

Predacious Fungi and Nematodes

By C. L. DUDDINGTON*

The existence of predacious fungi in the soil and elsewhere has been known since the classic paper of ZOPF (1888)¹ described the capture of nematodes by *Arthrobotrys oligospora*, *Dactylella ellipsospora* and others. Even before that time, the characteristic networks formed by the reticulate Hyphomycetes had been observed and recorded, though the function of these peculiar structures was not even guessed at. It was not for nearly half a century after the appearance of ZOPF's paper, however, that it was realized that the predacious fungi are not occasional biological curiosities, but common organisms that form an important part of the micro-flora of the soil, rotting vegetation, dung and other habitats where free-living nematodes abound. Even now we should probably know little about them but for the work of DRECHSLER²⁻⁴ in America, whose observations on the predacious fungi during the last quarter of a century will go down in history as one of the classic researches in mycology.

The predacious fungi that attack nematodes fall into two categories: those that capture their prey alive with the aid of various ingenious trapping devices, and those that are internally parasitic in nematodes, effecting entry into their host usually by means of sticky spores that adhere to the animal's body on contact and, when they germinate, intrude a germ tube through the integument of the host that gives rise to an endozoic mycelium.

Most of the nematode-trapping predacious fungi belong to the Moniliales (Hyphomycetes), an Order of the Fungi Imperfecti. They have a mycelium of colourless, septate hyphae on which the nematode traps are borne. The traps are of two main kinds: adhesive traps, by

which the prey is captured and held by means of a sticky secretion, and mechanical traps where no adhesive substance is needed.

The best known of the adhesive traps is the sticky network, such as is found in *Arthrobotrys oligospora*, the commonest of all the predacious fungi. The structure and functioning of the traps has been described in detail by DRECHSLER². The networks are formed by short lateral branches from the mycelium that curl round and join up to form loops (Figure 1) by anastomosis either with the parent mycelium or with other similar branches. The loops tend to be orientated roughly at right angles to one another, rather like the semicircular canals of the mammalian ear, so that a three-dimensional reticulum is formed.

The surface of the networks only is sticky: there is no sticky material produced by the rest of the mycelium. If a nematode happens to come into contact with any part of a network it is held firmly, and it is possible to see that a viscous adhesive fluid has been secreted by the cells of the network. The action of the sticky substance is highly efficient: a nematode seldom, if ever, escapes once it has been fairly held.

Immediately after capture the captive struggles violently, pulling the mycelium of the fungus this way and that, but without avail. In due course its struggles become less and less, until within two hours at the most it is quiescent and, apparently, moribund. The cause of death is uncertain: it may be that a toxin is produced by the fungus, but there is no evidence of this.

Once the captured nematode has become moribund, invasion of its body by the fungus begins. This process has been described in detail by SHEPHERD⁵. A swelling appears on the fungal network at the point where the nematode is held, and from this a minute outgrowth penetrates the integument of the animal and forms, inside its body, a globular infection bulb from which

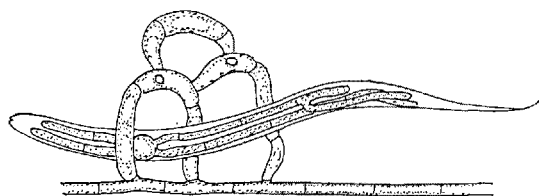


Fig. 1. *Arthrobotrys oligospora*. Diagram of a network with a captured nematode. Note infection bulb and trophic hyphae in the carcass of the captive.

* Biological Laboratories, The Polytechnic, London (England).

¹ W. ZOPF, Nova Acta Leop.-Carol. 52, 314 (1888).

² C. DRECHSLER, Mycologia 29, 447 (1937).

³ C. DRECHSLER, Phytopathology 31, 773 (1941).

⁴ C. DRECHSLER, Mycologia 42, 1 (1950).

⁵ A. M. SHEPHERD, Nature, Lond. 175, 475 (1955).

trophic hyphae grow out and fill the carcass, consuming its contents as they do so. In about twenty-four hours only the integument of the nematode is left, still attached to the network and filled with trophic hyphae. Finally, the contents of the trophic hyphae themselves are passed back to the parent mycelium.

Other variations of the sticky trap are found amongst the predacious Hyphomycetes. In *Dactylella cionopaga* (DRECHSLER)⁴ nematodes are captured by short lateral branches of the mycelium that are sticky and function in the same way as the sticky networks of *Arthrobotrys oligospora*. Each branch usually consists of one, two or three cells (Figure 2), though sometimes they proliferate and form simple networks: the complex three-dimensional networks shown by the reticulate species are, however, never formed.

