Interrelationships between fungal egg parasitism in *Heterodera schachtii* (Schmidt) and nematode population density

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SUMMARY

The results of two years of field experiments demonstrated a weak correlation between *Heterodera schachtii* population density and the proportion of eggs parasitized by fungi. More relevant data were obtained with a bioassay, designed to determine potential parasitic activity in soil, than with direct plating of eggs collected from cysts in soil samples. The results showed that the actual level of fungal parasitism of eggs or the parasitic potential at a specific time was independent of nematode density in the field as well as from the density of newly formed nematode populations produced in the bioassay containers. Furthermore, inoculation with large amounts of cysts containing eggs did not increase parasitic activity. Most fungal egg parasites are not dependent on nematode eggs for nutrition but are facultative parasites that may prefer the saprophytic as compared to parasitic mode of nutrition.

RÉSUMÉ

*Relations entre le parasitisme des œufs d'*Heterodera schachtii *par les champignons et le taux de population du nématode*

Les résultats obtenus après deux années d'expérimentation en champ montrent une corrélation faible entre le taux de population d'*Heterodera schachtii* et la proportion des œufs parasités par les champignons. Un essai en conteneurs visant à déterminer l'activité parasitaire potentielle du sol a fourni des données plus significatives que l'examen direct des œufs provenant de kystes extraits du sol. Ces résultats montrent que le niveau réel du parasitisme fongique des œufs, ou la potentialité parasitaire, à un moment donné, sont indépendants tant du taux de nématodes au champ que du niveau de la population des nématodes nouvellement formés dans le cas de l'essai en conteneurs. De plus, l'inoculation de quantités importantes de kystes contenant des œufs n'augmente pas l'activité parasitaire. De nombreux champignons parasites d'œufs ne dépendent pas en effet des nématodes pour leur nutrition mais sont des parasites facultatifs qui peuvent adopter un type de nutrition saprophytique.

Plant parasitic nematodes along with their hosts are not isolated in the ecological system, but are strongly influenced by antagonists, parasites and pathogens. The degree of dependence of a parasite on its host determines whether it is classified as obligate or facultative. Examples of obligate fungal parasites of nematodes are *Catenaria auxiliaris* (Tribe, 1977) and *Nematophthora gynophila* (Kerry, 1974), both parasites of young females of cyst nematodes. Endoparasitic fungi that parasitize mobile stages also are often obligate parasites.

Conversely, nematode trapping and egg parasitic fungi can survive saprophytically and are considered facultative parasites. This attribute presupposes the lack of dependence on the presence of nematodes as a nutrient source. It would be logical, however, to hypothesize that by increasing cyst density in soil, coincidental contact with the host is more likely, resulting in increased rates of parasitism. Furthermore, the question arises as to whether an increased nutrient level (host density) affects the parasitic potential of the fungi.

In this study we investigated levels of parasitism in field populations of *Heterodera schachtii* using a direct plating method (Kerry & Crump, 1977) and parasitism of newly formed eggs using a bioassay in an attempt to determine : *i)* whether a correlation exists between fungal egg parasitism or potential parasitic activity and nematode density in the field and *ii)* whether the fungi gain an ecological advantage when nematode density increases.

Material and methods

FUNGAL EGG PARASITISM IN FIELD POPULATIONS AS INFLUENCED BY INCREASING NEMATODE DENSITY

In 1986 and 1987, soil samples were taken from two fields at different dates to a depth of 0-25 cm. The cropping system in the experimental field at Bonn-Poppelsdorf was sugarbeet — winter wheat — winter

barley and in the experimental field at Dikopshof sugarbeet — winter wheat — winter wheat, respectively. Rape *Brassica napus* var. *napus* L. (cv. Akela and Willi) and *H. schachtii* resistant mustard *Sinapis alba* L. (cv. Emergo and Maxi) were planted as breakcrops after the cereals. Sixteen soil cores were removed from the 2 × 4 m plots at Bonn-Poppelsdorf and 18 from 3 × 9 m plots at Dikopshof. The samples for each plot were mixed and the cysts from 2 × 250 g soil extracted using a MEKU high pressure elutriator (MEKU Wennigsen, FRG). The cysts on the 250 µm sieve were cleaned by floatation in $MgSO_4$ (> 1.28 g/ml), hand picked and the egg and juvenile density/sample determined. Fungal egg parasitism was investigated on water agar by plating out the egg suspensions (Nicolay & Sikora, 1989).

