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THE EFFECT OF MACROARTHROPODS PATROLLING SOIL SURFACE ON SOIL NEMATODES: A FIELD EXPERIMENT IN A MOWN MEADOW

ABSTRACT: A field experiment was designed to estimate the effect of soil surface patrolling by macroarthropods on organic matter content in soil. One of the components of this experiment was the soil nematode community – density, trophic and dominance structure, the diversity and maturity indices. These parameters were compared between two types of mesocosms: accessible and inaccessible to macroarthropods. The experiment was performed under natural environmental conditions and did not reduce the diversity of the biota characteristic of the ecosystem. Most parameters of nematodes did not vary significantly between mesocosms. Differences between mesocosms observed over the 5-month period of each of the two experiments (1992 and 1993) concerned mainly, bacterivorous nematodes and, within this trophic group, colonizers. The densities of the taxon *Rhabditis* s.l. were statistically higher in the mesocosms accessible to macroarthropods, and the proportion of colonizers (r-strategists s.l.) among bacterivorous nematodes was also higher.

KEY WORDS: soil nematodes, bacterivores, macroarthropods, *Rhabditis* s.l.

1. INTRODUCTION

Predation by large, motile arthropods on saprophages in terrestrial ecosystems is relatively little known. It is known, however, that

predation can affect the rate of organic matter mineralization (Coleman *et al.* 1984, Kajak 1995). The hypothesis is that predatory macroarthropods can change proportions between bacteria and fungi by decreasing the density of fungivorous mesofauna, and, consequently, they can contribute to the carbon storage in the soil. Nonpredatory macroarthropods influence decomposition by comminution of plant material, by microbial grazing and by faeces ejection.

The relationship between decomposition processes and structures of heterotrophic communities in the litter and soil was already analysed by Kajak (1997), Kajak *et al.* (1998), and Kajak *et al.* (2000).

This paper analyses a part of the same problem with reference to soil-inhabiting nematodes. Soil nematodes are useful indices of soil processes, habitat quality, and of all kinds of management effects (Wardle *et al.* 1995, Ferris *et al.* 1996, Neher and Campbell 1996, Wasilewska 1997, Yeates and King 1997, Yeates *et al.* 1997a, Yeates *et al.* 1997b, Alpehi 1998, Porazińska *et al.* 1998). Thus, the variables compared here comprise the density of

nematodes, composition of taxa, trophic structures, and maturity indices in variants accessible to macroarthropods and in the control, not accessible to macrofauna. A special attention will be paid to bacterivorous nematodes, that increase in numbers in response to the addition of faeces (or dung) to the habitat (Bardgett *et al.* 1998, Wasilewska 1998). On the other hand, however, the role of macroarthropods as regulatory forces in the decomposer food-webs (fungivorous and predatory macroarthropods feed upon soil nematodes and compete for similar resources) should not be neglected (Wardle and Yeates 1993, Hyvönen and Persson 1996).

2. EXPERIMENTAL DESIGN

2.1. STUDY AREA

The experiment was conducted in a permanent, mown meadow situated near the village of Łomna at the peripheries of the Kampinos Forest, central Poland. The vegetation was of the order of Arrhenatheretalia, the soil was gleyed black earth (8% C in the sod layer, 1.85% in A₁ layer), with pH = 4.5, exchange capacity in A₁ = 12 cmol per 1 kg dry wt of soil. The soil was derived from loamy sand underlain by loose sand.

A detailed description of the experiment, its assumptions and parameters are presented in Kajak (1997), Kajak (2000) and Kajak *et al.* (2000). This paper presents a shortened description concerning the estimation of soil nematode density and community structure.

2.2. EXPERIMENTAL TREATMENTS

Two types of mesocosms were used in the experiment, one accessible (open) and the other one not accessible (closed) to macrofauna moving on the soil surface. The intensity of the penetration of the open mesocosms by macroarthropods (Formicidae, Carabidae, Araneae) was 6.9 mg dry wt per trap per day in 1992, and 3.6 mg dry wt

per trap per day in 1993, and it was over 100 times higher than in the closed mesocosms. The penetration of the open mesocosms by nonpredatory animals was only ten times that in the closed mesocosms (2.4 and 3.9 mg dry wt per trap per day in 1992 and 1993, respectively).

