Density-dependence and host-specificity of the nematode-trapping fungus *Monacrosporium ellipsosporum*

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SUMMARY

The infection rate of *Meloidogyne incognita* juveniles was reduced by more than 90 % following migration through soil infested with the nematode-trapping fungus, *Monacrosporium ellipsosporum* to tomato roots. *M. ellipsosporum* reduced the number of juveniles penetrating tomato roots and the number of juveniles remaining in the soil twelve days post-treatment. The number of *M. incognita* juveniles entering roots decreased with increased *M. ellipsosporum* inoculum density. *M. ellipsosporum* sticky knob traps were tested for adhesion specificity to fifteen different species of nematodes. *Acrobeloides* sp., *Aphelenchoides* sp., *Aphelenchus avenae*, *Criconemella xenoplax*, *Meloidogyne incognita*, *Pratylenchus scribneri*, *Seinura oxuris*, and *Tylenchulus semipenetrans*, adhered to the sticky knobs while *Longidorus africanus*, *Mesodorylaimus* sp., *Paratrichodorus minor*, *Xiphinema americanum*, and *Diplenteron* sp. adults did not. *Iotonchus brachylaimus* only rarely adhered. Fifteen sugars were tested for suppression of adhesion of *Panagrellus redivivus* to the sticky knobs of *M. ellipsosporum*. Fucose, D-fructose and lactose suppressed adhesion of *P. redivivus* to the knobs at 20 mM, but some nematodes adhered even at 200 mM concentrations. Alpha-methyl-D-mannoside, L-sorbose, D-arabinose, alpha-D-mellibiose, D (+) trehalose, and sucrose suppressed adhesion of *P. redivivus* at 200 mM but not at 20 mM concentrations. N-acetyl-galactosamine and L-xylose did not suppress adhesion at 20 mM or 200 mM concentrations.

RÉSUMÉ

Effet de la densité dans le sol et spécificité d'hôte chez le champignon piégeur de nématodes Monacrosporium ellipsosporum

Le taux d'infestation de racines de tomate par les juvéniles de *Meloidogyne incognita* est réduit de plus de 90 % s'ils migrent à travers un sol contenant le champignon piégeur de nématodes *Monacrosporium ellipsosporum*. Celui-ci diminue le nombre des juvéniles tant pénétrant dans les racines que demeurant dans le sol douze jours après le traitement. Le nombre de juvéniles de *M. incognita* pénétrant dans les racines décroît lorsque la densité de l'inoculum en *M. ellipsosporum* augmente. L'éventuelle adhérence spécifique des boutons collants de *M. ellipsosporum* a été testée envers quinze espèces de nématodes. *Acrobeloides* sp., *Aphelenchoides* sp., *Aphelenchus avenae*, *Criconemella xenoplax*, *Meloidogyne incognita*, *Pratylenchus scribneri*, *Seinura oxuris* et *Tylenchulus semipenetrans* adhèrent à ces boutons tandis que les adultes de *Longidorus africanus*, *Mesodorylaimus* sp., *Paratrichodorus minor*, *Xiphinema americanum* et *Diplenteron* sp. n'y adhèrent pas. *Iotonchus brachylaimus* adhère rarement. Quinze sucres ont été testés en vue de la suppression de cette adhérence de *Panagrellus redivivus* aux boutons collants de *M. ellipsosporum*. La fucose, le *d*-fructose et le lactose suppriment cette adhérence au taux de 20 mM, mais quelques nématodes adhèrent encore à des concentrations de 200 mM. L'α-méthyle-*d*-mannoside, le *l*-sorbose, le *d*-arabinose, l'α-*d*-mellibiose, le *d* (+) tréhalose et le saccharose suppriment l'adhérence de *P. redivivus* à une concentration de 200 mM mais non à 20 mM. La N-acétyle-galactosamine et le *l*-xylose aux concentrations de 20 mM ou 200 mM ne suppriment pas l'adhérence.

Two constraints that may limit the ability of nematode-trapping fungi (NTF) to reduce nematode numbers in soil are density-dependence and host-specificity. NTF are predators/parasites of juvenile and adult motile stages of nematodes but do not attack eggs or sedentary stages (Barron, 1977). NTF trapping organs are passive in the sense that nematodes must come in contact with the adhesive surface of hyphae or other trapping organs to be captured. Only nematodes migrating through soil are thus parasitized. Many important plant-parasitic nematodes are endo-parasites or sedentary for most of their life-cycle and therefore largely escape contact and capture.

