Induction of Nematode-Trapping Organs in the Predacious Fungus *Arthrobotrys oligospora* (Hyphomycetales) by Infective Larvae of *Ostertagia ostertagi (Trichostrongylidae)*

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Grønvold, J.: Induction of nematode-trapping organs in the predacious fungus *Arthrobotrys oligospora (Hyphomycetales)* by infective larvae of *Ostertagia ostertagi (Trichostrongylidae)*. Acta vet. scand. 1989, 30, 77–87. – Laboratory experiments were designed to study the influence of temperature, concentrations of nematodes, oxygen tension, light, and nutrient levels, on the induction of nematode-trapping hyphal nets in the predacious fungus *Arthrobotrys oligospora* When induced by infective *Ostertagia ostertagi* larvae, a maximum number of nets was produced at 20°C, at which temperature nets in surplus were produced at larval concentrations up to 1,000 larvae per cm^2. *A oligospora* did not produce nets in an anaerobic atmosphere containing 21 % CO_2 (v/v), and net induction was suppressed to a certain degree by exposure to light. The composition of the medium had an important influence on the saprophytic growth and the net-forming capability of *A oligospora* as a maximum number of nets was induced at a relatively low concentration of corn meal supporting the relatively sparse mycelium. It was shown that a proportion of trapping nets in *A. oligospora* maintained their trapping potential for more than 7 weeks when the temperature was below 25°C. Induction of nematode-trapping organs in *A oligospora* is discussed in relation to control of infective nematode parasite larvae in cow pats.

nematodes; cattle parasites.

Introduction

The predacious fungus *Arthrobotrys oligospora* is able to trap migrating nematodes in three-dimensional adhesive nets raised above the surface of the medium. Net formation starts by lateral branch growing out from the vegetative hyphae. This branch curls back and anastomoses with the parent or adjacent hyphae. From this primary loop other loops may be formed by hyphal anastomoses, and eventually a three-dimensional network is created (Fig. 1).

In *A. oligospora* trapping nets are formed only if the fungus is stimulated (induced) by factors of physio-chemical (e.g. electrical potentials or peptides) or biological (e.g. nematodes and several other soil animals) nature *Pramer & Stoll* (1959) were able to induce
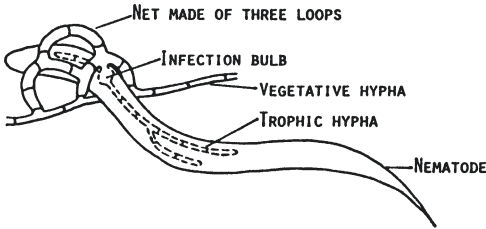
Figure 1. Schematic drawing of a nematode trapped by *Arthrobotrys oligospora* in a three-dimensional adhesive net made of 3 loops. Only the nets are sticky in *A. oligospora*. At the point of contact the fungus penetrate the cuticle. Inside the nematode an infection bulb is formed from which trophic hyphae grow out within the nematode and absorb its contents.

trap formation in predacious fungi by a substance isolated from nematodes. They called the substance nemin. Detailed investigations on peptide- and nematode-induced net formation in *A. oligospora* have been performed by *Nordbring-Hertz* (1973, 1977).

It was evident that the dipeptide phenylalanyl-valine (0.1 mg per ml medium) was effective in inducing nets in *A. oligospora* if the fungus was grown on a mineral salt medium of low nutrient value, supplied with thiamin and biotin (*Nordbring-Hertz* 1973). On nutrient-rich media, net induction was depressed. Other peptides, especially valyl peptides, also gave some activity, but the presence of non-polar and aromatic amino acids in the peptides seems important for net induction (*Nordbring-Hertz* 1973, *Nordbring-Hertz & Brinck* 1974). Most amino acids did not induce nets in *A. oligospora* (*Nordbring-Hertz* 1973).

The breakdown of proteins or peptides in the environment, or exudations of proteinaceous material from soil animals, may be important in starting the process of net formation. Nematodes excrete CO_2, ammonia, acetic acid, and propionic acid, but only ammonia showed a certain effect on net formation in *A. oligospora* (*Nordbring-Hertz & Odham* 1980). Nematodes also excrete small peptides capable of inducing nets in *A. oligospora* (*Nordbring-Hertz* 1977), but it is most likely that nematodes are capable of inducing nets in some way other than through peptides.

