

Biocontrol: Fungi as Nematode Control Agents¹

R. Mankau²

Abstract: The fungal antagonists of nematodes consist of a great variety of organisms belonging to widely divergent orders and families of fungi. They include the nematode-trapping fungi, endoparasitic fungi, parasites of nematode eggs and cysts, and fungi which produce metabolites toxic to nematodes. The diversity, adaptations, and distribution of nematode-destroying fungi and taxonomic problems encountered in their study are reviewed. The importance of nematophagous fungi in soil biology, with special emphasis on their relationship to populations of plant-parasitic nematodes, is considered. While predacious fungi have long been investigated as possible biocontrol agents and have often exhibited spectacular results *in vitro*, their performance in field studies has generated little enthusiasm among nematologists. To date no species has demonstrated control of any plant pest to a degree achieved with nematicides, but recent studies have provided a much clearer concept of possibilities and problems in the applied use of fungal antagonists. The discovery of new species, which appear to control certain pests effectively under specific conditions, holds out some promise that fungi may be utilized as alternatives to chemical control after a more thorough and expanded study of their biology and ecology. **Key Words:** Nematode-trapping fungi, nematode-destroying fungi, nematode egg parasites, nematode antagonists, nematode parasites, nematophagous fungi.

The fungal antagonists of nematodes consist of a great variety of organisms which include the nematode-trapping or predacious fungi, endoparasitic fungi, parasites of nematode eggs, parasites of nematode cysts, and fungi which produce metabolites toxic to nematodes. It is remarkable that fungi belonging to widely divergent orders and families occur in each of these groups. Predacious, parasitic, and biochemical relationships with nematodes have evolved among almost all major groups of soil fungi from the Phycomyces to the Basidiomycetes. Considering the long co-evolution of nematodes and fungi which obviously occurred in the close confines of the soil habitat, it is not surprising that a great variety of inter-relationships have developed between the two groups. A complete and readable account of these interesting organisms was recently published in a small book on the nematode-destroying fungi by G. L. Barron (4).

It is important to recognize the fact that fungi continuously destroy nematodes in virtually all soils. Microbial and fungal control of nematodes is of great biological importance. In some circumstances it may be of considerable economic importance. However, we are presented with great technical problems in the observation and assessment of the importance of these organisms be-

cause of the complexities of the soil habitat. Specialized techniques are required to extract, count, and isolate the fungal antagonists, and many of the fungi concerned are obligate parasites or do not sporulate readily.

Nematode-destroying fungi play a major role in recycling the carbon, nitrogen, and other important elements from the rather substantial biomass of nematodes which browse on microbial primary decomposers. Virtually every population expansion of microbivorous nematodes occurring in the soil is accompanied by epizootics of fungal antagonists. Thus, fungi help convert the reservoir of materials in the rather extensive nematode biomass back into microbial biomass, making basic materials available to plants. Phytophagous nematodes, migrating in soil to new host plants or deprived of proper hosts, face survival in an environment abundantly populated with fungal enemies. Once within plant tissue they are probably isolated from most antagonists.

The attention of investigators is often focused on plant-parasitic nematodes. However, other types which are often far more numerous have very important roles in the biology of soil. It is with these groups of nematodes that many, if not most, of the nematode-destroying fungi interact. Some fungus species, for example, have spores which must be ingested by the nematode host. These spores then germinate in the esophagus to develop and consume the nematode (1). Such fungi generally have no relationship with plant-parasitic nematodes

Received for publication 19 December 1979.

¹Symposium paper presented at the annual meeting of the Society of Nematologists, Salt Lake City, Utah, 23-26 July 1979.

²Professor of Nematology, Department of Nematology, University of California, Riverside, CA 92521.

which feed through a stylet whose aperture is too small to admit fungal spores. Such fungi cannot play any role in biological control of economically important nematodes. Species of *Harposporium* and similar genera fall into that category. However, other fungi have evolved spores specialized for adhesion to, or penetration of, the nematode cuticle, making them possible antagonists of plant-parasitic nematodes.