Mesocosms contained soil cores in isolators (bags) made up of a steelon screen with 0.24 mm meshes. The difference between the open (O) and closed (C) mesocosms was that the former had holes cut at the soil interface, so that even the largest invertebrates searching the soil surface could pass through. Soil cores were taken from a meadow with a cylindrical 100-cm² sampler, 15 cm deep. They were immediately put into isolators and returned to the same pits from which they were taken. To estimate nematodes, 100 mesocosms were established in 1992 (Experiment I), and 60 mesocosms in 1993 (Experiment II). Experiment I was run from June 1992 until April 1993, whereas experiment II from April 1993 until May 1994. In each year mesocosms were established separately. A part of mesocosms was used to determine numbers of microflora and mesofauna in the soil, also to determine the content of carbon and humic acids, and the rate of litter decomposition and colonization by biota (Kajak *et al.* 2000).

2.3. ESTIMATION OF SOIL NEMATODE DENSITY AND COMMUNITY STRUCTURE

Samples of soil nematodes were taken from the soil of open mesocosms (O), closed mesocosms (C), and from surrounding meadow soil on the following dates: 21 May 1992, 4 June 1992, 2 July 1992, 2 September 1992, 20 October 1992 (Exp. I), and 10 May 1993, 21 June 1993, and 27 September 1993 (Exp. II). On each sampling occasion, one soil core 1.8 cm in diameter and 10 cm deep was taken from 10 mesocosms in each variant. After being mixed together, these soil cores formed a single mixed sample. Identi-

cal 10 soil cores were taken from surroundings of the mesocosms.

Nematodes were extracted from three subsamples of 25 ml of soil by using a modified Baermann method. They were identified to the genus level or to the genus s.l. level, like in the earlier paper (Wasilewska 1979).

The year 1992 was very dry, whereas 1993 was rainy. In the period from May through October 1992, precipitation sums were lower than the long-term mean by at least 20%. In the period from May through September 1993, they were higher than on average by 40%, even up to 400%.

The following parameters were estimated: density, composition of taxa in the community, trophic structure (bacterivores – B, fungivores – F, obligate plant feeders – OPF, facultative plant feeders (partially fungivores) – FPF, omnivores – Om, predators – P, and parasites of insects – PI). Nematodes were assigned to trophic groups after Wasilewska (1971) with reference to the classification by Yeates *et al.* (1993). Also the relations between trophic groups were considered: B/F, (B+F+FPF)/OPF, and B+F/(OPF+FPF). The difference between the last two ratios is that the group FPF is considered as mycophilous in one case and as plant feeders in the other case. These ratios are indicative of differences in the contribution of nematodes to the mineralization occurring in the detritus food web and grazing food web (Wasilewska 1997). Also the number of taxa and the Shannon-Weaver H' index were estimated, along with several maturity indices developed by Bongers (1990) and described in more detail by Bongers *et al.* (1995), Bongers and Bongers (1998), and Wasilewska (1997). Maturity indices are based on the allocation of taxa according to life strategy. These indices are based on the proportions of taxa (genera) with different life strategy in the community, from colonizers (r-strategists s.l.) to persisters (K-

strategists s.l.). These are the following indices:

1) Maturity Index – MI, based solely on free-living taxa of nematodes i.e. omitting herbivores, and monitoring habitat colonization and succession,

2) Maturity Index for total nematodes – Σ MI, calculated for all taxa in a sample. It serves the same purpose as MI and responds in the same way, but a slightly different response can be expected when natural ecosystems are analysed,

3) Plant Parasite Index – PPI, constructed using phytoparasitic nematodes, seems to be positively correlated with primary production,

4) The MINO Maturity Index – MINO MI, for free-living nematodes, but excluding opportunists ($c - p = 1$),

5) The Σ MINO Maturity Index – Σ MINO MI, for free-living nematodes, excludes opportunists and includes plant parasitic nematodes. The last two indices, which exclude opportunists, record rather long-term changes,

6) Maturity Index for bacterivores – Ba MI, indicates the life strategies within this trophic group. It may be expected that its lower value points to enhanced microbial activity when nitrogen supply is increased (Wasilewska 1998).

2.4. STATISTICS

Two-way ANOVA was used to estimate differences in the density of taxa and in bio-coenotic parameters of the nematode community between particular sampling dates and between open and closed mesocosms. Also nonparametric Friedman test was used for analysing differences between open and closed systems. In all the remaining cases, the Student *t*-test was used.

