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Effects of Nematophagous Fungi on Numbers and Death Rates of Bacterivorous Nematodes in Arable Soil

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Abstract: In a series of microcosm experiments with an arable, sandy loam soil amended with sugarbeet leaf, the short-term (8 weeks) dynamics of numbers of nematodes were measured in untreated soil and in γ-irradiated soil inoculated with either a field population of soil microorganisms and nematodes or a mixed population of laboratory-propagated bacterivorous nematode species. Sugarbeet leaf stimulated an increase in bacterivorous Rhabditidae, Cephalobidae, and a lab-cultivated *Panagrolaimus* sp. Differences were observed between the growth rates of the nematode population in untreated and γ-irradiated soils, which were caused by two nematophagous fungi, *Arthrobotrys oligospora* and *Dactylaria* sp. These fungi lowered the increase in nematode numbers due to the organic enrichment in the untreated soil. We estimated the annually produced bacterivous nematodes to consume 50 kg carbon and 10 kg nitrogen per ha, per year, in the upper, plowed 25 cm of arable soil.

Key words: *Acrobeloides*, *Arthrobotrys*, bacterivorous nematode, carbon-nitrogen flow, *Dactylaria*, nematode, nematophagous fungus, organic amendment, *Panagrolaimus*, population dynamics, *Rhabditis*, soil ecology.

In Dutch arable soil, in particular, bacteria are the main decomposers of organic matter such as roots, root exudates, crop residues, manure, and green manure, while fungi seem to be of minor importance (34). For example, biomass estimates at Kjettslinge Experimental Field in Sweden amounted to 2,300 kg fungal carbon and 900 kg bacterial carbon per ha in the upper 15 cm of soil, whereas at the Lovinkhoeve Experimental Farm in the Netherlands these biomasses amounted to approximately 250 kg bacterial carbon and 3 kg fungal carbon in the upper 25 cm of soil (24). The bacteria serve as food for bacterivorous organisms such as protozoa (11), nematodes (17), and mites (9). The resulting contribution of nematodes to carbon and nitrogen mineralization is relatively large, as studies on energy conversion efficiencies indicate that bacterivorous nematodes use only a small proportion of their ingested food for growth (24,28,29) and excrete considerable amounts of carbon and nitrogen as CO_2 (12) and NH_4^+ (32).

In arable fields, nematode population densities in the upper 25 cm of soil are as large as $10^7/m^2$, the equivalent of 2.0 kg C and 0.25 kg N per ha (6,29). Bacterivores often dominate this fauna, particularly rhabditid and cephalobid species. Abiotic factors that influence the population densities of these nematodes include moisture conditions, because nematodes that have escaped from drought by anhydrobiosis may rapidly reproduce after wetting under dry conditions (22). Furthermore, aboveground arable management practices such as growing crops (6), incorporation of crop residues (7), and manuring (13) may stimulate either both Rhabditidae and Cephalobidae or stimulate one taxum selectively. Overall, the largest numbers of bacterivorous nematodes occur during crop growth and in the periods after organic enrichment of the soil. Soil fumigation may also affect differential recovery of both taxa (14). Biotic factors that influence the growth rates of nematodes concern the availability and quality of food (bacteria) (27), competition with other bacterivorous organisms (protozoa) (8), and predation (nematophagous organisms).

The amount of bacterial biomass that has been consumed by nematodes during a certain time period will depend not only on the measured population size of the nematodes but also on all the nematodes

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that have been consumed by predators or have died a natural death during that time (15). Nematophagous fungi are well-known predators of nematodes, and because of their almost complete assimilation of nematodes they hardly promote the growth of other microorganisms (3).

Nematode population changes in the field can be measured as the difference in nematode density between two samplings. This difference, however, does not adequately measure reproduction because, in addition to natural death, the nematodes are also subject to predation. Assimilation of bacterial biomass by nematodes can contribute considerably to the dynamics and composition of soil bacterial populations (31). Consequently, the unknown number of predated or otherwise deceased nematodes may have affected this flora during the time between two samplings. Therefore, to examine the effects of nematode populations on soil bacteria and the concomitant mineralization of C and N, information is required on both the effects of organic enrichments of the soil on nematode population levels as well as the growth and death rates of the nematodes, including death due to predation. The purpose of this investigation was to study the dynamics of bacterivorous nematodes in organically enriched arable soil in the presence and absence of organisms with nematophagous potential. Results were used to estimate the annual carbon and nitrogen flows through the bacterivorous nematode feeding categories that were involved in the decomposition processes in arable soil.

