FUNGAL PARASITES OF *MELOIDOGYNE ARENARIA* EGGS IN AN ALABAMA SOIL. A MYCOLOGICAL SURVEY AND GREENHOUSE STUDIES

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ABSTRACT

Godoy, G., R. Rodríguez-Kábana, and G. Morgan-Jones. 1983. Fungal parasites of *Meloidogyne arenaria* eggs in an Alabama soil. A mycological survey and greenhouse studies. Nematropica 13:201-213.

A survey of fungal parasites of *Meloidogyne arenaria* (Neal) Chitwood eggs was performed with isolates of the nematode from an Alabama peanut (*Arachis hypogaea* L.) field. Roots of Rutgers tomatoes (*Lycopersicon esculentum* Mill.) infected with the nematode were macerated enzymatically to extract eggs and females. After thorough washing with sterile water, the eggs were placed on acidified PDA and chitin agar. Four fungal parasites were isolated from single eggs of the nematode. The fungal species isolated were *Fusarium oxysporum* Schlect, *Paecilomyces lilacinus* (Thom) Samson, *Pseudopapulospora kendrickii* Sharma, and *Verticillium chlamydosporium* Goddard; *P. lilacinus* was the most frequently occurring egg parasite. Results of greenhouse studies indicated that *P. lilacinus* and *V. chlamydosporium* were effective in reducing *M. arenaria* infestations.

Additional key words: biological control, population dynamics, chitin, chitinase, nematode ecology, mucopolysaccharides, soil enzymes, pest management.

RESUMEN

Godoy, G., R. Rodríguez-Kábana, y G. Morgan-Jones. 1983. Parásitos fungosos de huevos de *Meloidogyne arenaria* de un suelo de Alabama. Un análisis micológico y estudios de invernadero. Nematrópica 13:201-213.

Se efectuó un examen de los parásitos fungosos de huevos de *Meloidogyne arenaria* (Neal) Chitwood proveniente de un campo de maní (*Arachis hypogaea* L.) en Alabama. Los huevos y hembras del nematodo se extrajeron de raíces de tomate (*Lycopersicon esculentum* Mill.) previa maceración enzimática de las mismas. Los huevos extraidos se lavaron repetidamente con agua esterilizada seguido lo cual se les colocaron en agar-papa-dextrosa y en agar-quitina para efectuar el aislamiento de los hongos. Se obtuvieron cuatro especies fungosas de los huevos que fueron: *Fusarium oxysporum* Schlect, *Paecilomyces lilacinus* (Thom) Samson, *Pseudopapulospora kendrickii* Sharma, y *Verticillium chlamydosporum* Goddard. La especie que se aisló con más frecuencia fué *P. lilacinus*. Resultados de experimentos de invernadero señalaron que tanto *P. lilacinus* como *V. chlamydosporium* pueden reducir infestaciones de *M. arenaria*.

Palabras claves adicionales: combate biológico, dinámica poblacional, quitina, quitinasa, ecología de nematodos, mucopolisacáridos, enzimas del suelo, manejo de plagas.

INTRODUCTION

Although the capacity of a number of opportunistic soil fungi to invade cysts and eggs of phytonematodes and function as facultative pathogens has been known for many years (15,21,33,35,41,42), it is only during the last decade that their role as potential or actual biocontrol agents has been considered. In the case of cyst nematodes belonging to the genus *Heterodera* Schmidt, a distinct mycoflora is now known to be associated with their pathology. This is made up of a consistently occurring group of species which is, bearing in mind the hundreds of species known to be ubiquitous in most soils, remarkably restricted in numbers. Investigations by Bursnall and Tribe (5), Graham and Stone (16), Nigh, et al. (31), and Morgan-Jones et al. (27,28) have confirmed the existence and regular occurrence in soil of fungi capable of invading cysts and eggs of *Heterodera avenae* Wollenweber, *H. glycines* Ichinohe, and *H. schachtii* Schmidt. Some of these induce disease and are destructive of the reproductive stages. Whether or not the consistent occurrence of particular fungi in association with cyst nematodes reflects a high degree of specialization, including enzymatic capacity, remains to be determined. Cysts and eggs exposed to the rhizosphere are particularly vulnerable to attack since root exudates and nutrients released following cortex disruption may enhance fungal growth activity and negate natural soil fungistasis.