Monacrosporium ellipsosporum (Grove) Cooke & Dickinson produces sticky knobs for capturing nematodes. These trapping organs are stationary and plant-parasitic nematodes come into contact with them as they migrate through soil in search of a host root. This

suggests that nematode mortality is dependent on the density of sticky knobs and on the distance that nematodes travel through trap-infested soil. Plant-parasitic nematodes such as *Meloidogyne* spp. are capable of migrating considerable distances through soil (Prot & Van Gundy, 1981). Although this relationship suggests density dependence, nematode numbers often increase after the addition of NTF to soil (Cook, 1962; 1968). It has been assumed that NTF traps are nonspecific and adhere to any nematode that contacts them (Jansson & Nordbring-Hertz, 1980; Rosenzweig, Premachandran & Pramer, 1985). The adhesion phenomenon in at least two NTF, *Arthrobotrys oligospora* Fres. and *Dactylaria candida* Nees ex Pers. has been linked to a lectin (Nordbring-Hertz, Firman & Mattiasson, 1981; 1982). Increases in nematode densities after the addition of NTF could result from selective survival and reproduction of nematodes resistant to capture.

The importance of *M. ellipsosporum* inoculum density and the distance traveled by *Meloidogyne incognita* (Kofoid & White) Chitwood, on nematode mortality were tested in this investigation. In addition, the traps of *M. ellipsosporum* were tested for lectin-mediated host-specificity.

Materials and methods

M. ellipsosporum (ME) was cultured on V 8 broth medium (200 ml V 8 ® juice, 800 ml water, 5.0 g CaCO$_3$) for seven days on an orbital shaker. ME infested soil consisted of 50 ml of the fungal suspension (approximately 135 mg dry wt in the form of mycelial fragments) mixed with each L/soil (pasteurized loamy sand). Soil and fungus were mixed in a V-shell mixer for 10 minutes. Three to four days were allowed for trap formation to occur after mixing the soil, since traps are not formed in V 8 broth cultures (Nordbring-Hertz, 1973). Propagule density of ME was not determined.

M. incognita was cultured on greenhouse tomatoes (*Lycopersicon esculentum* Mill. cv Tropic). Egg-masses from heavily galled roots were dissolved in 0.5 % NaOCl (Barker, 1978), collected on a sieve with 25 μm openings (SEA # 500) and placed on a modified Baermann funnel. Only second stage juveniles (J2) within 3 days after hatching were used.

Soil columns used in this experiment consisted of four 10 cm polyvinyl chloride (PVC, schedule 40) pipe sections (i.d. 7.5 cm) taped together to form 40 cm tubes. One end of each tube was placed in a 15 cm clay pot which was then filled with loamy sand to secure the empty tubes in an upright position. The tubes were filled with either ME infested soil or control soil. After partially filling the tubes, root-knot juveniles were applied in suspension and then covered with enough soil to fill the tubes forming a soil column (Fig. 1).
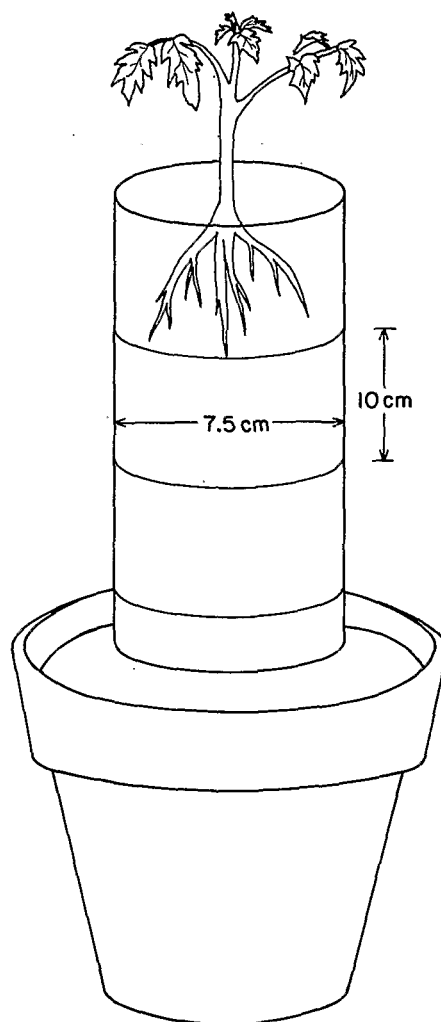

Fig. 1. Diagram of soil columns used to study density dependence of *Monacrosporium ellipsosporum* trapping activity.