The rate of predation of nematophagous organisms on nematodes was derived from measurements of "net increase," i.e., growth of populations minus death including death due to predation, and "potential increase," i.e., growth of populations minus death in absence of predation. Net population changes of nematodes were measured in a microcosm of untreated arable soil containing a natural set of nematophagous organisms after amendment with sugarbeet leaf. Potential population changes were measured in similar microcosms after γ-irradiation of the soil and reinoculation with microorganisms and nematodes. From these population dynamics, the annual carbon and nitrogen flows through bacterivorous nematodes in arable soil were estimated. Nematophagous organisms were surveyed in the soil used in the experiment, and their effect on nematode dynamics was tested in a separate experiment.

Materials and Methods

Soil: A calcareous silt loam soil (12% sand, 68% silt, 20% clay, 9% $CaCo_3$; pH-KCL 7.5; 2,5% organic matter) of recent marine origin from the Lovinkhoeve Experimental Farm (21) was used. From the 25-cm-deep plowed layer, 45 kg soil was removed, spread, air-dried (48 hours), sieved (10 mm-pore), and remixed. Of this sample, 25 kg was γ-radiated (1 megarad) to kill nematodes and non-spore-forming microorganisms (4). The remaining, untreated (non-γ-irradiated) soil was used to measure the net increase in numbers of nematodes and to isolate nematodes for addition to γ-irradiated soil. The γ-irradiated soil was used for measurements of the potential increase in numbers of nematodes and for the determination of the effects of nematophagous fungi on nematode population levels.

Organic amendment: In various treatments, 100 g soil was amended with 150 mg dried, milled (particle size <1 mm), and γ-irradiated sugarbeet leaf (*Beta vulgaris* cv. Regina), at the equivalent of ca. 2,000 kg C/ha and with a C/N-ratio of 12.

Establishment of the microcosms: For measurements of net increase in nematode numbers, 100 g untreated air-dried soil was mixed with 150 mg dried sugarbeet leaf and added to a 150-ml jar. Soil moisture content was adjusted to 20% w/w with tap water, and jars were sealed with air-permeable, high-density polyethylene mulch and incubated at 10 C for 0, 4, and 8 weeks. Incubations without sugarbeet leaf were also made. For measurements of the potential increase in nematode numbers, the same procedure was followed ex-

cept 1 g pulverized soil was mixed with γ-irradiated soil and 150 mg γ-irradiated sugarbeet leaf; subsequently, the soil was transferred into the jar in five layers of 20 g each, and 10 ml nematode suspension was pipetted onto the surfaces of the successive layers. Soil without sugarbeet leaf was similarly prepared for incubation. The number of replicates in each series of incubations differed (Table 1) because some nematode suspensions were spilled.

Microorganisms: For the reinoculation of γ-irradiated soil with the same microorganisms as present in the untreated soil, 200 g untreated soil was air-dried for 72 hours in the lab, pulverized in a mortar, and moistened with tap water. This procedure was repeated three times. One gram of this powder was mixed through the soil in the microcosms used for measurements on potential increase of nematode numbers. Metazoans, including nematodes, did not survive this procedure, in contrast to bacteria, fungi, and protozoa. The survival of protozoa (amoebae and flagellates) was determined in rewetted, incubated, pulverized soil. The absence of any other nematode species but the inoculated species in the treatments with γ-irradiated soil inoculated with agar-cultivated nematodes indicates that it is highly improbable that anhydrobiotic nematodes or nematode eggs survived the drying-wetting-pulverizing procedure.

Nematodes: For the measurements of potential nematode population levels, a series of treatments were inoculated with different aqueous suspensions of nematodes. In one treatment, approximately 1,200 nematodes, isolated by Oosterbrink's elutriation method (19) from 10 kg air-dried soil, were added to the γ-irradiated soil. In the second treatment, an aqueous mixture of approximately 500 agar-cultivated *Rhabditis* sp., *Acrobeloides bütschlii,* (Cephalobidae), and *Panagrolaimus* sp. was added to the microcosms. Nematode numbers were expressed per 100 g fresh weight soil with a dry matter content of 80%. The nematode species originated from Lovinkhoeve soil and were maintained for some generations in the lab; the species had been used already for other microcosm experiments (8,9).