Few published reports exist of fungi associated with the root-knot nematode genus *Meloidogyne* Goeldi. Investigations initially concentrated on nematode-trapping fungi (22) although egg masses are clearly susceptible to invasion. Stirling and Mankau (38,39) described *Dactylella oviparasitica* Stirling and Mankau as an active and specialized parasite of *Meloidogyne* egg masses in California. On potato roots in Peru, eggs of *Meloidogyne incognita* (Kofoid and White) Chitwood var. *acrita* Chitwood were found by Jatala et al. (18) to be heavily infected by *Paecilomyces lilacinus* (Thom) Samson. Following inoculation into nematode-infected potato plants this fungus was found to be capable of invading both females and egg masses of *Meloidogyne* and also cysts of *Globodera pallida* (Stone) Mulvey and Stone. Dunn et al. (9) have shown *P. lilacinus* to be capable of colonizing eggs of *M. incognita in vitro*.

Godoy et al. (13) investigated the capacity, *in vitro*, of thirteen fungal species isolated from cysts and eggs of *Heterodera glycines* to parasitize eggs of that nematode as well as those of *Meloidogyne arenaria* (Neal) Chitwood. Of these, only two succeeded in parasitizing the eggs of both

nematodes with high frequency. They were *Verticillium lamellicola* (F.E.V. Smith) W. Gams and *V. leptobactrum* W. Gams, which belong to section *Prostrata* W. Gams of the genus *Verticillium* Nees per Link; *Verticillium chlamydosporium* Goddard, another species belonging to this section, was encountered by Morgan-Jones et al. (29) as a parasite of females and eggs of *M. arenaria*.

In order to fully document the mycoflora associated with egg masses of *M. arenaria in vivo* in Alabama peanut field soil, a survey has been conducted. The two most frequently occurring fungi in this survey, which are also - - judging from the available literature - - among the most promising as biocontrol agents, were evaluated for this potential in greenhouse studies.

MATERIALS AND METHODS

A sandy soil infested with root-knot nematode (*M. arenaria*) was collected from a peanut field in Headland, Alabama. A decline in root-knot nematode infestation had been observed in the area from which the soil was collected. Rutgers tomato (*Lycopersicon esculentum* Mill.) was planted in pots with the soil and after two months roots were collected from the pots. Root pieces with galls (0.5 cm) were washed in running tap water for 24 hr and then treated with enzyme solution to soften tissues (14). The treated root pieces were blended for 30 seconds with 150 ml of sterile demineralized water in a Virtis® 45 homogenizer at low speed setting. The homogenate was passed through four 8-cm diam nested stainless steel sieves with openings of 250, 150, 75, and 30 μm respectively. Eggs retained in the 30 μm sieve were collected into a 100 ml beaker containing a solution of demineralized water and streptomycin sulphate (200 μg/ml). Aliquots (0.5 ml) of the egg suspension, containing approximately 300 eggs/ml, were pipetted into 10 U.S.B.P.T. watch glasses (Arthur H. Thomas Co., Philadelphia, PA). The watch glasses were placed in petri dishes and incubated at room temperature (25C) for six days. At the end of this period 25 eggs were randomly examined in each watch glass with a stereomicroscope and the number of parasitized eggs recorded. Eggs were considered parasitized when mycelial growth emerging from them was apparent. Parasitized eggs were carefully removed with fine, sterile needles and plated onto 0.2% colloidal chitin agar containing mineral salts (13) with added streptomycin sulphate (100 μg/ml) in petri dishes. The plates were incubated at 25°C for three or more days. After colony growth was observed the fungi were transferred onto potato dextrose agar (PDA) plates for identification. Eggs with no apparent fungal parasitism were also plated on chitin agar to serve as control.