DENSITY-DEPENDENCE

Approximately 5 000 J2 in suspension were added to each column and covered with 30 cm of soil. The columns were immediately planted with three week old tomato seedlings and were randomized on a greenhouse bench. After twelve days, the roots were washed free of soil, fixed in white boiling lactophenol, and stained with cold 0.5 % cotton blue lactophenol (de Guiran, 1967). Nematodes remaining in the soil were extracted with Cobb wet-sieving and centrifugal flotation (Barker, 1978). Treatments were replicated seven times (Experiment 1).

Approximately 1 000 J2 in suspension were added and covered with 30 cm of soil as before. The columns were immediately planted with tomato seedlings and were

randomized on a greenhouse bench. After twelve days, the sections were separated and the roots in each of the 10 cm sections were washed free of soil and stained. Treatments were replicated seven times (Experiment 2).

Approximately 750 J2 in suspension were added and covered with 7.5, 15.0, 22.5, or 30.0 cm of soil, respectively, as previously described. The columns were immediately planted with tomato seedlings and randomized on a greenhouse bench. After twelve days, the roots were washed free of soil and stained. Treatments were replicated ten times (Experiment 3).

ME infested soil (100 % propagule density) was mixed with loamy sand to obtain mixes with 0 %, 6 %, 12 %, and 50 % of the initial ME propagule density. Approximately 750 juveniles were covered with 30 cm of the diluted soil mixes or the unmixed infested soil and then the columns were planted with tomato seedlings and randomized on a greenhouse bench. After twelve days, the roots were washed free of soil and stained. Treatments were replicated twelve times (Experiment 4).

HOST-SPECIFICITY

The experimental design of Nordbring-Hertz, Firman and Mattiasson (1981) was used to investigate the involvement of lectins. *M. ellipsosporum* was cultured on strips (4.5 × 5.0 cm) of dialysis membrane (m.w. cutoff 12 000) placed on the surface of 10 % strength corn meal agar (1 part Difco® corn meal agar : 9 parts Difco Bacto-Agar®, CMA) in Petri dishes. Since *M. ellipsosporum* does not form sticky knobs spontaneously in culture (Nordbring-Hertz, 1973), sticky knob formation was induced by the addition of 300-500 *Panagrellus redivivus* in suspension to 3-4 day old cultures. After trap induction, strips of dialysis membrane with *M. ellipsosporum* forming sticky knobs (6-7 day old cultures) were transferred to empty 9 cm diameter plastic Petri dishes and flooded for 20-24 hours with the following sugars (20 and 200 mM solutions in 0.01 M phosphate buffered saline); N-acetyl-D-galactosamine, alpha-*d*-galactose, 2-deoxy-galactose, fucose, alpha-methyl-D-mannoside, L-sorbose, D-fructose, L-xylose, D-arabinose, alpha-D-mellibiose, lactose, D— (+) trehalose and sucrose. Alter draining the excess sugar solution from the Petri dishes, *P. redivivus* cultured on yeast cells was used to test adhesion. Under a dissecting microscope (100 ×), 25 *P. redivivus* were individually applied to sticky knobs of each dish flooded with a sugar solution to test suppression of adhesion. Sticky knobs in dishes flooded with the buffer solution were tested as a control. In cases where adhesion was suppressed an additional 50 nematodes were tested per dish. Petri dish treatments were replicated five times.