FUNGAL ADAPTATIONS

The fungal spore has undergone some remarkable adaptation and specialization to capture or penetrate nematodes. Among the lower fungi, motile zoospores appear to have positive tropisms toward nematodes. *Catenaria anguillulae* spores most often accumulate around the natural body orifices of the nematode cuticle. The many species with nonmotile zoospores have special adhesive properties to adhere instantaneously to the cuticles of passing nematodes. The most specialized and spectacular spore adaptation occurs in *Haptoglossa heterospora*, where spherical nonmotile spores are expelled through an exit tube from a zoosporangium within a parasitized nematode. The spores germinate to produce another oddly shaped, nonmotile spore which has a tongue-like lobe containing a minute projectile under tension. The spores inject the infective cell particle through the cuticle of passing nematodes upon mechanostimulation. Davidson and Barron have described the process in detail (8). Many fungi with spores that adhere to the nematode cuticle may have some specificity toward different groups or even species of nematode, but we have little information on the subject. *Scutellonema cavenessi* was observed to repeatedly pass through clumps of the adhesive spores of *Meristracum asterospermum* without any spores attaching, while various rhabditid and cephalobid nematodes had many spores per individual attach to their cuticles (Mankau, unpubl. observations). Even the spores of predacious hyphomycetes are remarkable in that they can germinate directly into a capture organ, or a vegetative hypha, depending on external stimuli.

Most nematologists are quite familiar with the unique hyphal adaptations which make up the traps of predacious fungi, and

there is no need to redescribe them here, but recent studies have revealed the interesting fact that in many species the traps, or infection pegs, which penetrate captured nematodes give off a toxin which immobilizes a nematode almost immediately (3,16,24). There are also fungi that apparently immobilize nematodes without any direct contact with the hyphae (11,12). Whether this could occur in the soil would be difficult to determine. These fungi have a variety of trapping organs: some coated with a mucilaginous material from which an average-sized soil nematode rarely escapes, some with constricting rings triggered by complex physiological processes, some whose traps have a fail-safe chemical system which intoxicates a nematode, and others whose trapping organs give off substances attractive to nematodes (3,10,15).

There is also evidence that the assimilative or haustorial hyphae of some trapping fungi release antibiotic inside the nematode which prevents the development of competing microorganisms (4). Secondary microorganisms enter moribund nematodes through the buccal cavity, excretory pore, vulva, and anus; however, in nematodes captured in the hyphal traps of most species of predacious fungi, secondary microorganisms seldom or never develop. The body contents of captured nematodes are consumed, leaving an empty cuticle filled with assimilative hyphae which eventually lyse. No other organisms develop in the victim.

The conidia of nematode-trapping fungi are much larger than those of most soil saprophytes. They have food reserves which can be utilized to produce quickly one or more traps upon which the fungus relies for nutrition and development in a predatory mode. The conidia of most of these fungi do not tolerate desiccation and therefore do not survive adverse conditions in the soil. They are easily lysed. The conidia apparently provide a short-term method of propagation and may be the stage at which a fungus can most conveniently switch from a saprophytic to a predacious nutritional mode or *vice versa*. Little is known about sporulation of nematode-trapping fungi in soil or about development of resistant structures. Many species have chlamydospores, but no information exists on their survival or germi-

nation in soil or on their role in the biology of these fungi. Some species produce thick-walled storage hyphae, others produce microsclerotia (Mankau, unpubl. observations), and still others have no resistant structures at all. Most attempts to produce inoculum on a commercial scale, as well as most experimental soil colonizations, have concentrated on the production of mycelia and conidia, but these may have very limited survival when introduced into soil. Predacious fungi tend to be poor saprophytic competitors and some soils are fungistatic to them (17).

DISTRIBUTION

Studies in several areas of the world show that the majority of species of nematode-trapping fungi and endoparasitic fungi are cosmopolitan. Surveys for nematode-trapping fungi in Canada, the United States, Western Europe, Russia, New Zealand, Australia, Taiwan, and India have revealed similar flora in each area. A few recently described species are controversial because they are close variants of already well-known species. I have isolated some unusual species (unpublished) from a few specialized areas such as arid desert soils and coastal dunes, but the flora of agricultural soils generally appears similar almost everywhere.