For the greenhouse studies cultures of *P. lilacinus* and *V. chlamydosporium* on PDA were used to inoculate sterilized boiled oat kernels in 500-ml Eryermeyer flasks. The oats were prepared according to the method of Epps et al. (10). The fungi were allowed to grow in the flasks at 28C with periodic shaking of the oats to assure uniform colonization of all the oat kernels in each flask. After 10 days, the colonized oats were spread evenly on aluminum foil and were allowed to dry at 25C. The dry kernels were stored at 4C in the dark until used. Fungi in the oats under these storage conditions remained viable for at least 6 months.

A moist (approx. 60% field capacity) sandy loam soil from a peanut field infested with *M. arenaria* was sieved (2mm mesh) and mixed well with an equal volume of fine sand ($\leq$0.5mm). The mixture, which will be henceforth referred to as soil, was apportioned in one kg quantities into polyethylene bags. Enough colonized oat kernels were added to the soil in each bag to have 0.5% (w/w) of the kernels. After thorough mixing the amended soils were transferred to cylindrical 10-cm diam PVC pots. Other amendments in the experiment were with uninoculated (no fungi) oat kernels prepared as described for the fungal amendments. Soil with no amendment was also included to serve as no treatment controls. All pots were placed in a greenhouse table where they were arranged in a completely randomized design. There were 10 pots (replications) per treatment. Seventy-two hrs after addition of the amendments, each pot was planted with 5 'Summer Crookneck' squash (*Cucurbita pepo* L.) seeds. The resulting plants were allowed to grow for 6 weeks when they were separated carefully from the soil. The roots were examined to determine the number of galls caused by *M. arenaria* and the effects of the treatments on shoot height and fresh weights of roots and shoots were recorded. Soil from each pot was analyzed to determine nematode numbers using an incubation procedure (34) and the number of chitinolytic fungal species in the soil was determined following procedures described before (26).

All data were analyzed following standard procedures for analysis of variance. Differences between means were evaluated for significance according to a modified Duncan's multiple range test (40). Unless otherwise indicated all differences referred to in the text were significant at the 5% or lower level of probability.

RESULTS

Of 250 *M. arenaria* eggs examined, fungal growth was observed in 96 of them. Four different fungal species were recovered. They were: *Fusarium oxysporum* Schlecht., *Paecilomyces lilacinus* (Thom) Samson, *Pseudopapulospora kendrickii* Sharma, and *Verticillium chlamydosporium*

Goddard. The fungus most frequently isolated was *P. lilacinus,* which occurred in 47% of the parasitized eggs. *V. chlamydosporium* and *F. oxysporium* were isolated from 19% and 18% of the eggs, respectively. The remaining 16% contained *P. kendrickii.* Healthy-looking larvae hatched from eggs in control plates seven days after inoculation. Two of the fungal species encountered, *P. lilacinus* and *V. chlamydosporium,* showed ability to clear the chitin agar medium, indicating chitinolytic capacity. The other two, although growing successfully on the medium, failed to demonstrate this capacity.

In the greenhouse studies all amendments reduced the number of galls per gm of fresh root (Table 1). Greatest reduction was observed in soils treated with oats colonized with *P. lilacinus* or *V. chlamydosporium.* Number of galls per gm of root in plants from soil treated with uninoculated oat kernels was 34% below the number in unamended control soil whereas the reduction in soils with *P. lilacinus* and *V. chlamydosporium* were 54% and 69%, respectively.

All amendments resulted in plants with heavier roots and shoots (Table 1) than those from untreated soil. Tallest plants were in soils treated with uninoculated oats or with the *V. chlamydosporium* amendment.

The addition of amendments with *P. lilacinus* or *V. chlamydosporium* to soil resulted in significant reductions in the number of larvae of *M. arenaria* in soil (Table 2). Also, these amendments resulted in severalfold increases in the number of chitinolytic fungi in soil as compared to the untreated control or in soils with the uninoculated oat amendment.