In *Dactylella ellipsospora* (DRECHSLER²) the eelworm traps consist of small subspherical knobs attached to the mycelium by short, two-celled stalks. Here the knobs are sticky, and nematodes are captured by adhesion (Figure 3). The sequence of events following capture is the same with the sticky branches and stalked knobs as with the networks: when the captive is dead or moribund its integument is penetrated by a slender process that gives rise to an infection bulb from which trophic hyphae arise and consume the body-contents of the nematode.

The mechanical traps, which do not depend on the production of a sticky secretion for their operation, are of two kinds: non-constricting rings and constricting rings, the latter being both commoner and more effective. The best-known fungus with non-constricting rings is *Dactylaria candida* (DRECHSLER²). The rings are formed by slender lateral branches that curl round and join up with themselves, forming three-celled rings attached to the mycelium by usually three-celled stalks (Figure 4). The internal diameter of a ring is such that, if a wandering nematode accidentally pushes its anterior end into the opening, it gets wedged in trying to force its way through. Capture is followed by the intrusion of trophic hyphae into the body of the captive, and the absorption of its body-contents, in the usual way.

The action of the non-constricting ring is entirely passive: there is no secretion of sticky material as far as we know, and the nematode is captured and held simply because it has, by its own misguided efforts, jammed its body into the ring. The constricting ring, on the other hand, captures nematodes by positive action. It works on the principle of a rabbit snare, or the lasso of an American cowboy. A nematode that thrusts its anterior end into a constricting ring is gripped by a sudden inflation of the ring cells, and held as in a garotte.

Predacious fungi with constricting rings are very common: *Dactylaria gracilis* (DUDDINGTON⁶) is an example. In appearance, the constricting ring is very

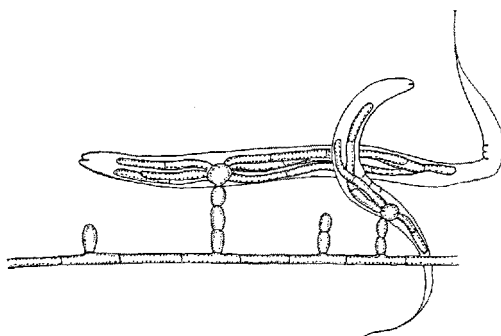


Fig. 2. *Dactylella cionopaga*. Diagram of part of the mycelium, with adhesive branches. Two nematodes have been captured.

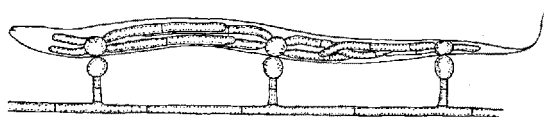


Fig. 3. *Dactylella ellipsospora*. Diagram of part of the mycelium, showing three adhesive knobs and a captured nematode.

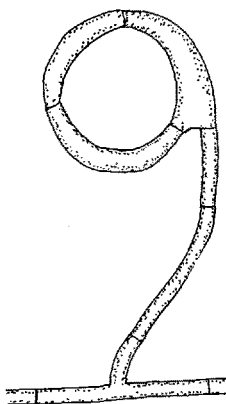


Fig. 4. A non-constricting ring of *Dactylaria candida*.

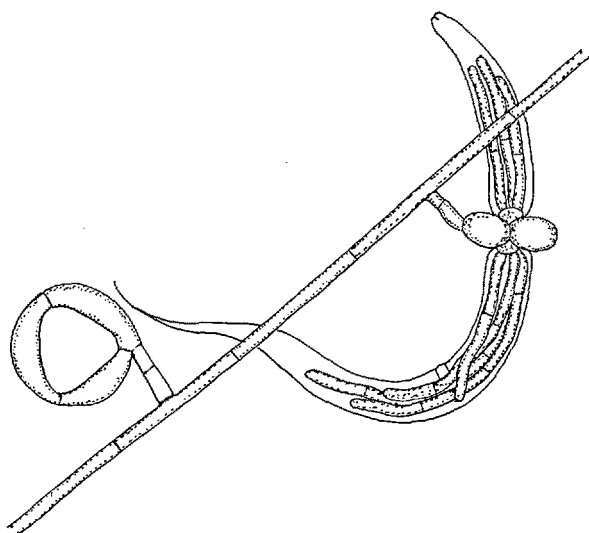


Fig. 5. *Dactylaria gracilis*. Diagram of part of the mycelium with one ring in its 'open' state and another, in side view, that has captured a nematode.