The development of numbers of nematodes belonging to different taxa was measured after 4 and 8 weeks incubation of the microcosms. Nematodes were isolated from 50 g soil by elutriation, collected on four 45-μm-pore sieves, placed on top of one another, and allowed to migrate through a double cottonwool filter for 24 hours (23). Nematodes were counted in three subsamples from a 100-ml suspension; 60 specimens per subsample were identified to family.

Nematophagous organisms: Because the aim of the experiment was to measure nematode density in the absence and presence of predation, air-dried untreated soil was examined for nematophagous organisms such as predatory nematodes (Dorylaimidae and Mononchidae) and nematophagous mites, springtails, and fungi. Soil microarthropods in three portions of 100 g, air-dried untreated soil were ex-

TABLE 1. Codes, treatments, and numbers of replicates of soil microcosms monitored for nematode population levels after 0, 4, and 8 weeks of incubation at 10 C.

Code	Treatment	Number of replicates		
		0 weeks	4 weeks	8 weeks
FNf	Untreated soil, field population of nematodes	6	12	10
FNfB	FNf with γ-irradiated sugarbeet leaf	8	10	10
SNf	γ-irradiated soil, field population of nematodes	8	12	10
SNfB	SNf with γ-irradiated sugarbeet leaf	8	11	9
SNl	γ-irradiated soil, laboratory-propagated nematodes[a]	8	12	9
SNlB	SNl with γ-irradiated sugarbeet leaf	8	12	10

[a] Laboratory-propagated nematodes comprised of a mixture of *Rhabditis* sp., *Acrobeloides bütschlii,* and *Panagrolaimus* sp.

tracted for 10 days with a modified MacFadyen high-gradient system (2) with a gradient of 5-45 C. For isolation of nematophagous fungi, 1.0 g air-dried untreated soil was sprinkled on 2% water agar in a petri dish and approximately 1,000 specimens of agar-cultivated *Rhabditis* sp. were added. The dish was incubated at 18 C (3).

Measurements of nematode dynamics: The following equations were used to estimate the rates of increases in numbers in the presence of predators (net increase) and in the absence of predators (potential increase), natural death, and death due to predation after organic enrichment of the soil: Potential rate of increase in population size of the nematodes (kg C/ha/yr) (i.e., no predation) can be described by:

$$\frac{dN}{dt} = (b - d)\,N, \qquad (1)$$

where N is the population size (kg C/ha or numbers of nematodes/weight unit soil), and b and d are the specific birth (per year) and death (per year) rates. For transformation of numbers of nematodes per 100 g soil into kg carbon per hectare (25-cm depth), a specific fresh mass of 0.1 μg was used for bacterivores, and carbon content of 10% of the fresh mass (8). Net rate of increase in population size (i.e., including predation by nematophagous fungi) can be described by:

$$\frac{dN}{dt} = (b - d - p)\,N, \qquad (2)$$

were p is the specific death rate due to predation (per year). These differential equations can be solved for potential increase in numbers

$$N(t) = e^{(b - d)t} \qquad (3)$$

and for net increase in numbers

$$N(t) = e^{(b - d - p)t} \qquad (4)$$

Effects of nematophagous fungi: The effect of the nematophagous fungi isolated from the untreated soil on numbers of laboratory-propagated nematodes in γ-irradiated soil amended with sugarbeet leaf was studied in a separate experiment. *Arthrobotrys oligospora* and *Dactylaria* sp. were each cultivated on malt-agar. Fungus-agar mixed suspensions were created from densely overgrown agar plates. Approximately 10 ml of these suspensions was autoclaved (ac) for 2 hours at 120 C. The *A. oligospora* suspension was diluted with tap water in 1, 10^{-1}, 10^{-2}, and 10^{-3} concentrations, and *Dactylaria* sp. was applied undiluted only. Microcosms with γ-irradiated soil amended with sugarbeet leaf and mixed with 1 g pulverized soil were established as already described; 1-ml fungal suspension was added to 9-ml nematode suspension containing approximately 1,100 laboratory-propagated *Rhabditis* sp. or *A. bütschlii* specimens, and this mixed suspension was pipetted onto the successive layers in the microcosm. Microcosms were incubated in quadruplicate at 10 C for 3 or 6 weeks. Single microcosms containing autoclaved *Dactylaria* sp. were incubated. The initial numbers of nematodes, isolated a couple of hours after incubation (0-week incubation), were counted in the four incubations containing autoclaved *A. oligospora*.