POTENTIAL FUNGAL EGG PARASITISM AS INFLUENCED BY INCREASING NEMATODE DENSITY

Soil samples were tested in a bioassay using the soil fractioning technique (Nicolay & Sikora, 1989). The soil substrate produced with this technique contains the natural soil flora and fauna as well as the eggs and juveniles separated from the original cysts in the soil sample. Fungal parasitism in the next *H. schachtii* generation formed after approximately eight weeks is then determined.

The relationships between the rate of parasitism and the initial density of cysts, eggs and juveniles/100 g soil or eggs and juveniles/cyst were calculated on a per replicate basis as described by Nicolay and Sikora (1989). Furthermore, the relationships between rate of parasitism and density of the newly formed population in the respective bioassay container were calculated.

POTENTIAL FUNGAL EGG PARASITISM AS INFLUENCED BY INCREASING NEMATODE DENSITY IN ARTIFICIALLY INOCULATED SOIL

Cysts were extracted from a greenhouse culture maintained on sterilized quartz sand and the average number of eggs and juveniles/cyst determined by examination of 3 × 25 cysts. The level of egg parasitism in the cysts varied from 0-2 % and was therefore, negligible at the beginning of the experiment. Increasing numbers of cysts were then added to an unsterilized field soil, the soil mixed thoroughly with a hand-mixer and 100 g of this soil added to 7 cm diam. plastic pots. The soil was taken from a cyst nematode uninfested field and inoculated with 0, 500, 1000, 2000, 4000, 6000, 10 000 or 15 000 eggs and juveniles in cysts. The spectrum of possible egg parasitic fungi was not measured.

The pots were placed into depressions in sand and maintained for 12 weeks at 21 °C in an incubator. Fungal egg parasitism was then determined using the soil fractioning technique (Nicolay & Sikora, 1989). The experiment was repeated twice.

Results

FUNGAL EGG PARASITISM IN FIELD POPULATIONS AS INFLUENCED BY INCREASING NEMATODE DENSITY

A negative correlation between the number of *H. schachtii* eggs and juveniles/100 g soil and their levels of parasitism was consistently detected in the experimental field at Bonn-Poppelsdorf (Table 1) and in the majority of cases in the experimental field at Dikopshof (Table 2). Parasitism decreased with increasing population density, with significant results sometimes obtained even at small correlation coefficients due to the large number of replicates involved. However, the generally low correlation coefficients indicated the presence of a weak relationship between the two factors. Similar weak and negative correlations were detected in the majority of cases between parasitism and cyst density as well as eggs and juveniles/cyst (Tables 1, 2).

The rates of parasitism at the individual sampling dates ranged between 0.8 and 73 % (Bonn-Poppelsdorf) and 0 and 71.5 % (Dikopshof) while the number of eggs and juveniles/100 g soil ranged from 48 - 5350 and 5 - 7335, respectively. The correlation coefficients, therefore, were determined from a highly variable data base.

At Dikopshof the rate of parasitism was highest directly after sugarbeet in 1987 and decreased with increasing time after the sugarbeet harvest. It could be assumed, therefore, that the rate of parasitism decreased with decreasing population density. The correlation coefficient of — 0.06 calculated for 133 samples in 1987, however, did not support this assumption. The rate of parasitism in the Bonn-Poppelsdorf field, conversely, did not decrease with time after sugarbeet harvest.

POTENTIAL FUNGAL EGG PARASITISM AS INFLUENCED BY INCREASING NEMATODE DENSITY

Influence of the newly formed population density on rate of parasitism

Although statistically significant correlations between parasitism of newly formed eggs and the density of newly formed eggs were detected, the correlation coefficients for the experimental field at Bonn-Poppelsdorf were low (Table 3). In addition, no correlation was detected between the level of parasitism and the density of newly formed cysts. Parasitism decreased as cyst content increased and, although the relationship was weak, it was statistically significant.

There was no correlation between parasitism and egg or cyst density in the pot in the samples from Dikopshof, regardless of the sampling date (Table 4).