Specificity of *M. ellipsosporum* sticky knob adhesion was tested with the nematodes *Acrobeloides* sp., *Aphelenchoides* sp., *Aphelenchus avenae* Bastian, *Criconemella xenoplax* (Raski) Luc & Raski, *Diplenteron* sp. *Helico-*

tylenchus sp., *Iotonchus brachylaimus* (Cobb) Andrássy, *Longidorus africanus* Merny, *Meloidogyne incognita* (Kofoid & White) Chitwood, *Mesodorylaimus* sp., *Paratrichodorus minor* (Colbran) Siddiqi, *Pratylenchus scribneri* Steiner, *Seinura oxuris* (Paesler) Goodey, and *Tylenchulus semipenetrans* Cobb. *C. xenoplax* sp., *Helicotylenchus* sp., *I. brachylaimus, P. minor* and *T. semipenetrans* were extracted from field soil using Cobb wet-sieving and centrifugal flotation (Barker, 1978). The other nematodes used were grown in laboratory monoxenic or oligoxenic agar cultures and were extracted directly from Petri dishes and rinsed in distilled water before use.

Twenty-five nematodes of each species were individually brought into contact with the sticky knobs of a dialysis membrane culture, as previously described, to test if adhesion occurred. *P. redivivus*, a nematode known to adhere to these sticky knobs was tested with each nematode as a control. If adhesion did not occur an additional 50 nematodes were tested per plate. Treatments were replicated five times as before.

Results

DENSITY-DEPENDENCE

The survival of J2 in ME infested soil was only 10 % of the numbers surviving in control soil after twelve days. An average of 1 983 J2 remained in the control soil and 198 J2 remained in the ME infested soil (P < 0.01). An average of only 16 J2 penetrated the tomato roots in the ME infested soil while 817 J2 penetrated in the control soil (P < 0.01) (Experiment 1).

The number of nematodes penetrating roots was significantly reduced when J2 migrated through ME infested soil but the distribution of nematodes in the four depths was similar in the treatment and the controls (Tab. 1). The majority of the J2 penetrated the roots in the top 10 cm of the columns indicating significant migration through trap-infested soil occurred (Experiment 2).

Increasing the distance nematodes migrated through soil did not reduce root penetration in the control soil (Fig. 2). The number of J2 penetrating roots in ME infested soil was substantially reduced from the control at all of the depths that J2 were added. In ME infested soil, there were also significantly more J2 in roots where nematodes were added at 7.5 cm than those added at the other depths (Experiment 3).

Decreasing the propagule density of ME resulted in an increase in root penetration (Fig. 3). Soils with 100 %, 50 %, or 25 % of the initial ME propagule density did not differ significantly from each other (P < 0.05), but those with 12 %, 6 %, and 0 % of the initial propagule density were significantly different from each other and from the 100 %, 50 %, and 25 % treatments (Experiment 4).

Table 1

Meloidogyne incognita in tomato roots at various depths
in soil columns infested with *Monacrosporium ellipsosporum*
or uninfested twelve days after adding 1 500 juveniles
at a depth of 30 cm

Depth (cm)	ME[a]	Control[b]
0-10	157 (74 %)	546* (71 %)
10-20	32 (15 %)	108* (14 %)
20-30	21 (10 %)	84* (4 %)
30-40	3 (1 %)	32* (4 %)
TOTAL	213 (100 %)	770* (100 %)

a = Number of juveniles in the roots at each depth of *M. ellipsosporum* infested soil and % of total at that depth.

b = Number of juveniles in the roots at each depth of control soil and the % of total at that depth.

* = The number of juveniles penetrating roots at this depth of the control soils is significantly greater than the penetration in ME infested soil (P < 0.01).