Recently I surveyed the nematode-destroying fungus flora of portions of West Africa and found, for the most part, species identical to those occurring in southern California soils. Barron's extensive examination of the flora of the soils of Ontario, Canada, (4) revealed that those temperate soils with long winter-dormant periods contain essentially the same flora we have observed in the sub-tropical soils of southern California. It may be that not many remarkably different or exotic species remain to be found. However, information on the occurrence of nematode-destroying fungi in the tropics is notably lacking, and the tropics may prove to be unique areas for these fungi.

We now need investigations of the relationships of various species of nematode-destroying fungi to biotic and abiotic factors in soil, to cropping sequences, to different soil types, and to microhabitats. Some differences in vertical distribution of these

fungi have been observed (18), but most species appear to occur in the top 10–20 cm of any given soil. A few species can be isolated at relatively great depths.

Some predacious fungi appear to be rhizosphere organisms, while others occur mainly in nonrhizosphere soil. The relationships to plant rhizospheres may be important aspects of the biological control capacity of these fungi. Species occurring in the rhizosphere appear better situated to influence plant-parasitic nematode populations. In my experience, *Arthrobotrys dactyloides*, *Dactylaria brochopaga*, *Monacrosporium ellipsosporum*, and *M. gephyropagum*, which are among species with restricted saprophytic capability, are consistently associated closely with plant roots and thus in a favorable position to prey upon economically important nematodes.

TAXONOMIC PROBLEMS

Most of the endoparasitic fungi belong to groups little known by most mycologists. They are minute and mainly obligate parasites, thus difficult subjects for study. Species must be separated largely on minute differences in spores, zoosporangia, or other aspects of their rather simple thalli. Barron (4) recently has described a number of new species and organized our knowledge of this group so that many of the biological and taxonomic problems are now apparent.

Species identification of both parasitic and nematode-trapping fungi is important if we are to advance our understanding of their biology and importance as biological control agents. Taxonomic characters are based on extremely simple morphological features whose subtle differences require a considerable commitment of time and energy from nematologists interested in developing expertise in their differentiation. Nevertheless, some fundamental and fruitful studies of these interesting organisms can be undertaken by nematologists without embarking on additional careers as mycologists.

The major genera of predacious fungi, *Arthrobotrys*, *Dactylaria*, *Dactylella*, and *Monacrosporium*, probably contain more than 100 species. Many of these have been described by Charles Drechsler (9) whose meticulous work delineated differences between most species in these genera. As one

collects more and more isolates, however, it becomes evident that there are continuums of gradations in the characteristics between most species, and it often becomes impossible to assign an isolate to a given species or to clearly focus on characteristics designating it a new species. A genus such as *Arthrobotrys* may, in fact, be as varied and complex as *Penicillium* and its relatives. We have collected approximately 50 geographic isolates which could be placed in the species *A. conoides*, yet most of the isolates were unique and could be separated from any of the others on some physiological, morphological, ecological, or biochemical basis (Mankau, unpublished data). They exhibited different patterns of sporulation and chlamyospore production, different responses and growth rates on a variety of comparative media, and different degrees of predaciousness or response to trap-stimulatory factors. What constitutes a species among these fungi is, or should be, a matter of controversy and a subject for a great deal of painstaking study.

NEMATODE CONTROL

Nematode-trapping fungi have long been considered promising biological agents for control of nematodes. Their spectacular predacious behavior on agar plates made them intriguing organisms for study and speculation. Some of the early tests in greenhouse pots and in the field were not designed to evaluate critically their effects on target nematodes and probably tended to exaggerate their potential. Most such experiments involved adding one fungus to soil which had been amended with organic matter on the assumption that the fungus would increase on the amendment and turn to predation on nematodes, hopefully the plant-parasites. All that was generally known about the test fungus was that it had trapped nematodes while under observation or culture in the laboratory. The criteria generally used in choosing the fungal agent were ready availability and easy culture, characteristics which may have some inherent value but are not necessarily those of a good natural enemy.

Cooke (7) showed that the chance of establishing "alien" nematophagous species in the predacious phase is small. None of

the fungi he tested rapidly colonized or exploited the soil microhabitat. They were poor competitive saprophytes, susceptible to antagonisms from other soil organisms. Added mycelia were nonpersistent in soil even in the presence of energy sources. Cooke concluded that it may be possible to alter the soil environment in favor of nematode-trapping fungi, but the means of doing so (or even the directions to pursue) are beyond present knowledge.