The levels of parasitism for each sampling date ranged between 0 - 67 % (Bonn-Poppelsdorf) or 0 - 93 %

Table 1

Correlation (r-values) between number of *Heterodera schachtii* cysts, eggs + juveniles/100 g soil or cyst contents, respectively, in the field and proportion of parasitized eggs in the field, Bonn-Poppelsdorf, 1986-1987.

Precrop	*Sampling date*	*Eggs + juveniles*	*Cysts*	*Eggs + juv./cyst*	*n*
SB	before SB	— 0.23 *	— 0.03 ns	0.00 ns	75
SB	after SB	— 0.32 **	0.05 ns	— 0.33 **	75
WB	before IC	— 0.28 *	— 0.11 ns	— 0.28 *	75
WB	after IC	— 0.08 ns	— 0.04 ns	— 0.11 ns	75
WW	before IC	— 0.50 *	0.26 ns	— 0.55 *	16
WW	after IC	— 0.49 ns	— 0.12 ns	— 0.48 ns	16
SB	b + a SB	— 0.21 *	0.01 ns	— 0.13 ns	150
WB	b + a IC	— 0.13 ns	— 0.05 ns	— 0.36 **	150
WW	b + a IC	— 0.44 *	— 0.01 ns	— 0.55 **	32
Total	value 1986	— 0.28 **	— 0.11 *	— 0.22 **	332
SB	in WW	— 0.37 **	0.20 ns	— 0.38 **	75
WB/IC	before SB	— 0.21 ns	0.03 ns	— 0.28 *	75
Total	value 1987	0.01 ns	— 0.30 **	— 0.14 ns	150

SB = sugarbeet; WB = winter barley; WW = winter wheat; IC = intercrop; b + a = before + after; ns = not significant; * (**) = significant at P ≤ 5 (1) %.

Table 2

Correlation (r-values) between number of *Heterodera schachtii* cysts, eggs + juveniles/100 g soil or cyst contents, respectively, in the field and proportion of parasitized eggs in the field, Dikopshof, 1986-1987.

Precrop	*Sampling date*	*Eggs + juveniles*	*Cysts*	*Eggs + juv./cyst*	*n*
WW2	before SB	— 0.57 *	— 0.57 *	0.26 ns	16
WW2	after SB	— 0.27 ns	0.43 ns	— 0.43 ns	20
SB	in WW1	— 0.38 ns	— 0.25 ns	— 0.28 ns	20
WW1	before IC	0.00 ns	0.31 ns	— 0.33 ns	18
WW1	after IC	— 0.24 ns	0.14 ns	— 0.33 ns	19
WW2	before IC	0.32 ns	0.25 ns	0.23 ns	19
WW2	after IC	— 0.09 ns	— 0.12 ns	0.07 ns	20
WW2	b + a SB	— 0.13 ns	0.34 *	0.22 ns	36
SB/	b + a IC +				
WW1	in WW1	0.06 ns	0.13 ns	0.00 ns	57
WW2	b + a IC	0.09 ns	— 0.01 ns	0.19 ns	39
Total	value 1986	— 0.12 ns	— 0.19 *	0.05 ns	132
WW2	before SB	— 0.16 ns	0.11 ns	— 0.14 ns	20
WW2	after SB	— 0.13 ns	0.13 ns	— 0.07 ns	20
SB	in WW1	— 0.43 ns	— 0.40 ns	0.00 ns	20
WW1	before IC	— 0.54 *	— 0.57 **	— 0.08 ns	20
WW1	after IC	— 0.55 *	— 0.58 **	— 0.03 ns	20
WW2	before IC	0.26 ns	0.23 ns	— 0.02 ns	20
WW2	after IC	— 0.20 ns	0.12 ns	— 0.39 ns	13
WW2	b + a SB	0.21 ns	0.06 ns	0.24 ns	40
SB/	b + a IC +				
WW1	in WW1	— 0.39 **	— 0.06 *	— 0.10 ns	60
WW2	b + a IC	0.08 ns	— 0.19 ns	— 0.08 ns	33
Total	value 1987	— 0.06 ns	— 0.10 ns	— 0.15 ns	133

SB = sugarbeet; WB1 (2) = first (second) winter wheat after SB; IC = intercrop; b + a = before + after; ns = not significant; * (**) = significant at P ≤ 5 (1) %.

Table 3

Correlation (r-values) between number of *Heterodera schachtii* cysts, eggs + juveniles/pot or cyst contents, respectively, in the bioassay and proportion of parasitized newly formed eggs, Bonn-Poppelsdorf, 1986-1987.