Living nematodes induce traps in *A. oligospora* more rapidly than peptides and extracts from nematodes (*Nordbring-Hertz* 1977). On low-nutrient media, net formation induced by the free-living soil nematode *Panagrellus redivivus* started within 2 h and a maximum of nets was reached after 4 h, the rapid response indicating an effect by direct contact between vegetative hyphae and nematodes. It is possible that electrical potentials arising from muscle concentrations of moving nematodes are capable of inducing net formation, as it has been shown that applied electrical potentials are able to bring about trap induction in *A. oligospora* (*Nordbring-Hertz* 1977). This agrees with the observation that fast-moving nematodes induce traps most rapidly (*Jansson & Nordbring-Hertz* 1980). Perhaps nematodes in this way affect the surface potential of the vegetative hyphae, giving an altered permeability of ions and peptides triggering the morphogenetic process. *Nansen et al.* (1988) have shown that the net-inducing capabilities of infective larvae of the cattle nematode parasite *Ostertagia ostertagi* and the free-living nematode *P. redivivus* were comparable.

Growing vegetative hyphae are rhythmically predisposed for peak production of nets. At 21°C, maximum numbers of nets in *A. oligospora* were formed periodically along hyphae with age differences of approximately 42 h (*Lysek & Nordbring-Hertz* 1981).

It has been found that *A. oligospora* produce substances that attract a wide range of nematodes (*Jansson & Nordbring-Hertz*

1980). This is in accordance with results of *Balan et al.* (1974) who found that the production of attractants in *A. oligospora* was potentiated by traps formed in the presence of nematodes.

The nets in *A. oligospora* are composed of hyphae that are more robust and with a cell wall often 4–5 times thicker than the vegetative hyphae (*Nordbring-Hertz & Stålhammer-Carlemalm* 1978). The trapping nets are covered with a mucilagineous coat that sticks to living nematodes, and there is experimental evidence for the presence of a lectin on the net surface which binds to a carbohydrate on the nematode cuticle (*Nordbring-Hertz & Mattiasson* 1979, *Mattiasson et al.* 1980). The adhesion mechanism has been shown to be equally effective against a range of bacteria-feeding and plant-parasitic nematodes (*Jansson & Nordbring-Hertz* 1980) as well as a range of animal-parasitic nematodes (*Nansen et al.* 1988). Observations by *Nordbring-Hertz & Stålhammer-Carlemalm* (1978) indicate that the struggling of captured nematodes trigger an increased secretion of adhesive substances between the fungal traps and the nematodes. Penetration of trapped *P. redivivus* was observed within 1 h by *Nordbring-Hertz & Stålhammer-Carlemalm* (1978). The mechanism by which the cuticle is penetrated is not known, but it is possible that it is partly mechanic and partly enzymatic (*Barron* 1981). Within 45 min. of penetration, an infective bulb is formed inside the trapped nematode (*Shepherd* 1955), at which time movements of the nematode ceased completely. Apparently nets in *A. oligospora* secrete a nematotoxin which paralyses or kills trapped nematodes (*Olthof & Estey* 1963). From this bulb, which reaches a size about half the diameter of the nematode, trophic hyphae grow out and extend throughout the body of the nematode (Fig. 1). After 6 h the whole

body of the *P. redivivus* was filled with hyphae (*Nordbring-Hertz & Stålhammer-Carlemalm* 1978).

Nansen et al. (1986) compared the predacious activity of *A. oligospora* on the preparasitic stages of the cattle nematode parasite *Cooperia oncophora* and the free-living soil nematode *P. redivivus*. The first and second larval stages of *C. oncophora* and *P. redivivus* were killed rapidly; in contrast, third-stage parasite larvae wriggled in the traps for many hours. This may be because it is time-consuming for *A. oligospora* to penetrate the outer cuticle of the previous moult which protects both *C. oncophora* and *O. ostertagi* larvae in their third and infective stage until infection of the host takes place.