⁶ C. L. DUDDINGTON, Trans. Brit. mycol. Soc. 34, 194 (1951).

like the non-constricting ring, and it is formed in much the same way, by a short lateral branch of the mycelium curling round to form a three-celled ring on a stalk (Figure 5). The constricting ring is, however, somewhat stouter in construction than the non-constricting ring, and its stalk is shorter, consisting normally of only two cells.

The three cells that make up a constricting ring are sensitive to touch on their inner sides. When a nematode introduces its body into a ring, the contact stimulus as it rubs against the ring cells is sufficient to trigger off the mechanism. The ring cells suddenly inflate inwards, greatly reducing the size of the opening of the ring and gripping the unfortunate nematode so tightly that its body is deeply constricted by the pressure of the inflated ring cells. The action of the cells is very quick: after a lag phase of a few seconds, the actual swelling takes only about one tenth of a second. The captured nematode struggles violently for a time after the ring has closed on it, but its movements become progressively weaker. When it has ceased to struggle, trophic hyphae grow from the ring cells into its body and consume its contents.

All the predacious fungi so far described are members of the Moniliales (Hyphomycetes), and they all appear to be closely related to one another. Another small group of nematode-capturing fungi is found in the Zoopagales, an Order of Phycomycetes showing strong taxonomic relationships with the Mucorales. The Zoopagales have non-septate hyphae, reproduce asexually by means of conidia borne singly or in groups on erect aerial fertile hyphae, and in many cases show sexual reproduction of a typically zygomycetous type. Most of the Zoopagales are predacious on amoebae and other Protozoa, but a number of species capture nematodes. No specialized organs of capture are formed: the prey is captured by adhesion, the mycelium apparently being sticky all over its surface. A typical example is *Stylopaga grandis* (DUDDINGTON⁷). Here the mycelium consists of a fairly stout, non-septate hyphae that branch occasionally. Nematodes coming into contact with the hyphae are held by a sticky secretion, and

capture is followed by the intrusion of trophic hyphae into the body of the victim, as in the Hyphomycetes that capture nematodes with sticky traps (Figure 6).

The nematode-trapping Hyphomycetes are not dependent on nematodes as a source of food, for when isolated into pure culture they will grow freely on most of the normal media used for cultivating fungi. Grown without nematodes, they do not usually form their characteristic traps, but, if nematodes are added to the cultures, traps are quickly formed and nematodes are captured. It is not even necessary to add living nematodes to the cultures, for most of the nematode-trapping Hyphomycetes that have been tested will form traps if given sterile filtered water in which nematodes have lived. It seems clear that trap formation can be initiated by a chemical stimulus, in this case a substance, the nature of which is at present unknown, that has diffused out of nematodes into the water surrounding them.

Nematode-trapping Hyphomycetes will sometimes form traps spontaneously in pure culture, without the addition of any stimulating substance: the fungi with constricting rings are especially prone to do this. The reason for this behaviour is as yet unknown, but recent work (FEDER, EVERARD and DUDDINGTON⁸) suggests that these fungi are heterocaryotic with regard to the capacity for spontaneous ring formation.

Fungi with constricting rings will form rings in pure culture in response to the presence of a wide variety of different substances (ROUBAUD and DESCHIENS⁹, LAMY¹⁰). The substances that gave positive reactions included blood serum of the horse and other animals, and aqueous extracts of various animal organs. Plant extracts were not effective.

The network-forming Hyphomycetes are less prone to develop their traps in pure culture, though they sometimes do so for no apparent reason. They will, however, produce networks fairly readily if treated with sterile filtered water in which nematodes have lived (COMANDON and DE FONBRUNE^{11,12}). PRAMER and STOLL¹³ obtained and partially purified a substance from nematode cultures containing an active principle that stimulated network formation in *Arthrobotrys* spp., and to this hypothetical stimulant they have given the name 'nemin'.