Fig. 3. Number of *M. incognita* penetrating roots twelve days after inoculating 750 juveniles at a depth of 30 cm to soil columns infested with various densities of *M. ellipsosporum*. (Points sharing a letter are not statistically different, P = 0.05).
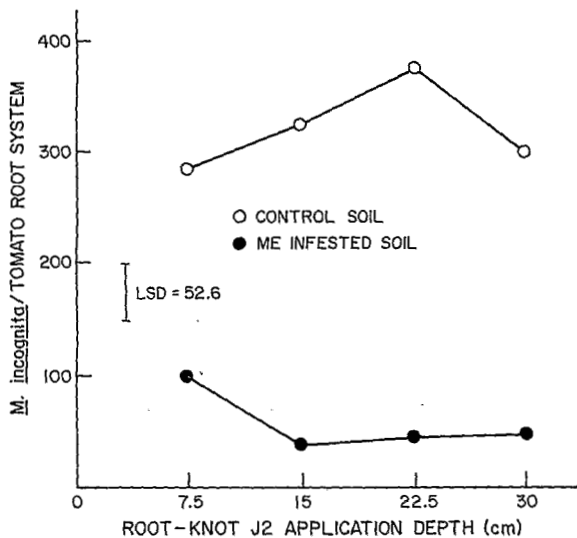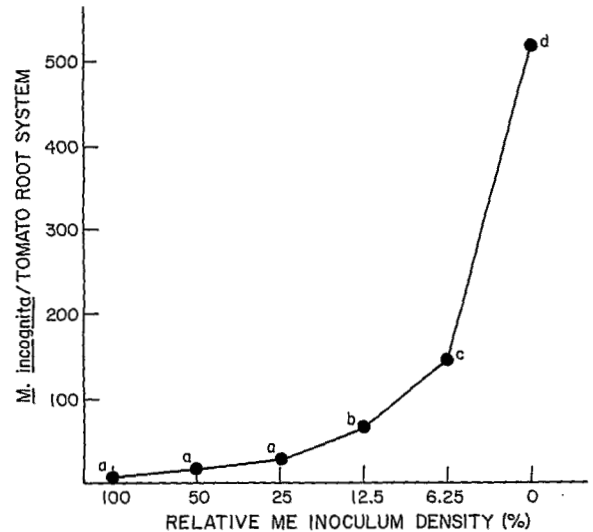

Fig. 2. Penetration of *M. incognita* into roots twelve days after inoculating 750 juveniles at various depths of soil columns infested or uninfested with *M. ellipsosporum*. (Bar represents least significant difference, P = 0.05).

Table 2

Effect of fifteen sugars on inhibition of adhesion
of *Panagrellus redivivus*
to sticky knobs of *Monacrosporium ellipsosporum*
at 20 mM and 200 mM concentrations

Sugars tested	% nematodes trappead[x]	
	20 mM[y]	200 mM[y]
N-acetyl-D-galactosamine	100 a	100 a
Alpha-D-galactose	100 a	24 ef
2 deoxy-D-galactose	100 a	80 abc
Fucose	88 a	60 cd
Alpha-D-glucose	100 a	44 de
2-deoxy-D-glucose	100 a	76 abc
Alpha-methyl-D-mannoside	100 a	56 cd
L-sorbose	100 a	84 abc
D-fructose	68 b	4 a
L-xylose	100 a	100 a
D-arabinose	100 a	12 f
Alpha-D-mellobiose	100 a	96 ab
Lactose	44 b	24 df
D (+) trehalose	100 a	76 bc
Sucrose	100 a	68 cd

x = At least 125 nematodes were tested with each sugar.

y = Within each column, percentages sharing the same letter are not significantly different (P = 0.05).

HOST-SPECIFICITY

Sticky knobs of ME were adhesive for a period of seven days, so only newly formed knobs at the margins of the colonies could be reliably tested. Fucose, D-fructose and lactose at 20 mM suppressed adhesion of *P. redivivus* to the sticky knobs (Tab. 2). N-acetyl-D-galactosamine and L-xylose did not suppress adhesion at 20 mM or 200 mM. The other sugars tested suppressed adhesion at 200 mM but not at 20 mM. ME sticky knobs showed nematode specificity (Tab. 3). *L.*

Table 3

Specificity of binding to the sticky knobs
of *Monacrosporium ellipsosporum*
to sixteen species of nematodes

Nematodes tested	% nematodes trapped*
Adenophorea	
Dorylaimida	
Longidorus africanus	0 a
Mesodorylaimus sp.	0 a
Paratrichodorus minor	0 a
Xiphinema americanum	0 a
Mononchida	
Iotonchus brachylaimus	8 a
Secernentea	
Rhabditida	
Acrobeloides sp.	100 c
Panagrellus redivivus	100 c
Aphelenchida	
Aphelenchoides sp.	100 c
Aphelenchus avenae	100 c
Seinura oxuris	100 c
Diplogasterida	
Diplenteron sp. (larvae)	100 c
(adults)	0 a
Tylenchida	
Criconemella xenoplax	88 b
Helicotylenchus sp.	92 bc
Meloidogyne incognita	100 c
Pratylenchus scribneri	100 c
Tylenchulus semipenetrans	100 c

* = At least 50 nematodes were tested of each species. Observations sharing the same letter are not statistically different (P = 0.05).

africanus, Mesodorylaimus sp., and *Diplenteron* sp. adults did not adhere to the sticky knobs. *I. brachylaimus*, rarely adhered to knobs. All other nematodes tested readily adhered to ME.