Cooke (7) reviewed some of the ecological relationships in which fungal predators were involved and identified some of the problems associated with using them as biological control agents. Before predation can occur, mycelial growth and trap formation must occur. Both these processes require energy, which can be supplied by a readily available carbon source. Consequently, the addition of organic amendments to soil is usually followed by a short period in which the activity of nematode-trapping fungi increases. Cooke suggested that nematode capture may have been a means of escaping competition during phases of intense microbial activity in microhabitats with readily available organic substrates. He also noted that, although the addition of organic amendments to soil results in an increase in the population of free-living nematodes, predation is apparently not related to the density of the nematode population. In fact, an increasing amount of amendment may result in a reduction in the predacious activity of a fungus. This occurs because of an intensification in the activity of the soil microbes competing with the predacious fungi for nutrients. Obviously complex interactions between predacious fungi, decomposing organic substances, and the remainder of the soil microbial population determine the final level of each in the soil. The dual nutritional capability of nematode-trapping fungi remains a puzzling aspect of their biology which requires further investigation to understand what initiates predacious activity and how long it can be sustained.

The factors which initiate trap formation in these fungi have been reviewed and investigated, most recently by Nordbring-Hertz and her co-workers (20,22). Although she has isolated a few valyl-peptides which

effectively trigger trap formation in one fungal isolate, such compounds still do not appear to elicit as strong and rapid a response as do living nematodes (21). A biochemical complex may be involved, and it may be quite different for various species and isolates. Many species form traps spontaneously and consistently even in pure culture, while others produce traps only feebly even in the presence of nematodes (Mankau, unpublished data). There is a wide range of facultative saprophytism and predation among different closely related isolates and certainly among different species. Nordbring-Hertz and Mattiasson (23) have just presented evidence for the presence of a lectin on the traps of *A. oligospora* which binds to a carbohydrate on the nematode surface leading to penetration of the cuticle by a hypha. These interesting findings open the possibility of solutions to the problem of specificity in these host-microorganism interrelationships. A method to assess the variable predacity of nematode-trapping fungi *in vitro* in order to select the most predacious ones for soil and field tests was developed by Heintz (13). After several decades of study we still have relatively little knowledge about the predacious habit of these fungi, but some is now accumulating on the physiology of trap formation.

With the exception of a few *Arthrobotrys* species, which are nearly always present, trapping fungi usually appear after intense microbial activity on organic substrates has subsided and secondary microbial browsers, such as nematodes, predominate. On agar plates seeded with soil one frequently observes a succession of species, with some appearing as much as several weeks to several months after the earliest species. The ecological relationships of nematode-destroying fungi are exceedingly variable and complex, and we are a long way from an adequate understanding of how effective they are in reducing specific nematode populations. It may be that under some agricultural conditions the reproductive capability of certain nematode pests far exceeds all of the combined biotic factors limiting population expansion, but there is not conclusive evidence that this is true. If we could tolerate nematode damage or population expansions for longer periods, we might find that antago-

nistic biological agents increase to a point where their activity is noticeable and economically advantageous. This is more apt to be true for perennial crops than for annual crops.

A salient consideration in the use of fungi as applied biological control agents against nematodes is the soil habitat in which most plant-parasitic nematodes exist. An average fertile field soil contains approximately 10^9 bacteria, 10^{5-8} actinomycete, 10^{5-6} fungus, and 10^{4-5} protozoa reproductive units per gram, plus a large number of fungivorous nematodes, tardigrades, Collembola, mites, and other assorted microfauna and meiofauna. To believe that adding one additional organism will have an immediate measurable effect requires credulity. But biological antagonisms are common in the soil, and biological control has often occurred there (2). The fungi under consideration are highly specialized in their roles as nematode consumers, and it would be unfortunate if we did not pursue our investigations of their biology and impact in the soil until we understand most of the possibilities and problems inherent in their use as biological control agents.