Generally, morphogenic processes are highly influenced by environmental factors. The series of experiments presented in this paper was performed to investigate the influences of temperature, concentrations of nematodes, oxygen tensions, light, and nutrient levels, on net formation in *A. oligospora* induced by infective larvae of the cattle nematode parasite *O. ostertagi*. The trapping capability of nets of increasing age was investigated using the free-living nematode *P. redivivus*.

Materials and methods

General experimental conditions
The fungi were grown on diluted Corn Meal Agar (Difco) (CMA 1:10) (*Lysek & Nordbring-Hertz* 1981): Temperature = 20°C; relative humidity = 90–100 %; pH = 6,5; normal atmosphere (21 % O_2 (v/v)); and darkness. Only deviations from these conditions are mentioned in the following descriptions of single experiments.

Saprophytic growth rate of different species of Arthrobotrys

This experiment was performed in large Petri dishes (diam.: 8.5 cm). Five *Arthrobotrys* species (*A. oligospora* (ATCC 24927), *A. musiformis, A. tortor* (4-182-3-INRA), *A. conoides* (CBS 109.52), and *A. arthrobotryoides* (CBS 118.54)) were inoculated in the centre of the dishes. Three Petri dishes with each species were placed at each of the following constant temperatures: 5°, 10°, 15°, 20°, 25°, 30°, and 35°C. The radii of the colonies were measured after 3 days, and the average saprophytic growth rate of each fungal species at each temperature was calculated in mm/3 days.

The influence of different factors on the induction of trapping nets in Arthrobotrys oligospora

These experimentswere performed in small Petri dishes (diam.: 3.5 cm; area: 9.6 cm²). The predacious fungus *A. oligospora* (ATCC 24927) was inoculated in the centre of the Petri dishes. One week later, when the fungus covered the whole surface, nets were induced by adding infective *O. ostertagi* larvae in 3 drops of non-sterile water to each culture. Infective *O. ostertagi* larvae had been kept in shallow water at 5°C for 1 week to 3 months. Immediately before use, the larvae were washed 3 times in tap water, using centrifugation followed by decantation of the supernatant. All larvae were living and motile when added to the fungal cultures.

After a period of some days, the number of trapping nets and the number of loops per net were determined. The number of nets were counted on 5 randomly selected areas of 3.14 mm² on the surface of each Petri dish situated between the centre and the rim of the dishes. The number of loops per net was counted on 2 randomly selected nets in each area. The average number of nets per cm² and the average number of loops per net could then be calculated for each treatment.

Net induction at different temperatures. Cultures of *A. oligospora* were induced by 50 infective *O. ostertagi* larvae per cm² at each of the following constant temperatures: 5°, 10°, 15°, 20°, 25°, 30°, and 35°C. Three petri dishes were incubated at each temperature. The numbers of nets and loops were counted after 3 days of contact with the parasite larvae.

Net induction at different concentrations of parasite larvae. Cultures of *A. oligospora,* grown on CMA 1:10 containing 0.02 % tetracycling chloride, were induced by 10, 100, 300, 600, and 1,000 infective *O. ostertagi* larvae per cm². The supernatant from the last larval washing was used in control Petri dishes without larvae. Tetracycline chloride was added to the medium to suppress bacterial growth, especially in dishes with high larval concentrations, as the larvae were non-sterile. For each larval concentration, 2 Petri dishes were incubated at 20°C for 5 days, after which time nets and loops were counted.

Net induction at different oxygen tensions (v/v). Cultures of *A. oligospora* were induced by 50 infective *O. ostertagi* larvae per cm². Three Petri dishes were placed in each of three 2.5-litre containers. In the first container O_2 was replaced by CO_2 by Anaerocult® A (Merck), in the second there was a normal atmosphere (21 % O_2), and in the third there was a pure O_2 atmosphere. The pressure was 750–770 mm Hg. The containers were incubated at 20°C for 2 days, after which time the numbers of nets and loops per net were countered. During the follow-

ing days all categories of Petri dishes were observed at normal atmosphere (21 % O_2).