Paecilomyces lilacinus was the most common chitinolytic species found in soil treated with kernels colonized by this species (Table 3); greater than 80% of the fungal species isolated from this soil were propagules of *P. lilacinus.* Several fungal species occurred in soils that received uninoculated oats or in untreated control soils (Table 3); however, there was no predominant species in these soils. The most common fungal species in soils with *V. chlamydosporium* were *Trichoderma* spp. (approx. 60% of the propagules) and *Humicola* sp. (approx. 25%). All other species occurred at frequencies of 5% or less; *V. chlamydosporium* occurred at a frequency of only 0.5%.

DISCUSSION

Our results suggest that the mycoflora associated with eggs of *M. arenaria,* while somewhat diverse taxonomically, is distinctly restricted in number of species. This is an analagous situation to that known to exist with other nematodes, particularly species of the cyst nematode genus *Heterodera* Schmidt (5,11,28,31,37). A consistent, but limited, myco-

Table 1. The effects of soil amendments with sterile uninoculated oat kernels and with oat kernels colonized with 2 fungal parasites of eggs of *M. arenaria* on galling caused by *M. arenaria* on roots of 'Summer Crookneck' squash (*Cucurbita pepo* L.) growing in field soil infested with the nematode.[x]

	Shoot height (cm)	Fresh shoot weight (gm)	Fresh root weight (gm)	No. of galls per gm root
Control	7.93 b	1.73 b	0.59 b	125 a
Uninoculated oat kernels	10.23 a	3.14 a	1.06 a	82 b
Paecilomyces lilacinus	8.48 b	2.79 a	1.05 a	57 c
Verticillium chlamydosporium	10.03 a	3.36 a	1.20 a	39 c

[x]Amendments were added at a rate of 0.5% (w/w) dry oats. Figures are the averages of 10 replications; those within each column followed by a common letter were not statistically different (P=0.01).

Table 2. The effect of soil amendments with uninoculated oat kernels and with kernels colonized with 2 fungal species parasitic of eggs of *M. arenaria* on numbers of larvae of *M. arenaria* and of fungi in soil.[a]

	Larvae per 100 cm^3 soil	Fungal propagules per gm soil
Control	9.3 a	1556 c
Uninoculated oats	7.0 a	2948 c
Paecilomyces lilacinus	4.8 b	18887 a
Verticillium chlamydosporium	3.3 b	7813 b

[a]All amendments were at the rate of 0.5% (w/w) dry kernels. Figures are the average of 10 replications; those within the same column with a common letter were not statistically different (P=0.01).

flora of opportunistic fungi is implicated in the pathology of eggs of all phytonematodes investigated to date. The identity of some of the fungal species isolated in the present study is significant since they have previously been reported to occur in association with other nematode species both in Alabama and elsewhere in the world. Several common denominators seem to exist among elements of these mycofloras, particularly ability to sporulate and compete successfully in soils and biosynthesis of exoenzymes instrumental in degrading chitin.

The occurrence of *Paecilomyces lilacinus* as an egg parasite of *M. arenaria* in Alabama soil represents the first report of its implication in phytonematode disease *in vivo* in the United States. Jatala et al. (18,19,20) have used this species in Peru to effect a biological control of *Meloidogyne incognita* and *Globodera pallida* on potatoes both in the laboratory and under field conditions. It has also been recovered by Dunn et al. (9) in the United States from sclerotia of *Sclerotinia minor* Jagger buried in agricultural soils. These authors demonstrated by scanning electron microscopy the capacity of some isolates to colonize nematode eggs *in vitro*. A morphologically closely similar fungus, *Paecilomyces nostocioides* Dunn, which may be but a mutated form of *P. lilacinus,* isolated from cysts of *Heterodera zeae* Koshy, Swarup and Seth, has also been shown to be capable of nematode egg colonization *in vitro* (8). *Paecilomyces lilacinus* is typically a soil-borne fungus and seems to be relatively common and ubiquitous in the tropics and subtropics (7). It also has a consistent association with insects on whose surface it produces a thin mycelial felt (36). The capability of this species to degrade chitin has been documented by Domsch (6) and Okafor (32). It has been recovered from chitin buried

Table 3. Fungal species isolated on Rose Bengal-chitin agar from soil previously amended with oat kernels and with two fungal pathogens of eggs of *M. arenaria*.