The physiology of the operation of the constricting ring traps of the predacious Hyphomycetes has cap-

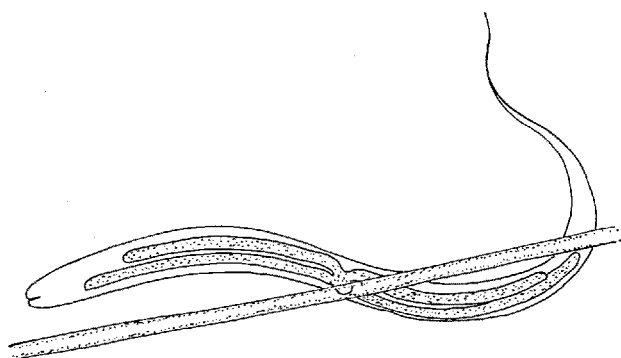


Fig. 6. Diagram of a nematode captured by the adhesive mycelium of *Stylopaga grandis*.

⁷ C. L. DUDDINGTON, *Mycologia* 47, 245 (1955).

⁸ W. S. FEDER, C. O. R. EVERARD, and C. L. DUDDINGTON, *Science* 131, 922 (1960).

⁹ E. ROUBAUD and R. DESCHIENS, *C.R. Acad. Sci. Paris* 209, 77 (1939).

¹⁰ L. LAMY, *C. R. Soc. Biol. Paris* 137, 337 (1943).

¹¹ J. COMANDON and P. DE FONBRUNE, *C. R. Soc. Biol. Paris* 129, 619 (1938).

¹² J. COMANDON and P. DE FONBRUNE, *C. R. Acad. Sci. Paris* 207, 304 (1939).

¹³ D. PRAMER and N. R. STOLL, *Science* 129, 966 (1959).

tured the attention of a number of workers. COUCH¹⁴ failed to induce closure of the rings of *Dactylella bembicodes* by passing a fine micromanipulator needle into them, an observation that is contradicted by COMANDON and DE FONBRUNE¹¹, who showed conclusively that the rings would close in response to a mechanical stimulus such as stroking the inner edges of the ring cells with a fine needle. The French workers also showed that the outer edges of the ring cells are insensitive to tactile stimuli. COUCH¹⁴ showed that the rings could be closed by the application of moderate heat, either by dropping warm water on to them or by holding a hot scalpel near them; this observation was confirmed by MULLER¹⁵.

The most striking feature of the action of the constricting rings is their great speed in closing. When suitably stimulated the ring appears to undergo a lag phase of several seconds, after which the ring cells suddenly inflate inwards, the time needed for the actual inflation being no more than one tenth of a second. When fully inflated, the ring cells occupy about three times their former volume – a very considerable increase. No completely satisfactory explanation of this sudden and rapid inflation has yet been put forward, but some observations by MULLER¹⁵ on the osmotic relationships of the ring cells are interesting. MULLER found that, after inflation, the osmotic potential of the cells was approximately the same as it was before inflation took place, in spite of the fact that the volume of the cells had increased threefold. This suggests that osmotically active material must be rapidly produced in the cells either during or immediately after inflation, and he favours the view that the swelling is due to a relaxation of turgor pressure in the cells brought about by a change in the elasticity of the inner cell wall, followed by the production of osmotically active material within the cell to counterbalance the intake of water. This theory is plausible, but needs confirmation, especially in view of the fact that MULLER, in his experiments, slowed down the rate of closure of the rings one hundredfold by treatment with sugar solution.

The predacious fungi that are internally parasitic in nematodes form a group distinct from the nematode-trappers. Here the mycelium of the fungus is entirely endozoic, only the fertile hyphae that bear the spores emerging from the body of the host. Some of these fungi are extremely common: *Harposporium anguilulae* (LOHDE¹⁶, KARLING¹⁷), for instance, is to be found in fertile soils over a wide area in this country and abroad.

A typical example of a hyphomycete internally parasitic in nematodes is seen in *Acrostalagmus obovatus* (DRECHSLER³), a species that is very common in soil. The small spores of the fungus adhere to the integuments of nematodes that come into contact with them. On germination, the spore puts out a germ tube that

penetrates the integument of the nematode and gives rise to an extensive mycelium of branched, septate hyphae within its body. As the mycelium of the parasite develops the body-contents of the host are consumed, until finally the carcass of the nematode is filled with hyphae. As this stage approaches, the reproductive phase of the fungus begins. Branches from the internal mycelium penetrate the integument of the host in an outward direction, and grow into procumbent fertile hyphae, on which numerous flask-shaped phialides are formed. Each phialide produces up to twenty small, obovate spores, which cohere in a bunch round the neck of the phialide (Figure 7). The spores are readily picked up by passing nematodes, and in this way the parasite is dispersed.

In *Acrostalagmus obovatus*, as in other Hyphomycetes, sexual reproduction is unknown.