Net induction in light and darkness. Cultures of *A. oligospora* were induced by 50 infective *O. ostertagi* larvae per cm^2, and incubated at 20°C. Six Petri dishes were placed under constant electric light at 500 Lux, while 6 other dishes were incubated in the dark. The trial was finished 7 days later by counting nets and loops per net.

Net induction at different concentrations of corn meal in the medium. The predacious fungus *A. oligospora* was cultivated on agar containing an increasing amount of corn meal per litre (0.0, 0.1, 0.2, 0.4, 1.0, and 2.0 g corn meal/l). The medium was a mixture of Bacto Agar (Difco) and Corn Meal Agar (Difco) with a constant amount of 15 g agar per litre (1.5 %) at each medium concentration. One week old *A. oligospora* cultures were induced by 50 infective *O. ostertagi* larvae per cm^2. Three cultures of each category were incubated at 20°C for 3 days, after which time the numbers of nets and loops per net were determined.

The influence of age and temperature on the activity of nets in Arthrobotrys oligospora
This experiment was performed in small Petri dishes (diam.: 3.5 cm; area: 9.6 cm^2) on CMA 1:10 containing 0.02 % tetracycline chloride. Tetracycline chloride was added to the medium to suppress bacterial growth during the long experimental period of 7 weeks. One week old cultures of *A. oligospora* were induced by 60 non-sterile individuals of *P. redivivus* per cm^2 at 20°C for 2 days. At that time, nets in excess were present in each culture (approx. 600 nets per cm^2).
The experiment started on day 2 by placing

a number of these cultures at the following temperatures: 5°, 10°, 15°, 20°, 25°, 30°, and 35°C. At intervals (1, 2, 4, and 7 weeks after the start of the experiment) 3 Petri dishes from each temperature were exposed to a known number (between 40 and 70 individuals) of *P. redivivus* per cm^2 for 2 h. No new trapping nets were produced during this period. Not-trapped nematodes were isolated from the dishes by Baermannization for 16 h according to *Jørgensen & Madsen* (1982). Control Petri dishes without *A. oligospora* were treated in the same way. The activity of the nets was calculated as the mean percentage of trapped *P. redivivus* in Petri dishes inoculated with the fungus, in proportion to those in control dishes.

Results
Saprophytic growth rate of different species of Arthrobotrys
As shown in Table 1, the tested *Arthrobotrys* species had growth rate optima at about 20° or 25°C. The fungi *A. oligospora, A. musiformis,* and *A. tortor* are fast-growing species. *A. oligospora* and *A tortor* grow well in the interval from 15° to 30°C. *A. musiformis* grows well between 15° and 25°C, but no growth was observed at 30°C. All species, except *A. oligospora,* grew slowly at 5°C, but none of the species showed any activity at 35°C.

The influence of different factors on the induction of trapping nets in Arthrobotrys oligospora
Net induction at different temperatures. Temperature had a significant influence on the production of trapping nets in *A. oligospora* when the fungus was induced by 50 infective *O. ostertagi* larvae per cm^2 (Fig. 2).

Table 1. The saprophytic growth rate in mm/3 days of 5 different *Arthrobotrys* species at different temperatures.

Arthrobotrys species	Temperature (°C)						
	5	10	15	20	25	30	35
A. oligospora	0.0	1.7	11.7	19.3	13.0	6.0	0.0
A. musiformis	0.3	2.3	9.7	17.0	20.0	0.0	0.0
A. tortor	0.3	0.8	5.3	13.3	11.3	11.3	0.0
A. conoides	0.3	1.3	3.7	5.7	6.0	1.2	0.0
A. arthrobotryoides	0.3	0.8	2.3	5.3	4.0	0.0	0.0

A maximum of 382 nets per cm^2 was induced at 20°C, but the fungus did not respond to larvae at 5°, 30°, or 35°C during the experimental period of 3 days. The nets were composed of 2–4 loops.