3. RESULTS

3.1. ESTIMATION OF "TYPICAL" CHARACTER OF A MEADOW BY USING TROPHIC STRUCTURE OF NEMATODE COMMUNITY

The densities of the total nematode community and trophic groups in the study area were compared with those in other regions of Poland (Table 1).

The experimental meadow was characterized by a low density of total nematodes (like another meadow located near Warsaw), and clearly by the lowest densities of omnivores and predators compared to several other meadows in different parts of Poland (Table 1). The ranges of densities of trophic groups associated with the detrital food web, that is, bacterivores, fungivores, and facultative plant feeders (which are partially fungivores) were lower than in the meadows of the lakeland and in the peat meadows of river valley (Biebrza). The ranges of bacterivore

densities were similar to those in the meadow of montane region (Table 1). The ranges of obligatory plant feeders were significantly different only from those in the meadows subjected to stress arising from acid rains, or from moorshing (mucking) processes, like river valley meadows (Table 1). Thus, mostly based on numbers of bacterivorous nematodes, the experimental meadow can be considered as biologically moderately active.

3.2. SEASONAL DIFFERENCES AND DIFFERENCES BETWEEN MESOCOSMS ACCESSIBLE AND INACCESSIBLE TO PREDATORS WITH RESPECT TO NEMATODE PARAMETERS

Significant seasonal differences were found (ANOVA) in densities of the following taxa: *Panagrolaimus*, *Rhabditis* s.l., *Plectus*, *Tylenchorhynchus*, *Paratrichodorus*, *Trichodorus*, and *Aporcelaimellus*, and bacterivore group, and also in such parameters as MI, Σ MI, and Ba MI (Table 2).

Table 1. Ranges of density (indiv. 10^6 m⁻²) of nematode trophic groups in Polish grassland soils, mainly Arrhenatheretalia (A) (to a depth of 25 cm), compared with experimental site (soil from surroundings of mesocosms, to a depth of 10 cm, 1992 and 1993) (after Wasilewska 1994, 1996)

Site	Bacterivores	Fungivores	Facultative plant feeders	Obligate plant feeders	Omnivores + predators	Total
Mineral soils:						
Present study (A)	0.5–2.2	0.06–1.0	0.02–0.2	0.3–1.5	0.04–0.2	1.0–4.9
Permanent meadow (A) (vicinity of Warsaw, Central Poland)	1.3	0.2	0.3	0.6	0.2	2.6
Permanent meadow (A)	1.6–5.4	2.5–1.4	0.7–1.9	0.8–1.9	0.4–2.7	7.3–11.6
Leys (\leq 4 years old) (A) (Lakeland, Suwałki Region, North-eastern Poland)	1.2–5.7	0.1–1.8	0.2–2.4	0.1–1.6	0.2–0.8	1.9–11.9
Montane pastures						
Pieniny Mts., 700 m a.s.l. (Southern Poland)	0.8–1.5	0.2–0.5	0.5–0.8	1.0–1.5	0.7–2.0	4.2–5.2
Izerskie Mts (900 m a.s.l., polluted area) (Southern Poland)	0.4–1.5	0.4–0.7	1.4–3.4	3.5–3.6	0.07–0.6	5.8–9.8
Peat soils:						
Permanent meadows in river valley (Biebrza, Narew, North- eastern Poland)	2.2–8.1	0.4–1.6	0.4–10.6	0.4–31.2	0.2–1.2	4.1–34.1

Table 2. Summary statistics ($P < 0.05$ significance level) of the density of nematode taxa or trophic groups and of the nematode community parameters between sampling dates and between mesocosms open (O) and closed (C) to macroarthropods. Two-way ANOVA was used, with sampling dates and mesocosms types, and also nonparametric Friedman test