Discussion

Density of trapping organs, and to a lesser extent the distance *M. incognita* juveniles migrated were important factors in nematode survival and root penetration. Capture of juveniles in ME infested soil reduced root penetration in all cases. The reduction of soil J2 in the first experiment, and the presence of large numbers of ME trapping organs and trapped nematodes in the soil washings from the ME infested soil supported the suggested role of ME trapping activity as the primary cause of reduction of J2 root penetration.

Root-knot, second stage juveniles, can effectively migrate 20 cm to an infection site (Prot & Van Gundy,

1981). Experiment 2 indicated that ME did not alter the migration behavior of J2. In both the control and the ME infested soil, root penetration occurred primarily in the top 10 cm of soil. Those juveniles in the top 10 cm of the soil columns migrated through at least 20 cm of trap-infested soil to locate a suitable infection site. Although the total number of J2 penetrating roots was reduced in ME soil, the distribution by depth of penetration was similar, suggesting that the proportion of nematodes captured in each 10 cm section was similar.

Varying the distance J2 traveled through soil in slightly influenced root penetration. J2 applied 7.5 cm from the soil surface of ME infested soil made significantly more successful penetrations than those applied further from the roots. The J2 added to control soil were not affected by the depth of addition; root penetration occurred to the same extent or increased at lower depths. Although the nematodes were added at varying depths and migrated up the columns, the tomato roots also grew toward the nematodes as they were migrating; twelve days after planting, tomato roots had reached the bottom of the soil columns. Therefore, the actual distance the nematodes had to travel to enter roots did not correspond to the depth of application and may have been responsible for the discrepancy between the expected and actual penetration of J2 in roots.

Decreasing the inoculum density of ME by serial dilution increased root penetration by J2. At the highest inoculum density, penetration was virtually blocked. At 50 % and 25 % of that density penetration increased but was not different from the 100 % level. Each subsequent dilution level and the uninfested soil had increased penetration. The increase in successful root penetrations by J2 agreed well with the reduction of trap density of ME infested soil from the soil dilutions, as inoculum density of ME increased, the rate of root-knot penetration decreased.

A density and motility dependent relationship is proposed to explain these experimental results. The traps of ME are passive in action. They are, in many ways, analogous to land mines in a mine field. Movement of J2 to these traps is required to initiate parasitism. Although traps of some NTF are attractive to nematodes (Field & Webster, 1977; Jansson & Nordbring-Hertz, 1979), attraction of J2 to the sticky knobs of ME has not been observed (Mankau & Wu, 1985).

Suppression of nematode adhesion to the sticky knobs of ME by flooding the knobs with specific sugars is indirect evidence of lectin involvement. Presumably the sugars bind to the lectins on the surface of the sticky knobs and prevent recognition of the carbohydrate residues on the surface of the nematode cuticle (Kocourek & Horesjsi, 1983; Zuckerman, Kahane & Himmelhoch, 1979).

Although it had previously been suggested that nematode-trapping fungi were not nematode specific (Rosenzweig, Premachandran & Pramer, 1985), the results

of this study show specificity that falls along taxonomic lines. Nematodes belonging to the class Secernentea were generally captured, while those of the Adenophorea were not. This may reflect fundamental differences in the cuticular structure of the two classes of nematodes (Spiegel, Cohn & Spiegel, 1982). In addition to taxonomic specificity, binding also was stage-specific in the nematode *Diplenteron* sp. Stage-specific binding has also been reported for the binding of *Pasteuria penetrans* spores to the cuticle of root-knot nematode. *P. penetrans* spores bind to juveniles but not adult males of *M. incognita* (Mankau, 1980). These results suggest ME is not a candidate for the biological control of those nematodes which are resistant to this lectin-like interaction and may partially explain why total nematode numbers sometime increase after the addition of NTF to soil.

REFERENCES

BARKER, K. R. (1978). Determining population responses to control agents. In : *Methods for evaluating plant fungicides, nematicides and bacteriocides.* St. Paul, MN, USA, Amer. phytopathol. Soc. : 114-127.