Treatment	Fungi isolated
Control	*Chaetomium cochliodes* Pall. *Aspergillus niger* Van Tieghem *Fusarium oxysporum* Schlecht *Trichoderma harzianum* Rifai
Uninoculated oat kernels	*Chaetomium cochliodes* Pall. *Humicola fuscoatra* Traaen *Myrothecium verrucaria* (Alb. & Schw.) Ditm. *Rhizopus nigricans* Ehrenb. *Trichoderma harzianum* Rifai
Paecilomyces lilacinus	*Fusarium oxysporum* Schlecht. *Humicola fuscoatra* Traaen *Myrothecium verrucaria* (Alb. & Schw.) Ditm. *Paecilomyces lilacinus* (Thom) Samson *Trichoderma harzianum* Rifai *Verticillium chlamydosporium* Goddard
Verticillium chlamydosporium	*Chaetomium cochliodes* Pall. *Humicola fuscoatra* Traaen *Myrothecium verrucaria* (Alb. & Schw.) Ditm. *Penicillium* spp. *Trichoderma harzianum* Rifai *Verticillium chlamydosporium* Goddard

in agricultural soil (6). It has also been shown to have some antagonistic activity and therefore competitive capacity against bacteria (2,24) and fungi (3,4). In soils treated with some fungicides, such as benomyl, captan and PCNB, *P. lilacinus* has been found with high frequency (43).

There is sufficient evidence to suggest that *P. lilacinus*, a heavy sporulator, is a strong competitor capable of successfully establishing itself in natural soil when introduced artificially. Our results from the greenhouse experiment support this view since *P. lilacinus* became the predominant isolate from soil amended with oats infested with this fungus. This ability to compete effectively and colonize natural soil and to exercise a degree of control against *M. arenaria* suggest that *P. lilacinus* may be a good candidate for development as a biological control agent.

Verticillium chlamydosporium, which has been previously encountered in Alabama as a female and egg parasite of *M. arenaria* (29), has been described as a principal egg parasite of *Heterodera schachtii* (5,44). It is also known from cysts of *H. avenae* Wollenweber in Australia (37). It has been isolated from a variety of soils (7) and from snail eggs (1). Capacity to degrade both cellulose (12,23,30) and chitin (17) has been demonstrated as has antibiotic activity against several bacteria *in vitro* (25).

Results from the greenhouse test suggest that *V. chlamydosporium* is capable of effecting considerable control of *M. arenaria.* However, results also indicate relatively low frequency of isolation of this fungus from soil amended with it. Although this may indicate inability of *V. chlamydosporium* to establish itself in soil we believe it more likely that our method of isolation was not adequate or suitable for assessment of *V. chlamydosporium* populations in soil. We have observed in studies on *Heterodera glycines* that frequently when chlamydospores of *V. chlamydosporium* occur within cysts, the fungus fails to grow out and produce colonies when these are plated on chitin agar. This suggests that the cultural requirements of this fungus may be considerably more exacting than those for *P. lilacinus.* Germination of chlamydospores of *V. chlamydosporium* may only occur within a narrow range of conditions. The development of this fungus as a biological control agent will require more knowledge of its physiology.

Isolates of *Fusarium oxysporum* have previously been reported to be destructive of eggs of *Heterodera schachtii* from sugar beet fields in California (31) and those of *H. glycines* in Alabama soybean fields (27). Infraspecific biotypes probably exist which are peculiarly adapted to exploit particular ecological niches and substrates.

Reduction in numbers of galls obtained by the addition of uncolonized oat kernels to soil was not unexpected. It is well established that the addition of some organic amendments to soil can result in a degree of nematode control (26). This can be attributed to increased soil microbial activity detrimental to nematode survival. Apparently, the uncolonized oat kernels stimulated development of a broad spectrum of microbial species, some of which were antagonistic to *M. arenaria.* In addition, the uncolonized oat kernels contained nutrients which enhanced plant growth resulting in taller shoots and heavier shoots and roots.

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