Taxon / Parameter	ANOVA		Friedman test
	Sampling date	O versus C	O versus C
<i>Anaplectus</i>	ns	ns	ns
<i>Panagrolaimus</i>	0.02	ns	ns
<i>Rhabditis</i> s.l.	0.04	0.07*	0.03
<i>Acrobeloides</i>	ns	ns	ns
<i>Heterocephalobus</i>	ns	ns	ns
<i>Plectus</i>	0.01	ns	ns
<i>Eucephalobus</i>	ns	ns	ns
<i>Araeolaimida</i> „1”	ns	ns	ns
<i>Cephalobus</i>	ns	ns	ns
<i>Alaimus</i>	ns	ns	ns
<i>Wilsonema</i>	ns	ns	ns
<i>Prismatolaimus</i>	ns	ns	ns
<i>Monhystera</i>	ns	ns	ns
<i>Aphelenchoides</i>	ns	ns	ns
<i>Paraphelenchus</i>	ns	ns	ns
<i>Aphelenchus</i>	ns	ns	ns
<i>Nothotylenchus</i>	ns	ns	ns
<i>Deladenus</i>	ns	ns	ns
<i>Boleodorus</i>	ns	ns	ns
<i>Aprutides</i>	ns	ns	ns
<i>Tylenchorhynchus</i>	0.001	ns	ns
<i>Helicotylenchus</i>	ns	ns	ns
<i>Paratylenchus</i>	ns	ns	ns
<i>Paratrichodorus</i>	0.01	ns	ns
<i>Filenchus</i>	ns	ns	ns
<i>Ditylenchus</i>	ns	ns	ns
<i>Tylenchus</i>	ns	ns	ns
<i>Rotylenchus</i>	ns	ns	ns
<i>Aglenchus</i>	ns	ns	ns
<i>Trichodorus</i>	0.04	ns	ns
<i>Pratylenchus</i>	ns	ns	ns
<i>Mesodorylaimus</i>	ns	ns	ns
<i>Aporcelaimellus</i>	0.02	ns	ns
<i>Eudorylaimus</i>	0.05	ns	ns
Steinernematidae juv.	ns	ns	ns
Bacterivores – B	0.04	ns	ns
Fungivores – F	ns	ns	ns
Facultative plant feeders – FPF	ns	ns	0.03
Obligate plant feeders – OPF	ns	ns	ns
Omnivores – Om	ns	ns	ns
Density total	ns	ns	ns
Ratio B/F	ns	ns	ns
Ratio (B+F+FPF)/OPF	0.07	ns	ns

Table 2 continued

Taxon / Parameter	ANOVA		Friedman test
	Sampling date	O versus C	O versus C
Obligate plant feeders – OPF	ns	ns	ns
Omnivores – Om	ns	ns	ns
Density total	ns	ns	ns
Ratio B/F	ns	ns	ns
Ratio (B+F+FPF)/OPF	0.07	ns	ns
Number of taxa – S	ns	ns	ns
Shannon Index – H	ns	ns	ns
Maturity Index – MI	0.04	ns	ns
– Σ MI	0.001	ns	ns
– MINO MI	0.006	ns	ns
– Σ MINO MI	ns	ns	ns
– Ba MI	0.001	ns	ns
Plant Parasite Index –PPI	ns	ns	ns

ns – not significant

* This figure is given because of the importance of this taxon to further analyses

No significant differences were found in densities of taxa and in biocoenotic parameters between open and closed mesocosms, except for the taxon *Rhabditis* s.l. (O > C, ANOVA, $P = 0.07$, Friedman test, $P < 0.03$). The group of facultative plant feeders (FPF) showed differences in their densities between the mesocosms (C > O, Friedman test, $P < 0.05$) (Table 2).

As no differences were found between the open and closed mesocosms (except for *Rhabditis* s.l. over the two study years (1992 and 1993) combined, they were considered separately, especially because climatic conditions markedly differed between these years.

The dominance structure of taxa, trophic structure, and relations between functional groups were considered separately for Exp. I (1992) and Exp. II (1993).

Dominant taxa (over 4%) were identified which accounted for about 75% of the community when combined. In Exp. I these were *Pratylenchus*, *Panagrolaimus*, *Acrobeloides*, *Aphelenchoides*, *Rhabditis* s.l., and *Rotylenchus* (only in C). A similar composition was

observed for dominants in Exp. II: *Pratylenchus*, *Acrobeloides*, *Panagrolaimus*, *Aphelenchoides*, *Plectus* (as dominant only in Exp. II), and *Rhabditis* s.l. in O, also *Ditylenchus* in C (Table 3).

Statistically significant differences in density were found for only a few taxa: *Eudorylaimus* (O > C) in 1992, *Rhabditis* s.l. (O > C), and *Plectus* (C > O) in 1993 (Table 3).

Both similarities and differences in the trophic structure were found between the two study years (Table 4). The similarities included a total absence of predatory nematodes in the two years. Differences mostly referred to a higher abundance of nematodes in the more humid year (1993) as a result of an increase in the number of nematodes associated with the detrital food web (groups B, F, and FPF) (Table 4). The group of bacterivores was most abundant in the two study years. Together with fungivores, it accounted for over half of the total community, 54–58% in Exp. I and 58–62% in Exp. II).