Net induction at different concentrations of parasite larvae. In the interval between 0 and 100 infective *O. ostertagi* larvae per cm^2, increasing numbers of nets per cm^2 were produced in *A. oligospora* with increasing numbers of larvae (Fig. 3). The supernatant from larval cultures in control Petri dishes did not induce any nets at all. But when *A. oligospora* was induced by more

than 100 infective larvae per cm^2, 1,300–1,8000 nets per cm^2 were induced. Even at a concentration of 1,000 infective larvae per cm^2, all parasites were trapped, and still some nets were not occupied with larvae, as was also the case at the lower larval concentrations. At the high larval concentrations, more than one larva was trapped in many nets, which was possible as 4–8 loops were produced in each net.

Net induction at different oxygen tensions. The results presented in Table 2 show that *A. oligospora* does not produce nets under anaerobic conditions (0 % O$_2$). In
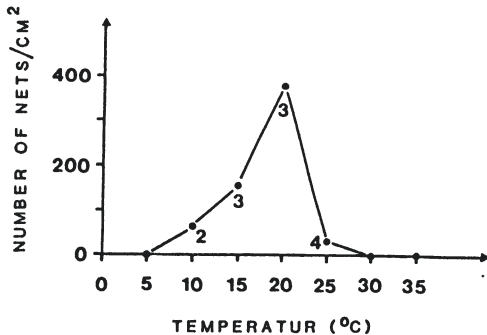

Figure 2. The average number of trapping nets/cm^2 in *Arthrobotrys oligospora* when the fungus was induced by 50 infective *Ostertagi ostertagi* larvae/cm^2 in 3 days at different temperatures. Numbers under the curve refer to the average number of loops per net.
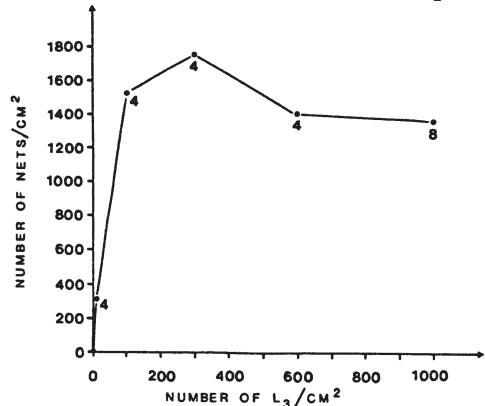

Figure 3. The average number of trapping nets/cm^2 in *Arthrobotrys oligospora* when the fungus was induced by increasing numbers of infective *Ostertagia ostertagi* larvae (L$_3$)/cm^2 in 5 days at 20°C. Numbers under the curve refer to the average number of loops per net.

Table 2. The average number of trapping nets/ cm² in *Arthrobotrys oligospora,* when the fungus was induced by 50 infective *Ostertagı ostertagı* larvae/cm² in 2 days at different oxygen tensions (v/v). In brackets are shown the average number of loops per net.

Anaerobıc atmosphere (0 % O₂ and 21 % CO₂)	Normal atmosphere (21 % O₂ and 0 03 % CO₂)	Pure oxygen atmosphere (100 % O₂ and 0 % CO₂)
0 (0)	651 (3)	641 (3)

normal (21 % O_2) and pure oxygen atmosphere (100 % O_2) the fungus produced nets at normal rate in comparable numbers, and all larvae were trapped and killed. The infective larvae survived anaerobic conditions for 2 days and so did the fungus, as it produced nets when transferred to a normal atmosphere.

Net induction in light and darkness. As shown in Table 3, light had a negative effect on the numbers of nets induced in *A. oligospora.* In the present experiment only one loop was produced in each net.

Net induction at different concentrations of corn meal in the medium. The results in Fig. 4 indicate that net induction in *A. oligospora* was optimal at a concentration of 0.2 g corn meal per litre. This concentration is identical to the diluted Corn Meal Agar (CMA 1:10) which was generally

Table 3. The average number of trapping nets/ cm²in *Arthrobotrys oligospora,* when the fungus was induced by 50 infective *Ostertagıa ostertagı* larvae/cm² in 7 days under electric light at 500 Lux or ın darkness. In brackets are shown the average number of loops per net.