Results

Potentially nematophagous organisms: Nematophagous fungi *A. oligospora* and *Dactylaria* sp. were present in all treatments with incubated untreated soil (FNf, FNfB) at all sampling dates and were not isolated from any microcosms with γ-irradiated soil inoculated with a field population of nematodes (SNf, SNfB). Dorylaimidae and Mononchidae, at the rate of 14 ± 21 and 25 ± 18 specimens per 100 g soil, respectively, were isolated from untreated soil. Numbers of Dorylaimidae increased slightly in incubated untreated soil during the course of the experiment and remained very low in γ-irradiated soil. Numbers of Mononchidae decreased gradually in incubated untreated soil in the course of the experiment and were not isolated from incubated γ-irradiated soil. Microarthro-

pods were not isolated from untreated, non-incubated soil, and incubated soil was not assayed for their presence.

Nematode population levels: Table 2 presents the numbers of nematodes of the different taxa in the various treatments after incubation. In the untreated soil (FNf), the relatively sparse population of ca. 1,000 specimens comprised 46% bacterivores (Rhabditidae and Cephalobidae with some Plectidae), 36% fungivores (Tylenchidae with some Aphelenchoidea, genus *Aphelenchoides*), 14% herbivores (Pratylenchidae with some Hoplolaimidae), and 4% omnivores or predators (Dorylaimidae, Mononchidae).

In untreated soil (FNf), Cephalobidae excepted, numbers of most taxa decreased during the experiment. In the amended untreated soil (FNfB), both microbivorous feeding categories, the bacterivores, and the fungivores increased in numbers, in particular the bacterivorous Rhabditidae (analysis of variance, $P < 0.01$) and Cephalobidae ($P < 0.05$). In the γ-irradiated soil inoculated with the field population of nematodes (SNf), the initial nematode density (ca. 500 specimens) was 0.5 times the density in untreated soil. Selective death due to the isolation and inoculation procedure changed the total numbers of some taxa in this treatment and, consequently, the proportions of the various feeding categories. In particular, Rhabditidae, Dorylaimidae, Mononchidae and fungivores did not survive the procedure, but the numbers of the various herbivorous taxa were not affected. After 8 weeks, the number of bacterivores in unamended γ-irradiated soil, inoculated with a field population of nematodes (SNf), had reached the level of those in untreated soil (FNf). In the amended γ-irradiated soil inoculated with a field population of nematodes (SNfB), bacterivores had larger densities than in the amended untreated soil (FNfB) at both sampling dates (4 and 8 weeks) ($P < 0.05$; Table 2). In the γ-irradiated soil inoculated with the laboratory-cultured bacterivorous nematodes (SNI), densities increased to approximately the same level as observed for the total numbers in the untreated soil after 8 weeks (FNf) (Table 2).

In the amended γ-irradiated soil inoculated with the laboratory-propagated nematodes (SNIB), total numbers were higher than in amended untreated soil (FNfB) at both sampling dates (4 and 8 weeks) ($P < 0.001$) and used for the calculation of the specific rate of increase (Fig. 1). Densities of *Rhabditis* sp., *Panagrolaimus* sp., and, to a lesser extent, *A. bütschlii* increased to a greater extent ($P \leq 0.1$) in this treatment than in the amended soils with the field populations of nematodes (FNfB and SNfB) (Table 2).

The rates of specific increase in population size of nematodes: Figure 1 gives the net and potential growth-rate curves and the densities in amended untreated soil including the calculated numbers of nematodes killed by predators. Net growth rate was estimated by fitting equations (3) and (4) in the amended untreated soil (FNfB) and potential growth rate in the amended γ-irradiated soil (SNIB). This parameter fitting yielded estimates of the specific rates of increase without predation ($b - d = 0.35$ per week) and with predation ($b - d - p = 0.09$ per week).

Effect of A. oligospora and Dactylaria sp.: After 3 and 6 weeks incubation, the reduction in numbers of *Rhabditis sp.*, and *A. bütschlii* in amended γ-irradiated soils by *A. oligospora*, was dependent on the dilution of the inoculated fungus; effects were most drastic after 6 weeks of incubation, and numbers of *Rhabditis sp.* were considerably more reduced than numbers of *A. bütschlii* in all treatments except concentration 10^{-3} after 3 weeks incubation.