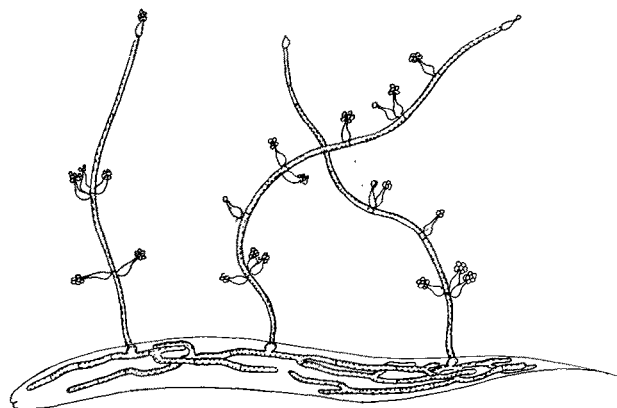


Fig. 7. *Acrostalagmus obovatus*. Body of an infected nematode, with internal mycelium and three emergent fertile hyphae bearing phialides and spores.

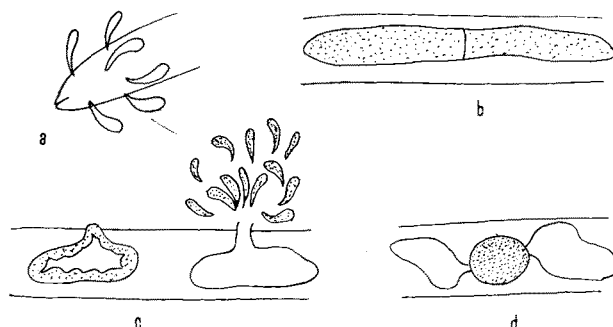


Fig. 8. *Protascus subuliformis*. a, Spores sticking to the anterior end of a nematode. b, Young thallus in the body of a nematode. c, a young sporangium, and an old sporangium that has discharged its spores. d, a developing zygospor.

¹⁴ J. N. COUCH, J. Elisha Mitchell Sci. Soc. 53, 301 (1937).

¹⁵ H. G. MULLER, Trans. Brit. mycol. Soc. 41, 341 (1958).

¹⁶ G. LOHDE, Einige neue parasitische Pilze. Tageblatt der 47. Versammlung deutscher Naturforscher und Ärzte in Breslau (1874), p. 203.

¹⁷ J. S. KARLING, Mycologia 30, 512 (1938).

A small but interesting group of fungi that are endozoic in nematodes is found in the Lagenidiales, a primitive Order of Phycomycetes most of which are parasitic in fresh-water algae. *Protascus subuliformis* DANGEARD¹⁸, KARLING¹⁹) is a not uncommon example. Here the spores are club-shaped and slightly curved (Figure 8), and they adhere to the bodies of nematodes by their pointed ends, which appear to be sticky. When a spore germinates, the germ tube penetrates the integument of the nematode and forms a naked protoplast within its body. This grows at the expense of the body-contents of the nematode, forming an elongated thallus. Multiple infection from a number of spores is common.

As the thallus of the fungus grows it forms a wide, irregular filament, which eventually becomes septate. Finally, the thallus fragments at the septa. Each segment then becomes a sporangium in which the cytoplasm divides up to form a large number of spores: an exit tube grows out through the integument of the host, and the spores are discharged to the exterior. Sometimes the fungus undergoes sexual reproduction, adjacent segments functioning as male and female gametangia and conjugating with one another, the contents of the male gametangium passing through a conjugation tube into the female gametangium. Conjugation is followed by the formation of a thick-walled zygosporangium.

Protascus subuliformis is unusual in that its asexual spores are non-motile, whereas in most of the Lagenidiales they are motile zoospores. It seems likely that this is connected with the type of host: nematodes are motile and gregarious, and it is reasonable to suppose that, in attacking such prey, motile spores would carry no advantage, and might well be inferior to sticky aplanospores. It is worthy of note that most of the Lagenidiales that parasitize nematodes have non-motile spores.

Various other species of lower fungi are internally parasitic in nematodes: descriptions of these can be found in the literature (DUDDINGTON²⁰, SPARROW²¹).

Unlike the nematode-trapping Hyphomycetes, the endozoic predacious fungi appear to be obligate parasites: there are no fully-confirmed accounts of their isolation into pure culture. The same applies to nematode-trapping species of Zoopagales such as *Stylopaga grandis*.