Precrop	*Sampling date*	*Eggs + juveniles*	*Cysts*	*Eggs + juv./cyst*	*n*
WB	after IC	— 0.51 *	— 0.32 ns	— 0.62 **	20
SB	after SB	— 0.16 ns	0.14 ns	— 0.28 **	100
Total	value 1986	— 0.17 ns	— 0.15 ns	— 0.30 **	120
WB/IC	before SB	— 0.29 **	— 0.17 ns	— 0.42 **	119
WB/IC	after SB	— 0.16 ns	0.01 ns	— 0.29 **	136
Total	value 1987	— 0.23 **	— 0.10 ns	— 0.34 **	255

SB = sugarbeet; WB = winter barley; IC = intercrop; ns = not significant; * (**) = significant at P ≤ 5 (1) %.

Table 4

Correlation (r-values) between number of *Heterodera schachtii* cysts, eggs + juveniles/pot or cyst contents, respectively, in the bioassay and proportion of parasitized newly formed eggs, Dikopshof, 1986-1987.

Precrop	*Sampling date*	*Eggs + juveniles*	*Cysts*	*Eggs + juv./cyst*	*n*
WW2	before IC	— 0.26 ns	— 0.06 ns	— 0.43 *	24
WW2	after IC	— 0.20 ns	— 0.14 ns	— 0.19 ns	24
WW2/IC	after SB	0.24 ns	0.32 ns	— 0.18 ns	24
Total	value 1986	— 0.04 ns	— 0.19 ns	— 0.24 *	72
WW2/IC	before SB	— 0.11 ns	—0.18 ns	— 0.22 ns	19
WW2/IC	after SB	0.04 ns	0.32 ns	— 0.23 ns	23
WW1	before IC	— 0.03 ns	0.07 ns	— 0.06 ns	21
WW1	after IC	0.15 ns	0.28 ns	— 0.03 ns	23
WW2	before IC	0.32 ns	0.17 ns	0.21 ns	22
WW2	after IC	0.19 ns	0.21 ns	0.05 ns	21
WW2/IC	b + a SB	0.00 ns	0.16 ns	— 0.22 ns	42
WW1	b + a IC	0.00 ns	0.09 ns	0.01 ns	44
WW2	b + a IC	0.05 ns	— 0.03 ns	0.06 ns	43
Total	value 1987	0.06 ns	0.19 *	— 0.24 *	129

SB = sugarbeet; WW1 (2) = first (second) winter wheat after SB; IC = intercrop; b + a = before + after; ns = not significant; * = significant at P ≤ 5 %.

(Dikopshof), the number of eggs and juveniles/pot between 60 - 49 800 or 170 - 38 700, respectively. The results, therefore, are based on a wide array of population densities and levels of parasitism.

Influence of the population density in the field on rate of parasitism

A significant negative correlation was observed between the number of eggs and juveniles in the field samples and the rate of parasitism of the newly formed eggs for one in three sampling dates at Bonn-Poppelsdorf and for two in nine sampling dates at Dikopshof, respectively (Tables 5, 6). The correlations in general were negative indicating a decrease in parasitic activity with increasing nematode density. This negative correlation was detected at Bonn-Poppelsdorf and in one case at Dikopshof after sugarbeet. For 75 % of the sampling dates, however, there was no significant correlation

Table 5

Correlation (r-values) between number of *Heterodera schachtii* cysts, eggs + juveniles/100 g soil or cyst contents, respectively, in the field and proportion of parasitized newly formed eggs in the bioassay, Bonn-Poppelsdorf, 1986-1987.

Precrop	*Sampling date*	*Eggs + juveniles*	*Cysts*	*Eggs + juv./cyst*	*n*
WB	before IC	− 0.28 ns	− 0.20 ns	− 0.21 ns	20
SB	after SB	− 0.42 *	0.27 ns	− 0.47 **	30
Total	value 1986	− 0.21 ns	0.11 ns	0.29 *	50
WB/IC	before SB 1987	0.00 ns	− 0.18 ns	0.13 ns	35

SB = sugarbeet; WB = winter barley; IC = intercrop b + a = before + after; ns = not significant; * (**) = significant at P ≤ 5 (1) %.