The undiluted *Dactylaria* sp. was more effective in reducing nematode numbers and almost eradicated *Rhabditis* sp., and considerably reduced *A. bütschlii* after 6 weeks incubation (Table 3).

Discussion

Numbers and dynamics of Dorylaimidae and Mononchidae in the various treat-

TABLE 2. Numbers (per 100 g soil) of bacterivorous, fungivorous, herbivorous, and omnivorous nematodes of various taxa in 0-, 4-, and 8-week incubations of microcosms established as presented in Table 1.

Nematode taxa and feeding categories	Incubation time (weeks)	FNf	SNf	SNl	FNfB	SNfB	SNlB
				Bacterivores			
Rhabditidae	0	211	49	12			14
	4	132	64	30	611	2,856	1,842
	8	122	127	247	786	8,626	8,478
Cephalobidae	0	257	129	41	257		44
	4	218	205	60	334	729	959
	8	332	277	56	664	1137	819
Panagrolaimidae	0	0	0	24			27
	4	8	3	51	2	3	1171
	8	2	0	574	19	171	5,391
Plectidae, Araeolaimidae	0	3	2				
	4	19	1		26	0	
	8	7	11		28	20	
Totals	0	471	180	77			85
	4	377	273	141	973 a	3,588 b	3,972 b
	8	463	415	877	1,497 c	9,954 d	14,688 e
				Fungivores			
Tylenchidae	0	347	192				
	4	238	112		351	418	
	8	218	146		394	281	
Aphelenchoididae	0	24	11				
	4	12	6		38	15	
	8	17	16		66	59	
Totals	0	371	203				
	4	250	118		389	433	
	8	235	162		460	340	
				Herbivores			
Pratylenchidae	0	118	119				
	4	42	44		82	74	
	8	38	67		40	99	
Hoplolaimidae	0	14	16				
	4	20	22		34	22	
	8	10	13		14	0	
Paratylenchidae	0	11	9				
	4	9	12		36	37	
	8	21	16		53	41	
Totals	0	143	144				
	4	71	78		152	133	
	8	69	96		107	140	
				Omnivores and Predators			
Dorylaimidae	0	14	2				
	4	44	1		19	0	
	8	25	2		29	0	
Mononchidae	0	25	0				
	4	10	0		16	0	
	8	6	0		0	0	
Totals	0	39	2				
	4	54	0		35	0	
	8	31	2		29	0	
Totals	0	1,024	529				
	4	752	470		1,549	4,154	
	8	798	675		2,093	10,434	

Values followed by different letters are significantly different (analysis of variance, $P < 0.0001$).

The microcosms inoculated with laboratory-propagated nematodes (SNL and SNLB) did not contain fungivores, herbivores, omnivores, and predators.

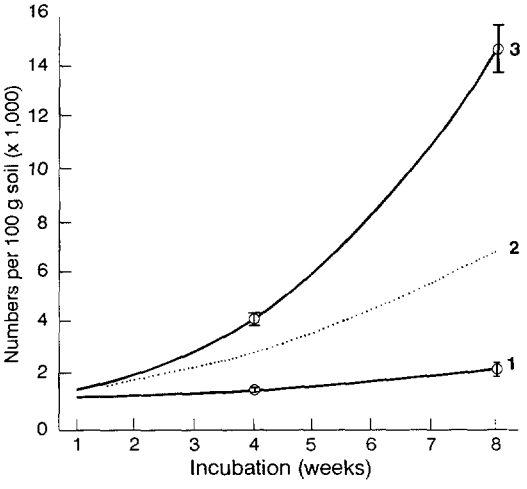

FIG. 1. Numbers of nematodes per 100 g soil amended with 150 mg dried and ground sugarbeet leaf, measured during an 8-week incubation at 10 C in untreated soil (1 = net nematode densities) and in γ-irradiated soil inoculated with laboratory-propagated nematodes (3 = potential nematode densities). The dotted line (2) represents the net nematode densities plus the calculated numbers of nematodes killed by predators. Bars indicate SE.