Until recently, the occurrence of nematode-attacking predacious fungi in the soil had not been closely studied, though it has been known that they are abundantly represented. LINFORD and OLIVEIRA²² found no less than seventeen different species in soil from Hawaiian pineapple fields, and a survey of predacious fungi from British arable soils (DUDDINGTON²³) produced eighty-two records from forty-nine samples, at least twenty different species being represented. The predacious fungi are, in fact, an important fraction of the natural

biome of the soil. They are probably absent from extreme mineral soils where there is a marked lack of organic matter, such as the soil of Wareham Heath, Dorset (England), and in my experience the acid peats are also inhospitable to them, though they contain plenty of free-living nematodes.

The state of activity of the nematode-trapping fungi in the soil has long been a matter of speculation. Most of these fungi can live and reproduce freely without nematodes if supplies of nourishment are sufficient; they are facultative saprophytes, and may even be facultative predators, depending on a diet of nematodes only when food is limited. Since the abundance of predacious fungi in the soil may be a biotic factor of some importance in the lives of soil nematodes, this is a matter on which information is badly needed.

Shortly before the second world war, LINFORD et al. in Hawaii, working on the biological control of the pineapple root-knot eelworm, showed that the efficacy of predacious fungi in keeping down the soil population of root-knot eelworm was greatly enhanced by the addition to the soil of easily-decomposable organic matter such as chopped green pineapple tops (LINFORD²⁴, LINFORD and YAPP^{25, 26}, LINFORD, YAPP and OLIVEIRA²⁷). This effect of organic matter on predacious fungi has been confirmed by more recent work in England (DUDDINGTON²⁸, DUDDINGTON and DUTHOIT²⁹, DUDDINGTON, DUTHOIT, and EVERARD³⁰). LINFORD advanced the theory that the stimulating effect of organic matter on soil predacious fungi was an indirect one, postulating that the presence of the organic matter produced a great increase in the numbers of free-living nematodes, and that the rise in the nematode population then reacted on the fungi. For many years this view was generally accepted, but recent work by COOKE³¹ indicates that it is no longer tenable.

COOKE investigated the effect of organic matter on the activity of predacious fungi in the soil by an ingenious agar disk technique. COOKE buried disks of

¹⁸ P. A. DANGEARD, C. R. Acad. Sci. Paris 136, 627 (1903).

¹⁹ J. S. KARLING, *Simple Holocarpic Biflagellate Phycomycetes* (New York 1942).

²⁰ C. L. DUDDINGTON, Biol. Rev. 31, 152 (1956).

²¹ F. K. SPARROW, *Aquatic Phycomycetes*, 2nd ed. (University of Michigan Press, Michigan 1962).

²² M. D. LINFORD and J. M. OLIVEIRA, Phytopathology 28, 14 (1938).

²³ C. L. DUDDINGTON, Nature, Lond. 173, 500 (1954).

²⁴ M. B. LINFORD, Science 85, 123 (1937).

²⁵ M. B. LINFORD and F. YAPP, Phytopathology 28, 14 (1938).

²⁶ M. B. LINFORD and F. YAPP, Phytopathology 29, 596 (1939).

²⁷ M. B. LINFORD, F. YAPP, and J. M. OLIVEIRA, Soil Sci. 45, 45, 127 (1938).

²⁸ C. L. DUDDINGTON, *The Friendly Fungi* (Faber and Faber, London; The Macmillan Company, New York 1957).

²⁹ C. L. DUDDINGTON and C. M. G. DUTHOIT, Plant Pathology 9, 7 (1960).

³⁰ C. L. DUDDINGTON, C. M. G. DUTHOIT, and C. O. R. EVERARD, Plant Pathology 10, 108 (1961).

³¹ R. C. COOKE, Nature, Lond. 191, 1411 (1961).

agar in soil contained in large petri dishes under carefully controlled conditions, and enriched the soil with various quantities of chopped cabbage leaf. The agar disks were removed each week and replaced with fresh ones: in this way COOKE was able to study the behaviour of predacious fungi in his soil samples over a period of time.

The results obtained by COOKE were most interesting. He found that the addition of chopped cabbage leaf to the soil produces a dramatic increase in the population of free-living nematodes. He also found, on studying the fungal flora of his agar disks, that the activity of predacious fungi, as indicated by the number of traps formed, increased to a notable extent. On comparing the effects of organic amendment of the soil on the nematode population and on the activity of predacious fungi, however, a discrepancy appeared. On the addition of the chopped cabbage leaf to the soil, the figures for nematode population and fungal activity rose together to a maximum. The activity of the fungi then rapidly fell away, while the increase in nematode population was maintained for several weeks, declining only slowly. At a time when the activity of the predacious fungi had dropped back to its former value before organic amendment, the eelworm population was still very high—higher, in fact, than it was when predacious activity was nearing its peak. It did not look as if the increase in predacious activity was due solely to the increase in nematode population, for if that had been the case the fungal activity should have remained high as long as the increase in nematode population was maintained.