BARRON, G. L. (1977). *Nematode-destroying fungi.* Topics in mycobiology No. 1. Guelph, Canada, Can. Biol. Publ. Ltd., 140 p.

COOKE, R. C. (1962). Ecology of nematode-trapping fungi in soils. *Annls appl. Biol.,* 50 : 507-513.

COOKE, R. C. (1968). Relationships between nematode-destroying fungi and soilborne phytonematodes. *Phytopathology,* 58 : 909-913.

FIELD, J. I. & WEBSTER, J. (1977). Traps of predaceous fungi attract nematodes. *Trans. brit. mycol. Soc.,* 68 : 467-469.

DE GUIRAN, G. (1976). Coloration des nématodes dans les végétaux par le bleu coton à froid. *Nematologica,* 12 : 646-647.

JANSSON, H. B. & NORDBRING-HERTZ, B. (1979). Attraction of nematodes to living mycelium of nematophagous fungi. *J. gen. Microbiol.,* 112 : 89-93.

JANSSON, H. B. & NORDBRING-HERTZ, B. (1980). Interactions between nematophagous fungi and plant-parasitic nematodes : attraction, induction of trap formation and capture. *Nematologica,* 26 : 383-389.

KOCOUREK, J. & HORESJSI, V. (1983). A note on the recent term " lectin ". In : Bog-Hansen, T. C., & Spengler, G. A. (Eds). *Lectins : Biology, Biochemistry and Clinical Biochemistry,* Vol. 3, Berlin, Walter de Grayter : 3-5.

MANKAU, R. (1980). Biocontrol : Fungi as nematode control agents. *J. Nematol.,* 12 : 244-252.

MANKAU, R. (1980). Biological control of nematode pests by natural enemies. *Ann. Rev. Phytopathol.,* 18 : 415-440.

MANKAU, R. & WU, X. Y. (1985). Effects of the nematode-trapping fungus, *Monacrosporium ellipsosporium* on *Meloidogyne incognita* populations in field soil. *Revue Nématol.,* 8 : 149-153.

McCLURE, M. & ZUCKERMAN, B. M. (1982). Localization of cuticular binding sites of concanavalin A on *Caenorhabditis elegans* and *Meloidogyne incognita. J. Nematol.,* 14 : 39-44.

NORDBRING-HERTZ, B. (1973). Peptide-induced morphogenesis in the nematode-trapping fungus *Arthrobotrys oligospora. Physiol. Plant.,* 29 : 223-233.

NORDBRING-HERTZ, B., FIRMAN, E. & MATTIASSON, B. (1981). Host-micro-organisms interaction : Developmentally regulated lectin-mediated capture of nematodes by nematode-trapping fungi. In : Bog-Hansen, T. C. (Ed.). *Lectins : Biology, Biochemistry and Clinical Biochemistry,* Vol. 1. Berlin, Walter de Grayter : 43-50.

NORDBRING-HERTZ, B., FIRMAN, E. & MATTIASSON, B. (1982). A recognition mechanism in the adhesion of nematodes to nematode trapping-fungi. In : Bog-Hansen, T. C., & Spengler, G. A. (Eds). *Lectins : Biology, Biochemistry and Clinical Biochemistry,* Vol. 2. Berlin, Walter de Grayter : 83-90.

NORDBRING-HERTZ, B. & MATTIASSON, B. (1979). Action of nematode-trapping fungus shows lectin mediated host-microorganisms interaction. *Nature,* 281 : 477-479.

PROT, J. C. & VAN GUNDY, S. D. (1981). Soil texture and migration. *J. Nematol.,* 13 : 213-217.

ROSENZWEIG, W. D., PREMACHANDRAN, D. & PRAMER, D. (1985). Role of trap lectins in the specificity of nematode capture by fungi. *Can. J. Microbiol.,* 31 : 693-695.

SPIEGEL, Y., COHN, E. & SPIEGEL, S. (1982). Characterization of sialyl and galactosyl residues on the body wall of different plant-parasitic nematodes. *J. Nematol.,* 14 : 33-39.

ZUCKERMAN, B. M., KAHANE, I. & HIMELHOCH, S. (1979). *Caenorhabditis briggsae* and *C. elegans :* Partial characterization of cuticle surface carbohydrates. *Exp. Parasitol.,* 7 : 419-424.