The introduction of predacious fungi into soil to effect biological control should probably be attempted with those organisms that research has demonstrated to be inherently effective in regulating target prey populations. They may not already be doing this in given areas because of controllable environmental factors, because they are not synchronized with susceptible stages of the host, or because they do not occur in the problem area. The nonspecific nature of nematode predation by most fungi may be a serious hindrance to their use as biological control agents. Most predacious and some parasitic species can be cultured easily and produced commercially. It is likely that the more effective biological control agents will be difficult to culture because of obligate parasitism or predation and will be somewhat specific for tylenchid nematodes.

Despite the generally equivocal performance of predacious fungi in applied biological control in the past, a few recent examples of successful results promotes some optimism. By systematically testing a group of predacious fungi for compatibility with

Agaricus bispora, Cayrol et al. (6) developed the use of a commercially prepared isolate *Arthrobotrys* to protect the commercial mushroom from attack by the destructive mycophagous nematode *Ditylenchus myceliophagus*. They tested six fungi commonly found in the horse manure used for mushroom compost in the south of France for compatibility with *A. bisporus*. Three species stopped the growth of the mushroom mycelium, and one eventually destroyed it completely, but two species, *M. doedycoides* and *A. robusta (antipolis)*, had no effect on development of the mushroom mycelium. They chose the latter, more rapidly growing species for development as a biological control agent (Royal 300). Trials with the fungus seeded simultaneously with *A. bisporus* into mushroom compost at a rate at 1% each increased harvests of mushroom by more than 20% and reduced *Ditylenchus* populations in the compost by about 40%. Substantial numbers of nematodes still remained in the compost, and a second trial had less response; nevertheless, the authors were convinced that the results justified commercial use of the fungus for nematode control in mushroom culture.

Cayrol and Frankowski (5) had another isolate of *Arthrobotrys* grown commercially (Royal 350) and developed it as a biological control agent against a root-knot nematode problem in tomato. Trials in fields of several vegetable growers in the Alpes-Maritimes Departement utilized the fungus on granules of oat seed medium at a rate of 140 g/m² incorporated 1 month in advance of the crop. This rate was the maximum that was economically feasible, and it resulted in good protection of tomato against *Meloidogyne* and satisfactory colonization of the soil by the fungus. In the case of heavy populations of *Meloidogyne*, however, Cayrol and Frankowski indicated that the Royal 350 fungus would be more appropriate as a secondary control measure after an initial (presumably nematicide) treatment. If the experience of these researchers is repeatable, then even the less specific nematode antagonists may show some promise under proper conditions.

The discovery of fungi parasitic on the eggs of plant-parasitic nematodes has been very recent. Barron (4) considered only

Rhopalomyces elegans to be a confirmed egg parasite; however, it has never been associated with the eggs of a crop pest. The difficulty of observing nematode eggs in soil, or of extracting them from soil, had led to few observations of egg parasites. The sugar-flotation methods commonly used to extract eggs from soil generally halt any further development of fungal antagonists present in or on the eggs. Most of the fungi attacking eggs appear to produce quite similar internal hyphae, and they can only be identified after isolation and subsequent sporulation. Because of their importance as major plant parasites, and also their easy recovery, the eggs of the root-knot (*Meloidogyne* spp.) and cyst nematodes (*Heterodera* spp.) have been examined most frequently. Occasionally they have been found to be parasitized.

The viability of *Heterodera* eggs generally declines over time as the cyst remains in the soil, and fungi are suspected to be involved. Tribe (32) reviewed the relationship of fungi to cyst pathology and listed *Verticillium chlamyosporium* and another nonsporulating "contortion fungus" as the major pathogens of eggs within *H. schachtii* and *H. avenae* cysts. *Cylindrocarpon destructans* and several unidentified fungi were listed as minor pathogens, but the status of this group was considered unclear without further study of the ecology of cysts in soil over a long period of time. Tribe also discussed the relationship of a number of relatively common soil fungi which are often reported associated with *Heterodera* cysts.