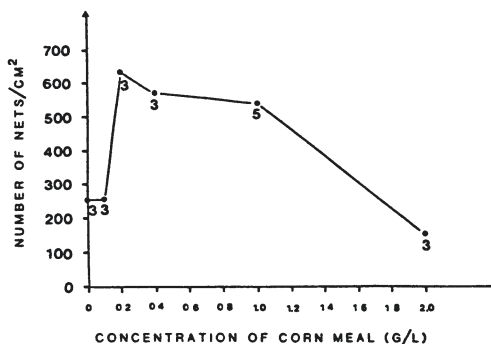| Lıght	Darkness
191 (1)	478 (1)

Figure 4. The average number of trapping nets/cm² in *Arthrobotrys oligospora* when the fungus was induced by 50 infective *Ostertagia ostertagı* larvae/cm² in 3 days. The growth medium contained different amounts of corn meal. Numbers under the curve refer to the average number of loops per net.

used. On increasing concentrations of corn meal the fungus produced a mycelium of increasing density. Nevertheless, *A. oligospora* produced significantly fewer nets per cm² at the highest mycelial density on 2 g corn meal per litre than at low mycelial density on 0.2 g corn meal per litre.

The influence of age and temperature on the activity of nets in Arthrobotrys oligospora
In Fig. 5 it appears that a proportion of the trapping nets in *A. oligospora* will maintain their trapping potential for more than 7 weeks when the temperature is below 25°C. Traps kept at 30° and 35°C lose their trapping capability after 7 and 4 weeks, respectively. But this may partly be due to drying-out of the agar medium at these high temperatures.

Discussion
As pointed out by *Eren & Pramer* (1978), both growth and trap formation are prerequisites to nematode capture. Experiments have shown that conidia of the predacious
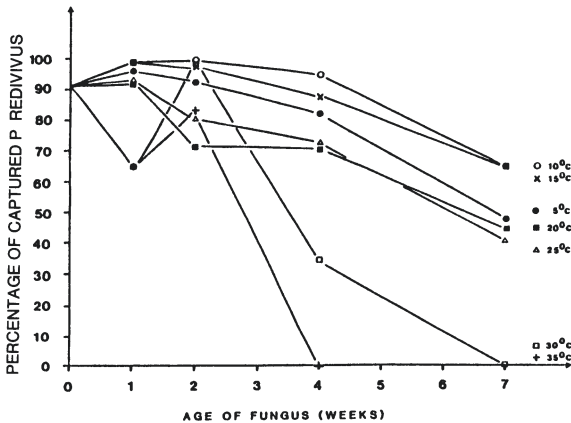
Figure 5. The effect of temperature on the average percentage of captured *Panagrellus redivivus* added to *Arthrobotrys oligospora* culture of different age.

fungus *A. oligospora,* when added to cattle faeces, resulted in a reduction of infective larvae og *Cooperia* spp. (*Grønvold et al* 1985) and *Ostertagia ostertagi* (*Grønvold et al.* 1988). Moreover, the trapping effect in faeces was shown to depend on the level of inoculation. This may be explained in two different ways. First, results from the present experiments have shown that *A. oligospora* has a high saprophytic growth rate in pure cultures. In competition with other microorganisms in the cow pat, saprophytic growth may be suppressed by fungistasis. In antagonistic environments germinating conidia may form traps immediately with minimal hyphal extension (*Mankau* 1962). In such situations it is obvious that the trapping effect depends on the inoculum level. However, in contact with other microorganisms, only a small percentage of germinating *A. oligospora* conidia quickly gave rise to trapping organs (*Cooke* 1964). Secondly, it is also possible that a high inoculum level is necessary for *A. oligospora* to grow successfully in competition with other micro-

organisms, as pointed out by *Cooke* (1963). If this is the case, a high inoculum level will ensure that the fungus is able to colonize the faeces with a mycelium on which nets may be induced in high numbers. Above all, the present experiments have been dealing with factors influencing induction of trapping nets on a well-established *A. oligospora* mycelium.

Contact with nematodes was necessary for induction of trapping nets on no more than 1 week old vegetative hyphae in this strain of *A. oligospora.* Spontaneous trap formation was never seen under the present experimental conditions. Furthermore, non-sterile supernatants from the nematode cultures were not able to induce nets.