ments indicate a low activity of these taxa. Knowledge of the feeding habits and type of food of Dorylaimidae is fragmentary. Ferris and Ferris (16) presented an overview of the feeding behavior of dorylaimid and mononchid species, cultured on agar, with most species feeding on bacterivorous nematodes but some species also feeding on fungi and algae. Russell (26) observed that *Mesodorylaimus* sp. would feed on bacterial colonies, and Yeates (33) observed that the younger stages of Mononchidae were feeding on bacteria. This wide range of prey types suggests that these taxa have omnivorous capacities where the actual feeding probably depends on life stage and the type of food available. In Lovinkhoeve soil, various dorylaimid species occur, mainly concentrated in the upper soil layers (8). In microcosm experiments with this soil, Dorylaimidae and Mononchidae did not respond numerically to enrichment of mixed soil with organic matter, in contrast to the bacterivorous nematodes; however, in one experiment with an undisturbed soil core with organic matter applied to the surface, the Dorylaimidae increased their numbers significantly under a wet moisture regime during 1 month of incubation in the dark (8). In the present experiment, Dorylaimidae and Mononchidae seemed not to have affected the numbers of other nematode taxa in the untreated soil (FNf, FNfB) because their numbers were too small; even in the presence of high densities of potential prey nematodes in the γ-irradiated soil, no increase in dorylaimid or mononchid nematodes was observed.

In the Netherlands, and occasionally in the Lovinkhoeve soil (pers. obs.), various nematode species have been observed with endospores of the parasitic bacterium *Pasteuria penetrans* attached to their cuticle. However, no attached endospores were observed during the identification of nematodes in this experiment. Sturhan (30) observed endospores attached to the cuticles of *A. bütschlii* and *Rhabditis* sp.; due to the slow growth rate of the parasite and the fast growth rate of the bacterivorous nematodes, the bacteria are assumed not to develop on the nematodes, at least not at the prevailing temperature of 10 C in this experiment. Thus, any significant reduction in numbers of nematodes in the untreated soil treatment by *P. penetrans* seems highly improbable.

Furthermore, γ-irradiation can cause a sudden burst of easily decomposable organic matter, including dead biomass (4); this extra substrate for bacterial or fungal growth in the γ-irradiated treatments did not yield a substantial increase in numbers of bacterivorous or fungivorous nematodes.

The observations indicate the presence of an effective predation system on bacterivorous nematodes in the alkaline silt loam arable soil used in the experiment. This system did not affect fungivorous and herbivorous nematodes, as the dynamics of these organisms did not differ significantly between untreated (FNfB) and γ-irradiated (SNfB) amended soil. It is assumed that in more acid soils, which promote the decomposition of organic matter by fungi, predation on fungivorous nema-

TABLE 3. Numbers (per 100 g soil) of *Rhabditis* sp. and *Acrobeloides bütschlii* in γ-irradiated soil amended with sugarbeet leaf, incubated at 10 C with decreasing concentrations of *Arthrobotrys oligospora* and with a non-diluted suspension of *Dactylaria* sp., for 3 and 6 weeks.

		Weeks of incubation					
		Rhabditis sp.			*Acrobeloides bütschlii*		
Fungus	Dilution	0	3	6	0	3	6
Arthrobotrys oligospora	ac[a]	208	5,744 ± 1,572	5,444 ± 1,046	513	4,362 ± 370	26,550 ± 2,270
	1×10^{-3}		5,519 ± 642	2,688 ± 661		3,412 ± 474	15,988 ± 2,122
	1×10^{-2}		1,319 ± 140	533 ± 263		2,919 ± 263	13,025 ± 1,895
	1×10^{-1}		688 ± 327	294 ± 172		2,600 ± 388	9,231 ± 688
	1×10^{0}		338 ± 48	194 ± 175		2,144 ± 432	10,044 ± 1,438
Dactylaria sp.	ac		6,550	7,725		6,325	25,050
	1×10^{0}		263 ± 101	50 ± 54		5,550 ± 805	6,288 ± 942

Data are means ± standard error of four replications, with the exception of concentration ac, 0 weeks of incubation (single observation).

[a] Autoclaved suspension.

At 0 weeks of incubation, numbers were counted only in the treatment with autoclaved fungus (ac) and were considered not to differ among the various treatments.

todes could also be stimulated by incorporation of fresh organic matter into the soil.

With respect to the soil used in the experiment, the initial density of ca. 1,000 specimens/100 g soil was less than half the numbers usually counted in field samples such as collected in the Lovinkhoeve soil (34); however, the distribution of specimens over the various feeding categories was typical (8).

