloidogyne* populations (Table 1). Apparently, population levels of nematode-trapping fungi were related to factors other than the presence of root-knot nematodes. Nematodes trapped or parasitized by nematode-trapping fungi were not observed in soil from Lovell peach orchards, even when nematodes were extracted by methods designed to obtain inactive nematodes. The addition of relatively high numbers of *Meloidogyne* larvae to soil did not stimulate trapping, although the occurrence of open *A. dactyloides* traps showed that the predacious phase of this species occurred in soil. Failure to observe predation by nematode-trapping fungi in soil

TABLE 3. *Meloidogyne incognita* egg masses containing eggs parasitized by *Dactylella oviparasitica* on tomato plants growing in rhizosphere or nonrhizosphere soil diluted with sterile soil

	Egg masses with parasitized eggs (%)[a]					
	Orchard 1		Orchard 2		Orchard 3	
Field soil: Sterile soil	Rhizosphere soil	Nonrhizosphere soil	Rhizosphere soil	Nonrhizosphere soil	Rhizosphere soil	Nonrhizosphere soil
1:0	85	4	30	8	70	1
1:1	74	3	4	0	9	1
1:3	35	1	21	0	9	1
1:7	21	0	26	3	3	4
0:1	0	0	0	0	0	0

[a]Based on 80 egg masses (20 from each of four plants).

has been noted previously (3,4).

These results are compatible with the theory that nematode-trapping fungi grow saprophytically in the soil and are not dependent on nematodes as a food source. They utilize nematodes as a source of nutrition only when the soil organic substrate is nutritionally deficient or when the associated microflora compete for the available nutrients (2,5,12).

In contrast to the nematode-trapping fungi, *D. oviparasitica* had many of the attributes of a successful biological control agent against *Meloidogyne*. The fungus (i) actively parasitized *Meloidogyne* eggs, which are more vulnerable to attack than are the larvae (24), (ii) occasionally parasitized *Meloidogyne* females, particularly on hosts where the nematode produced eggs relatively slowly, (iii) occurred in the rhizosphere close to its nematode host, and (iv) was able to survive periods when the nematode was absent by growing saprophytically on dead roots (22) or by parasitizing eggs of other nematodes (25).

We suggest that the capacity of *Meloidogyne* females to produce eggs on Lovell peach is limited and that parasitism by *D. oviparasitica* is often high enough to significantly reduce nematode populations. On plants such as grape and tomato, where *Meloidogyne* females produce eggs over a longer period and egg masses contain large numbers of eggs, some parasitism occurs but is not always sufficient to decrease nematode populations unless a particularly virulent isolate of the fungus is present or unless environmental conditions favor the parasite or are unsuitable for the nematode.

The discovery of an active parasite of *Meloidogyne* eggs associated with relatively low numbers of *Meloidogyne* in fields that had been planted to hosts of the nematode for at least 45 yr resembled a situation recently recorded in England. An *Entomophthora*-like fungus was found actively parasitizing *Heterodera avenae* in areas where the nematode population had decreased after years of cereal monoculture (6,13,14). Both situations confirm that areas in which a pathogen does not occur, has declined, or cannot develop despite a susceptible host are likely areas in which to search for potentially useful antagonists (1). A search of similar areas might yield other potentially useful biological control agents of plant-parasitic nematodes.

TABLE 4. Influence of three isolates of *Dactylella oviparasitica* on Lovell peach-*Meloidogyne incognita* host-parasite relationship

D. oviparasitica isolate		Root galls (no.)	Larvae per 500 g of soil (no.)
C	present	47 c[z]	127 b
	absent	375 b	431 a
K	present	68 c	40 b
	absent	700 a	410 a
S	present	178 bc	274 ab
	absent	630 a	390 a

[z]Means followed by the same letter are not significantly different ($P=0.05$) by Duncan's multiple range test.

TABLE 5. *Meloidogyne incognita* eggs per egg mass on Pearson tomato, Lovell peach, and Thompson seedless grape at intervals after inoculation

	M. incognita eggs[a]		
Days after inoculation	Pearson tomato	Thompson grape	Lovell peach
25	322	275	223
30	936	1,065	347
35	985	1,103	270
40	1,004	1,530	120
45	1,120	1,664	95

[a]Means of 30–50 egg masses.

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