When induced by infective *O. ostertagi* larvae, *A. oligospora* had a high trapping potential. Maximum of nets was produced at 20°C, at which temperature nets in surplus were induced at larval concentrations up to 1,000 larvae per cm^2. As each loop in a net is a potential trap, the trapping capacity of *A. oligospora* was even higher than indicated by the number of nets, because each net normally consisted of several loops.

The present experiment indicates that trap formation in *A. oligospora* is an aerobic process. But it is also possible that the replacement of O_2 by CO_2 in the experimentally created anaerobic atmosphere had a negative effect on net induction. *Nordbring-Hertz & Odham* (1980) have shown that increased CO_2 in air to 5–10 % (v/v) totally inhibited trap formation. The trapping capability of *A. oligospora* is probably restricted to surface areas of the cow pats with high O_2 and low CO_2 tensions. In this part of the cow pats, infective *O. ostertagi* larvae may also be found in high concentrations (*Rose* 1961). On the surface of the cow pats net induction may be suppressed to a certain degree by exposure to light, as shown by the present ex-

periment. On the other hand light, whether continuous, intermittent, or absent, has little influence on the saprophytic growth rate (*Olthof & Estey* 1965).

The composition of the medium has an important influence on the saprophytic growth and the net-forming capability in *A. oligospora*. Nematodes alone cannot provide the sole energy for *A. oligospora* (*Hayes & Blackburn* 1966). In their work, *Hayes & Blackburn* (1966) showed that the vitamins biotine, thiamine, and p-aminobenzoic acid, stimulated saprophytic growth but had little effect on predacity. Nitrogen supplied as nitrate, nitrite, or urea supported both growth and predacity in *A digospora*. *Hayes & Blackburn* (1966) also found that a range of carbohydrates was able to support saprophytic growth in *A. oligospora*. However, extensive mycelial growth was not always correlated with high predacity. On some carbohydrates *A oligospora* produced little mycelium, but predacity was high. *Nordbring-Hertz* (1973) found that on low-nutrient media phenylalanyl-valine induced trap formation in *A oligospora,* but the effect was greatly reduced or annulled in a nutrient-rich medium or on water agar. These informations correspond with the present results where maximum numbers of nets were induced at a relatively low concentration of corn meal which supported a relatively sparse mycelium. Based on the above-mentioned results it is possible that the nutrient level in cow pats are not always optimal for net induction.

The long survival of trapping nets at high humidity and temperatures below 25°C is surprising, as vegetative hyphae were observed to collapse within a couple of weeks. The present results indicate that capture of infective parasite larvae in the cow pats may continue for a long time under suitable conditions. As parasite nematode larvae do not multiply, the only result of predacious activity is a reduction of the population of infective larvae. Furthermore, old nets may act as survival structures.

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Sammendrag

Induktion of nematod-fangende organer hos rovsvampen Arthrobotrys oligospora (Hyphomycetales) ved hjælp af infektive larver af Ostertagia ostertagi (Trichostrongylidae)

Ved en serie laboratorie-forsøg blev indflydelsen af temperatur, koncentration af nematoder, ilt-tension, lys og substratstyrke målt som antallet af nematod-fangende svampe-net, der kunne induceres hos rovsvampen Arthrobotrys oligospora. Når

rovsvampen blev induceret med infektive *Ostertagia ostertagi* larver fandtes en maksimal produktion af net ved 20°C. ved denne temperatur dannede rovsvampen net i overskud ved koncentrationer af larver op til 1.000 larver pr. cm². *A. oligospora* dannede ikke net under anaerobe forhold i en atmosfære indeholdende 21 % CO_2 (rumfang/Rumfang), og induktionen af net blev undertrykt til en vis grad, når rovsvampen var udsat for lys. Mediets sammensætning havde en afgørende indflydelse på væksten og net-dannelsen hos *A oligospora,* idet en maksimal produktion af net kunne induceres ved en relativ lav koncentration af maj mel, som gav anledning til et relativt sparsomt mycelium. En del af nettene hos *A oligospora* bevarede deres fangst-potentiale i mere end 7 uger ved temperaturer lavere end 25°C. Induktion af nematod-fangende organer *A oligospora* diskuteres i relation til kontrol af infektive parasitiske nematodlarver i kokasser.