Tribe (33) analyzed 112 populations of *H. schachtii* from several countries; slightly over a fourth of this population was comprised of females and cysts taken from roots. Fourteen percent of full cysts taken from soil were diseased, but under some conditions of monoculture with sugar beet, slightly over 50% were diseased. Tribe observed great variability in infection, with some samples containing no diseased cysts. A similar percentage of females taken from roots were attacked by fungi, but these fungi were specific, probably obligate parasites; in their absence infection of cysts was very low. *Catenaria auxiliaris* and some of the egg parasites already mentioned were

the principal fungi involved. Tribe recognized two phases of fungal attack on cysts and eggs; the first occurs on the roots of the host among females and young cysts, and the second among cysts in soil over a long period of time.

Strains of *Acremonium strictum* and *Fusarium oxysporum* were isolated from eggs in *H. schachtii* cysts from a majority of sugar beet soils examined by Nigh in California (19). Both fungi readily attacked eggs of several nematode species offered on agar *in vitro* or mixed with the fungi in amended soils, and they also grew saprophytically on dead eggs. It was concluded that these common facultative saprophytes were responsible for the destruction of some *H. schachtii* eggs under certain conditions in the fields studied.

It is possible that many other strains of facultative saprophytes are able to attack cyst nematode eggs under circumstances where the eggs are accessible to fungi before completion of the first molt and possibly also under some stress. Second-stage larvae within eggs generally appear to be resistant to attack by any of the fungi thus far reported to be associated with cysts. Some of the weakly pathogenic root-inhabiting fungi and mycorrhizal fungi may be capable of invading sedentary nematode endoparasites in root tissue. Such fungi invaded *Sarisodera africanus* cysts in fixed and sectioned *Panicum* roots from West Africa (D. P. Taylor, personal comm.). Close examination of cyst nematodes in late stages of development within roots, and further meticulous study of the degradation of cysts remaining in the soil, may eventually establish consistent fungal-egg interactions among the many fungi isolated from cysts. A number of nonsporulating fungi present special problems in determining their roles and importance. Much more work is required to understand the importance of fungal attack on cyst nematode population dynamics. In some cases there appears to be a significant amount of biological control occurring.

Stirling (26) examined some peach orchards on Lovell rootstock in California's San Joaquin valley which had relatively low root-knot nematode populations despite susceptible host and ideal conditions for development of the nematode pest, a situation

cited as a likely area for potentially useful antagonists by Baker and Cook (2). It was suspected that the nematode was under natural biological control in these orchards, and close examination of the egg masses revealed that a substantial percentage of the eggs were parasitized by a new fungus, *Dactylella oviparasitica* Stirling and Mankau (29). The fungus appeared to keep *Meloidogyne* populations in the orchards at a level which had little or no economic impact on the crop. Nematode-trapping fungi, however, appeared to play no more than a minor role (31).

D. oviparasitica required special enriched laboratory media for growth and sporulation (29) and had many attributes of a successful biological control agent against *Meloidogyne*. The fungus (i) actively parasitized *Meloidogyne* eggs, which were more vulnerable to attack than were the larvae (28); (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 (27) or by parasitizing eggs of other nematodes (30).

The specific host-parasite relationship of Lovell peach and *Meloidogyne* influenced the dynamics of the parasitism. The somewhat restricted capacity of *Meloidogyne* females to produce eggs on Lovell peach allowed the parasite to destroy a large percentage of them. Stirling et al. (31) observed that 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 egg parasitism occurs. However, this parasitism is not sufficient to decrease nematode populations unless a particular virulent isolate of the fungus is present or environmental conditions favor the parasite or are unsuitable for the nematode. *D. oviparasitica*, although capable of limited saprophytic growth, appears to be one of the most specialized hyphomycete parasites of nematodes yet discovered.

CONCLUSIONS

Nematophagus fungi have interested a

number of researchers for several decades as interesting subjects for study and as potential biological control agents. To date, however, not a single fungal strain has demonstrated any sustained capacity to control nematodes as effectively as chemicals. Perhaps this is an unrealistic comparison, and such levels of control are unattainable by fungal agents. All of the commonly used nematicides have been broad spectrum general biocides with which a large variety of soil organisms were killed to reduce and control target nematodes. Nematode antagonists have seldom been considered in applying nematicides, and use of nematode antagonists often resulted in increased disease problems in subsequent seasons. Biological agents have very limited activities and generally operate from a highly variable population base which is difficult to control and sustain after their addition to soil. They must also interact with hundreds of active soil organisms, other than hosts and prey, in many complex ways.