COOKE then tried sucrose as a soil amendment instead of chopped cabbage leaves, and here his results were even more striking. He found that the addition of sucrose produced a sharp rise in the activity of predacious fungi, without a corresponding increase in the nematode population. In this case the increase in predacious activity could not possibly be attributed to increased numbers of nematodes.

In view of COOKE's results, it is impossible to retain LINFORD's hypothesis that the stimulating effect of organic matter on the activity of soil predacious fungi is simply a function of the rise in nematode population that follows the addition of easily-decomposable organic matter to the soil. We must look for some other explanation. It looks as if the organic amendment of the soil has some direct action on the predacious fungi, but what that action may be we cannot even guess. Further work is badly needed to elucidate this point.

LINFORD and COOKE agree on one very interesting point. Both found that there was an optimum amount of organic soil amendment for the activity of predacious fungi. If this optimum was exceeded, the activity of the fungi fell off. The reason for this has not yet been explained.

In view of the fact that predacious fungi are abundant in soil, it is not surprising that a number of workers have seen in them a possible means for the biological control of nematodes that attack crops. The first work in this field was carried out by LINFORD et al.^{22, 24–27}, working on the pineapple root-knot eelworm in Hawaii. They found that direct inoculation of the soil with cultures of five different predacious Hyphomycetes was ineffective, but that incorporation of chopped green pineapple tops into the soil produced a useful degree of control, which they attributed to the increased activity of soil predacious fungi. This work was given up shortly before the outbreak of World War II, and was not resumed.

During the war, a great deal of work on the use of predacious fungi for the control of nematodes, both in plants and animals, was carried out in France. This work has been summarized by DOLLFUS³². Most of the French work was concentrated on methods of growing the fungi in bulk, and on demonstrating that they could effectively attack pathogenic nematodes and that they were harmless to crop plants and domestic animals. Only two experiments on nematode control were carried out, both of which were inconclusive owing to their small scale.

Experiments on the biological control of nematodes by predacious fungi in England began in 1951, and are still in progress. Initially, the work was mainly concerned with the control of the potato root eelworm (*Heterodera rostochiensis*), and a preliminary series of pot experiments confirmed LINFORD's observation that the activity of the fungi was much affected by the presence of organic matter in the soil. The results of experiments in the field were inconclusive, though indications that the fungi might be of potential value were obtained (DUDDINGTON²⁸). Later trials with cereal root eelworm (*Heterodera avenae*) in oats again confirmed LINFORD's experiments on the effect of organic matter, and demonstrated that the use of predacious fungi in conjunction with organic soil amendment produced a marked reduction in the number of *Heterodera* larvae invading the roots of oat seedlings (DUDDINGTON and DUTHOIT²⁹, DUDDINGTON, DUTHOIT, and EVERARD³⁰).

In a recent series of trials, HAMS and WILKIN³³ used cultures of predacious fungi grown in deep culture. In pot experiments against potato root eelworm, pea root eelworm and cereal root eelworm, the incidence of nematode attack on the plants was reduced, but later experiments on a field scale were inconclusive. The design of the field trials, however, and the method of assessing the results, were not beyond criticism.

³² R. P. DOLLFUS, *Parasites (animaux et végétaux) des helminthes* (Lechevalier, Paris 1946).

³³ A. F. HAMS and G. D. WILKIN, *Ann. appl. Biol.* 49, 515 (1961).

In recent years, a great deal of work has been done in Russia on the biological control of nematodes by predacious fungi, and some interesting and encouraging results have been reported. The work has been monographed by SOPRUNOV³⁴. In a more recent paper, SOPRUNOV and TENDETNIK³⁵ state that they have found *Arthrobotrys oligospora* and *A. dolioformis* the most useful fungi for eelworm control, and recommend chopped maize and oatmeal as the best culture substrates. After growth and sporulation of the fungi the cultures are dried and powdered, and the authors claim that a powder with up to 2000000 spores/g is effective and can be produced at a cost of about 4.50 roubles/kg. The value of the Russian work is difficult to assess at present, but, if their results are substantiated, they appear to be well ahead of the rest of the world in the field of biological control of nematodes.