Nematode population densities after organic amendment in arable soil depended strongly on the activity of nematophagous fungi. In the experiment with γ-irradiated soil inoculated with nematodes and nematophagous fungi, the fungi were as effective in reducing bacterivorous nematodes as the complete set of organisms with nematophagous potential in the amended untreated soil. The effect of the fungus *A. oligospora* on the numbers of nematodes was not affected by 10^{-2} dilution of the initial fungal suspension. Although densities of endoparasitic nematophagous fungi have been demonstrated to depend on the density of nematodes in microcosms (20), particularly after organic amendment of the soil (5), the relationship between density of predatory nematophagous fungi and their prey nematodes is more complex. Trap forming by *A. oligospora*, for example, and consequent predatory activity is also affected by decomposition of proteinaceous organic matter (23) and probably also by nematode-associated bacteria (10). Effects of nematophagous organisms on C and N mineralization are less straight-forward: they may be positive or negative, differ for C and N, and vary strongly in time (8). In the untreated soil, the nematode population doubled in the 8 weeks after amendment of the soil with sugarbeet leaf mainly because of an increase in numbers of Rhabditidae and Cephalobidae. In reinoculated and organically amended γ-irradiated soil, the neutralization of nematophagous activities allowed numbers of Rhabditidae to increase an order of magnitude higher than in the amended untreated soil in the presence of nematode predators, mainly nematophagous fungi; Cephalobidae doubled under these conditions.

Specific birth (b), death (d), and predation (p) rates and the concomitant annual flows of carbon and nitrogen through the bacterivorous nematodes in the plowed layer of the Lovinkhoeve arable fields were calculated. According to Anderson et al. (1) and Hunt et al. (18), the natural specific death rate (d) of bacterivorous nematodes under conditions without predation is 2.68 year = 0.0515/week; therefore, b becomes 0.35 + 0.0515 = 0.4015/week, and since ($b - d - p$) = 0.09/week (Fig. 1), p = 0.26/week. Total death M (natural death plus

death due to predation) becomes 0.26 + 0.0515 = 0.3115/week. The experiments indicate that in the treatments with amended untreated soil the nematode densities were low as compared to the densities in γ-irradiated soil; this was probably due to a high total death rate when organic matter is decomposing rapidly. In arable soil this will occur during crop growth and after crop residue or green manure addition; tillage can also cause the release of easily decomposible organic matter as can wetting-drying and freezing-thawing cycles. Under Dutch climatic conditions, total death rate is probably low in winter and early spring, when there is no external input of organic matter. Therefore, we assume that the death rate is high for 35 weeks, from May until January (0.3115/week), and negligible for the remaining 4 months. Thus, the total annual death rate is $M = 0.3115 \times 35 = 11$/year. For an average population of bacterivorous and omnivorous nematodes of ca. 0.70 kg C/ha (B), as measured in the upper 25 cm soil in the integrated managed fields at the Lovinkhoeve under winter wheat (1986, 1990) and under sugarbeet (1987) (8), and a production/feeding ratio (E) of 0.12 (30) or 0.24 (24), total feeding (F), necessary for maintenance is: F = MB/E = 32 kg C/ha/yr for E = 0.24, and 64 kg C/ha/yr for E = 0.12. From this feeding rate, nitrogen mineralization can be estimated, assuming C/N ratios of bacteria and nematodes of five, an assimilation/consumption ratio of 0.4, and a production/assimilation ratio of 0.375 (18). For 32 kg C consumed, the amount of N taken from the bacterial population is ca. 6.4 kg/ha/yr, from which 3.5 kg/ha/yr is returned in organic form to the environment, 1.2 kg/ha/yr is used for the production of nematode biomass, and 1.7 kg/ha/yr is mineralized (25). Using a consumption of 64 kg bacterial C, the figures for N are proportionally higher. These estimated C and N flows are close to the values presented by Sohlenius et al. (29), who estimated the annual flow of C and N passing through the nematode feeding categories located in the plowed upper 20-cm layer of an arable clay loam soil cropped with barley based on measured biomass and estimated respiration; they calculated a total annual consumption of ca. 82 kg C, corresponding to ca. 8 kg N for the entire nematode fauna, and for herbivores 29 kg C, fungivores 10 kg C, bacterivores 35 kg C, and omnivores 8 kg C. Thus, different approaches result in comparable flow rates for C and N in arable land.

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