Any biological control accomplished with fungi will probably be slow and erratic and may never completely suppress pest populations to the economically effective, albeit temporary, levels attained with nematicides. On the other hand, enough information might be gathered on the natural control already operating under certain conditions to develop practices enhancing biological control. We also may be able to tolerate higher economic threshold levels of pest damage related to long-term biological control and accept some short-term losses if they are balanced by longer term benefits in reduced pesticide costs and pollution problems. There is always the hope that the right organism, or combination of organisms, will be found to provide an almost permanent population balance of a nematode pest to a degree which would never be attainable with chemicals. There has not been enough effort expended in the search for such organisms to justify pessimism.

The experience gained by entomologists in the use of biological control suggests that the most desirable characteristics of natural enemies are mobility and ability to search out prey, adaptability to the environment, host specificity, synchronization with the host, and the ability to survive host-free

periods (14). While these characteristics require some modification in consideration of the soil habitat, they should apply equally to the natural enemies of nematodes. As has already been noted, many of the known fungal enemies of nematodes are inadequate with regard to at least some of these characteristics, and this may explain why they have rarely been used successfully against plant-parasitic nematodes. Now we have the example of a recently discovered fungus, *D. oviparasitica*, which has more of the desirable attributes than most other fungi, and this will stimulate continued diligence in the search for more effective agents. *Bacillus penetrans*, discussed elsewhere in this symposium (25), is another example of an organism with most of the apparent characteristics of an effective biological control agent.

We still know so little about the fungal antagonists of nematodes that we can afford a good deal of optimism about biological control. The search for antagonists and the attempt to understand the total soil community with respect to nematode populations never has been pursued systematically. With the demise of one of our most important nematicides and the threatened loss of others, there is some urgency in this search. We have never really searched the original habitats of nematode parasites for antagonists as have the entomologists, nor have we imported agents for trial in problem areas. There is obviously no lack of research opportunity in this area.

LITERATURE CITED

1. Aschner, M., and S. Kohn. 1958. The biology of *Harposporium anguillulae*. J. Gen. Microbiol. 19:182-189.
2. Baker, K. F., and R. J. Cook. 1974. Biological control of plant pathogens. W. H. Freeman & Co., San Francisco.
3. Balan, J., and N. N. Gerber. 1972. Attraction and killing of the nematode *Panagrellus redivivus* by the predaceous fungus *Arthrobotrys dactyloides*. Nematologica 18:163-173.
4. Barron, G. L. 1975. The nematode-destroying fungi. Can. Biol. Publications Ltd. Guelph, Canada.
5. Cayrol, J.-C., and J.-P. Frankowski. 1979. Une methode de lutte biologique contre les nematodes a galles des racines appartenant au genre *Meloidogyne*. Revue Horticole 193:15-23.
6. Cayrol, J.-C., J.-P. Frankowski, A. Laniece, G. D'Hardemare, and J.-P. Talon. 1978. Contre les nematodes en champignonniere. Mise au point d'une

methode de lutte biologique a l'aide d'un hyphomycete predateur: *Arthrobotrys robusta* souche anticipis (Royal 300). *Revue Horticole* 184:23-30.

7. Cooke, R. C. 1968. Relationships between nematode-destroying fungi and soil-borne phytonematodes. *Phytopathology* 58:909-913.

8. Davidson, J. G. N., and G. L. Barron. 1973. Nematophagous fungi: *Haptoglossa*. *Can. J. Bot.* 51:1317-1323.

9. Drechsler, C. 1941. Predacious fungi. *Biol. Rev.* 16:265-290.

10. Field, J. I., and J. Webster. 1977. Traps of predacious fungi attract nematodes. *Trans. Brit. Mycol. Soc.* 68:467-469.

11. Giurma, A. Y., and R. C. Cooke. 1973. Thermostable nematoxins produced by germinating conidia of some endozoic fungi. *Trans. Brit. Mycol. Soc.* 60:49-56.

12. Giurma, A. Y., and R. C. Cooke. 1971. Nematotoxin production by *Nematoconus haptocladus* and *N. concurrens*. *Trans. Brit. Mycol. Soc.* 56:89-94.