Table 6

Correlation (r-values) between number of *Heterodera schachtii* cysts, eggs + juveniles/100 g soil or cyst contents, respectively, in the field and proportion of parasitized newly formed eggs in the bioassay, Dikopshof, 1986-1987.

Precrop	*Sampling date*	*Eggs + juveniles*	*Cysts*	*Eggs + juv./cyst*	*n*
WW2	before IC	− 0.48 ns	− 0.15 ns	− 0.61 ns	6
WW2	after IC	− 0.54 ns	− 0.21 ns	− 0.30 ns	6
WW2/IC	after SB	− 0.95 **	− 0.91 *	− 0.69 ns	6
Total	value 1986	0.20 ns	0.21 ns	0.48 *	18
WW2/IC	before SB	− 0.82 *	− 0.34 ns	− 0.68 ns	6
WW2/IC	after SB	− 0.18 ns	− 0.45 ns	0.20 ns	6
WW1	before IC	0.30 ns	0.63 ns	− 0.54 ns	6
WW1	after IC	0.10 ns	0.19 ns	0.09 ns	6
WW2	before IC	0.50 ns	− 0.37 ns	0.39 ns	6
WW2	after IC	− 0.05 ns	− 0.59 ns	0.78 ns	6
WW2/IC	b + a SB	− 0.58 *	− 0.63 *	− 0.52 ns	12
WW1	b + a IC	0.07 ns	0.28 ns	− 0.35 ns	12
WW2	b + a IC	0.00 ns	− 0.45 ns	0.37 ns	12
Total	value 1987	− 0.16 ns	− 0.05 ns	− 0.19 ns	36

SB = sugarbeet; WW1 (2) = first (second) winter wheat after SB; IC = intercrop; b + a = before + after; ns = not significant; * (**) = significant at P ≤ 5 (1) %.

between population density in the field samples and the rate of parasitism of newly formed eggs in the bioassay.

A clear relationship between the number of eggs and juveniles/cyst and the rate of parasitism also was not detected (Tables 5, 6).

The level of parasitism for each sampling date ranged between 1 - 41 % and 1 - 58 % and the number of eggs and juveniles/100 g soil of the selected plots between 48 - 3081 and 9 - 7335 for Bonn-Poppelsdorf and Dikopshof, respectively.

Potential fungal egg parasitism as influenced by increasing nematode density in artificially inoculated soil

No correlation was found between parasitic activity and nematode density after 12 weeks incubation. Nonsignificant correlation coefficients of r = 0.26 and r = 0.26 demonstrated the lack of a correlation between parasitism in the newly formed generation and the number of inoculated eggs and juveniles or cysts.

The levels of parasitism averaged 11 % and ranged between 4 - 18 %. The average density of newly formed

eggs and juveniles was 38 495 (4005 — 83 025), of cysts 144 (45 — 320) per pot. The average cyst content was 255 (89 — 399) eggs and juveniles/cyst. A relationship between the rate of parasitism and these values could not be detected (r = 0.02, 0.01 and — 0.04, respectively).

The results of both tests were comparable, therefore, the data were combined.

Discussion

A strong correlation between rate of parasitism and *H. schachtii* population density in field samples could not be detected. In the vast majority of cases it was negative in both experimental fields. The data demonstrated that parasitism decreased with increasing nematode density. However, since the correlation coefficients in general were very low the relationship between the two parameters should be considered weak. There was no correlation between the number of eggs/g soil and the level of fungal parasitism in studies of Nigh, Thomason and Van Gundy (1980) involving the determination of rates of parasitism in 32 fields with different nematode densities.

Whereas, parasitism in the Bonn-Poppelsdorf field remained equally high at different sampling dates, in the field at Dikopshof parasitism decreased with time after sugarbeet harvest. Schlang, Steudel and Müller (1988) observed high levels of egg parasitism after sugarbeet which decreased continuously during the following years under cereals. Although the results indicate an interrelationship between decreasing nematode population density and rate of parasitism, our results, based on correlation coefficients, do not support this hypothesis.

The relationship between level of egg parasitism and the number of cysts extracted from the sample, or with the number of eggs and juveniles/cyst, was weak and predominantly negative. A negative correlation between the *H. schachtii* cyst density in soil and the number of cysts colonized by fungi was also detected by Rademacher and Schmidt (1933). They assumed that parasitism did not keep pace at high levels of nematode infestation, but decreased with increasing cyst density.