In the United States, interest in the use of predacious fungi for the control of soil nematodes has recently been aroused, and a number of very able workers have entered the field. It is as yet too soon to evaluate what is going on, but if the vigorous American attack on the problem continues it is unlikely that the Russians will hold their lead for long.

Zusammenfassung. Die zahlreichen, sich von Nematoden ernährenden Pilzarten zerfallen in zwei Gruppen.

Die eine Gruppe fängt die Würmer mit klebrigen, netz- oder knopfförmigen Mycelien oder mit Zellringen, in denen sich die Nematoden verfangen oder durch plötzliches Quellen des Ringes aktiv festgehalten werden. Die zweite Gruppe dringt von am Wurm haftenden Sporen in seinen Körper ein.

Die Pilzmycelien besitzen keine Fangeinrichtungen, wenn sie ohne Nematoden gezüchtet werden. Zugabe von sterilem Wasser, in dem sich früher Nematoden aufgehalten hatten, bringt die Wurmfallen zur Entwicklung. Auch zahlreiche andere Substanzen, wie Pferdeserum oder wässrige Auszüge verschiedener tierischer Organe wirkt bei den Formen mit quellbaren Fangringen als Bildungsreiz. Es wurde ausserdem festgestellt, dass gewisse organische Stoffe ihre Aktivität im Nematodenfang beträchtlich erhöhen.

Nematodenfangende Pilze sind häufige Bodenbewohner und ihre Bedeutung als Nematodenvertilger ist erwiesen. Es sind Versuche im Gang, sie für die biologische Kontrolle von Feldwürmern auszunutzen, die als Erreger von Pflanzenkrankheiten schädlich sind.

³⁴ F. F. SOPRUNOV, *Predacious Fungi—Hyphomycetes and their Application in the Fight against Pathogenic Nematodes* (Ashkabad 1958).

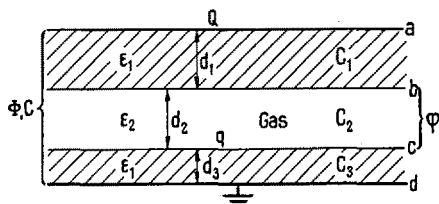
³⁵ F. F. SOPRUNOV and YU. YA. TENDETNIK, *Trud. gel'mint. Lab.* 10, 192 (1960).

Brèves communications – Kurze Mitteilungen – Brevi comunicazioni – Brief Reports

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Intermittierende elektrische Entladungen im Gasraum zwischen zwei Dielektrika

Wird in einem dielektrischen System, das einen Gasraum einschliesst, z.B. einem zusammengesetzten, unendlich ausgedehnten Plattenkondensator, wie ihn die Abbildung im Schema zeigt, ein von $+E$ bis $-E$



alternierendes Potential Φ angelegt, so tritt im mittleren Gasraum (Dielektrizitätskonstante ϵ_2 , Kapazität/cm² C_2) jeweils eine Entladung ein, wenn das dort herrschende Potentialgefälle Φ den Wert der Zündspannung $\Phi = A$ erreicht hat, und die Entladung hört auf, wenn $\Phi = B$,

gleich der Löschspannung geworden ist. Durch die Entladung, die in Form einer stillen elektrischen Entladung abläuft, solange kein Durchschlag durch das Dielektrikum erfolgt, entstehen an den Dielektrikumsflächen b und c elektrische Ladungen, die das Absinken des Potentials Φ von A auf B bedingen, was eine Nachlieferung von Elektrizität durch die Stromquelle auf die Belegungen a und d des Kondensators erfordert zur Aufrechterhaltung des angelegten Potentials Φ . Dass diese Nachlieferung von Elektrizität, auch wenn die Entladung im Gasraum sehr rasch abläuft, ohne vorübergehendes Absinken von Φ vor sich geht, wird angesichts der geringen Menge der transportierten Elektrizität als sehr wahrscheinlich erachtet, denn der im Hochspannungstromkreis gemessene Strom, der den aus den Gasentladungen resultierenden Leitungsstrom enthält, hat eine Stärke in der Grössenordnung von nur 10^{-2} bis 10^{-3} mA pro cm² Kondensatorfläche. Tatsächlich haben SPRETER und BRINER¹ in Versuchen mit stiller elektrischer Ent-

¹ V. SPRETER und E. BRINER, *Helv. chim. Acta* 32, 2527 (1949).