13. Heintz, C. E. 1978. Assessing the predacity of nematode-trapping fungi *in vitro*. *Mycologia* 70:1086-1100.

14. Huffaker, C. B., P. S. Messenger, and J. DeBach. 1971. The natural enemy component in natural control and the theory of biological control. Pp. 16-67 in C. B. Huffaker, ed. *Biological Control*. Proc. of AAAS Symposium on Biological Control, Boston, Massachusetts, Dec. 1969.

15. Jansson, H-B., and B. Nordbring-Hertz. 1979. Attraction of nematodes to living mycelium of nematophagous fungi. *J. Gen. Microbiol.* 112:89-93.

16. Krizkova, L., J. Balan, P. Nemeč, and A. Koložvary. 1976. Predacious fungi *Dactylaria pyriformis* and *Dactylaria thaumasia*: production of attractants and nematocides. *Folia Microbiol.* 21:493-494.

17. Mankau, R. 1962. Soil fungistasis and nematophagous fungi. *Phytopathology* 52:611-615.

18. Mankau, R., and M. V. McKenry. 1976. Spatial distribution of nematophagous fungi associated with *Meloidogyne incognita* on peach. *J. Nematol.* 8:294-295.

19. Nigh, Elizabeth L. 1979. *Acremonium strictum* and *Fusarium oxysporum*, two fungal egg parasites of *Heterodera schachtii*, the sugarbeet cyst nematode. Ph.D. thesis, University of California, Riverside.

20. Nordbring-Hertz, B. 1973. Peptide-induced morphogenesis in the nematode-trapping fungus *Arthrobotrys oligospora*. *Physiol. Plant* 29:223-233.

21. Nordbring-Hertz, B. 1977. Nematode-induced morphogenesis in the predacious fungus *Arthrobotrys oligospora*. *Nematologica* 23:443-51.

22. Nordbring-Hertz, B., and C. Brinck. 1974. Qualitative characterization of some peptides inducing morphogenesis in the nematode-trapping fungus *Arthrobotrys oligospora*. *Physiol. Plant.* 31:59-63.

23. Nordbring-Hertz, B., and B. Mattiasson. 1979. Action of a nematode-trapping fungus shows lectin-mediated host-microorganism interaction. *Nature* 281:477-479.

24. Olthof, Th. H. A., and R. H. Estey. 1963. A nematotoxin produced by the nematophagous fungus *Arthrobotrys oligospora* Fresenius. *Nature* 197:514-515.

25. Sayre, R. M. 1980. Biocontrol: *Bacillus pene-trans* and related parasites of nematodes. *J. Nematol.* 12:260-270.

26. Stirling, G. R. 1978. The role of *Dactylella oviparasitica* and other antagonists in the biological control of root-knot nematodes (*Meloidogyne* sp.) on peach (*Prunus persica*). Ph.D. thesis, University of California, Riverside.

27. Stirling, G. R. 1979. Techniques for detecting *Dactylella oviparasitica* and evaluating its significance in field soils. *J. Nematol.* 11:99-100.

28. Stirling, G. R., and R. Mankau. 1978. Parasitism of *Meloidogyne* eggs by a new fungal parasite. *J. Nematol.* 10:236-240.

29. Stirling, G. R., and R. Mankau. 1978. *Dactylella oviparasitica* a new fungal parasite of *Meloidogyne* eggs. *Mycologia* 70:774-783.

30. Stirling, G. R., and R. Mankau. 1979. Mode of parasitism of *Meloidogyne* and other nematode eggs by *Dactylella oviparasitica*. *J. Nematol.* 11:282-288.

31. Stirling, G. R., M. V. McKenry, and R. Mankau. 1979. Biological control of root-knot nematodes (*Meloidogyne* spp.) on peach. *Phytopathology* 69:806-809.

32. Tribe, H. T. 1977. Pathology of cyst-nematodes. *Biol. Rev. Cambridge Phil. Soc.* 52:447-508.

33. Tribe, H. T. 1979. Extent of disease in populations of *Heterodera*, with especial reference of *H. schachtii*. *Ann. Appl. Biol.* 92:61-72.