Utilization of actual rates of parasitism in eggs extracted directly from field soil is not considered to be a suitable indicator of potential fungal egg parasitic activity (Nicolay & Sikora, 1989). Consequently, we investigated the relationship between the rate of parasitism and nematode density solely on activity in a new generation of the nematode. This allowed measurement of parasitism at a time when empty egg shells are not or are only present in small numbers. This approach yielded no consistent correlation between egg parasitism and number of newly formed eggs or cysts.

Using this bioassay technique, correlations between nematode density in the field and activity of fungal egg parasites were not detected in 75 % of the sampling dates. The fungal parasites, even at high nematode densities either did not multiply or were not able to cause increased parasitism on the newly formed *H. schachtii* generation. Nicolay and Sikora (1989) showed that a high host density in this host-parasite-system is not associated with increased parasitic activity.

The addition of an extremely high and specific source of nutrition (in the form of encysted eggs) to the system did not give the facultative fungal parasites an ecological advantage. Although they had sufficient time to parasitize the host eggs, increased parasitic activity was not detected. The results indicate that the fungi in our experiments were not dependent nutritionally on *H. schachtii.*

Khan and Hussain (1986) considered *Meloidogyne incognita* a poor substrate for the fungal parasite *Fusarium solani* because the fungus only produced chlamydospores instead of conidia. *Verticillium chlamydosporium,* an important egg parasite, has been isolated from clover and rye-grass roots (Thornton, 1965). According to Kerry, Simon and Rovira (1984) *V. chlamydosporium* is not dependent on nematode sources of nutrition. It can be assumed, however, that once cysts are penetrated they act as survival and dissemination structures. The fact that parasitism in cysts proceeds very slowly, also indicates that these fungi may be poor or only erratic parasites.

In vitro tests demonstrated that approximately 14 of 30 fungal isolates collected from our experimental fields were non-pathogenic and probably colonized dead eggs saprophytically (Nicolay, 1989). The egg parasites detected were *V. chlamydosporium,* two isolates of *Fusarium oxysporum, F. solani, Cylindrocarpon destructans* and a species of *Acremonium.*

The correlation between number of eggs and juveniles/cyst in the field and parasitism of newly formed eggs with a few exceptions was statistically not significant. Cyst contents in the field, therefore, did not influence parasitic activity. A weak, but significant, correlation was detected between the contents of the newly formed cysts and parasitic activity in samples from Bonn-Poppelsdorf, while in the Dikopshof samples no such correlation was found. According to Kerry, Crump and Mullen (1982) the number of eggs and juveniles in *Heterodera avenae* females was high in samples where the eggs were only weakly parasitized. They compared, however, samples from only three different fields whereby the tendency was not distinct. The timing of infection of young females by fungi plays an important role in determining interdependence between cyst contents and fungal activity. The number of eggs and juveniles/cyst probably does not determine parasitic activity. Instead, the timing of the infection in maturing females is decisive in determining the number of eggs available for parasitism and their susceptibility. The weak correlation may also be influenced by the fact that parasitism of the developing female on the root may be more important in

population density regulation than egg parasitism. The simultaneous parasitism of young females and eggs still in embryogenesis makes use of the term egg parasites misleading and may be responsible for the weak correlation between parasitism of eggs and population density.

Thielemann and Steudel (1973) demonstrated that the number of *H. schachtii* cysts increased continuously while the number of eggs and juveniles/cyst decreased in a 9 year sugarbeet monoculture. Steudel (1985) reconfirmed these results after 20 years of sugarbeet and assumed that the *H. schachtii* population density was more strongly reduced by parasites under monoculture *versus* three year rotation. Tribe (1979) found high levels of " diseased cysts " in soil of the same monoculture as compared to the normal rotations. In spring the cysts were more heavily colonized by " minor pathogens " than by *V. chlamydosporium*. The hypothesis could be made that the increasing numbers of cysts in this experiment had decreasing numbers of cysts with viable contents which were then colonized by weak facultative parasites or saprophytic fungi.

We conclude from our results that the level of fungal egg parasitism of *H. schachtii* is not dependent on nematode density because of the strong saprophytic nutritional nature of the facultative parasitic fungi associated with cyst nematodes.

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