Differences in the densities of trophic groups between the mesocosms were statistically confirmed only for bacterivores (C > O)

Table 3. Densities of nematode taxa (indiv. 10^3 m^{-2}) in open (O) and closed (C) mesocosms separately for Exp. I (1992), $n = 5$, and Exp. II (1993), $n = 3$. B – bacterivores, F – fungivores, FPF – facultative plant feeders, OPF – obligate plant feeders, Om – omnivores, PI – parasites of insects; c-p – ranks on the scale colonizers-persisters (Bongers 1990)

c-p value	Trophic group	Taxon	1992		1993	
			O	C	O	C
2	F	<i>Nothotylenchus</i>	4			6.7
5	Om	<i>Mesodorylaimus</i>	2			
3	B	<i>Araeolaimidae</i> „1”	2			
2	B	<i>Anaplectus</i>	2			
2	B	<i>Wilsonema</i>	1		40	53.3
4	B	<i>Alaimus</i>	3	2		
2	FPF	<i>Aglenchus</i>	2	2		6.7
2	F	<i>Deladenus</i>	2	4		
2	F	<i>Boleodorus</i>	2	2	6.7	
2	B	<i>Prismatolaimus</i>	2	2		
2	FPF	<i>Ditylenchus</i>	8	16	40	166.7
2	B	<i>Eucephalobus</i>	13	16	6.7	20
2	B	<i>Cephalobus</i>	15.5	44	33.3	46.7
4	Om	<i>Eudorylaimus</i>	19	4**	73.3	126.7
2	F	<i>Aphelenchus</i>	20	18	46.7	40
2	FPF	<i>Filenchus</i>	22	34	33.3	53.3
2	B	<i>Heterocephalobus</i>	26	12	6.7	13.3
4	OPF	<i>Paratrichodorus</i>	31	42	6.7	
5	Om	<i>Aporcelaimellus</i>	31	16		
2	B	<i>Plectus</i>	33	42	213.3	440*
3	OPF	<i>Rotylenchus</i>	34	108	66.6	86.7
2	FPF	<i>Tylenchus</i>	44	18	40	66.7
2	OPF	<i>Paratylenchus</i>	44	76	80	106.7
2	F	<i>Paraphelenchus</i>	52	22	26.7	80
3	OPF	<i>Tylenchorhynchus</i>	52	28	126.7	133.3
3	OPF	<i>Helicotylenchus</i>	80	68	60	33.3
1	B	<i>Rhabditis</i> s.l.	119	80	240	126.7 *
2	F	<i>Aphelenchoides</i>	176	136	306.7	320
2	B	<i>Acrobeloides</i>	418	408	446.7	553.3
1	B	<i>Panagrolaimus</i>	456	228	346.7	640
3	OPF	<i>Pratylenchus</i>	612	464	486.7	860
2	B	<i>Monhystera</i>	2	2		
2	F	<i>Aprutides</i>		2		
4	OPF	<i>Trichodorus</i>			26.7	26.7
–	PI	<i>Steinernematidae</i> juv.	116	30	53.3	20

Significance of differences between O and C: * $P < 0.05$, ** $P < 0.02$, Student's t – test.

in 1993 and omnivores ($O > C$) in 1992 (Table 4).

In the next step, differences between mesocosms O and C were analysed by comparing two basic nematode groups: associated with the detrital food web and those associated with the grazing food web. Numerical relations between these two functional groups of nematodes can serve as an index of matter and energy flux in a biocoenosis, and they make it possible to estimate the possible predominance of organic matter decomposition either in the detritus food web

(*via* bacteria and fungi) or in the grazing food web (by sucking plant sap) (Wasilewska 1996, 1997). Thus, these two functional groups of nematodes were compared (based on data in Table 4). As the group of facultative plant feeders, partly fungivorous, without well known trophic status, represents a difficulty in the classification, then a ratio between two functional groups (one associated with the detrital food web, and the other directly using primary producers) was compared in which the group FPF had variable position. In one case it was included to the detrital food web (No. 1 in Table 4) and in other

Table 4. Trophic structure of nematode communities: numbers of indiv. 10^3 m^{-2} ; in parentheses there is percentage in open (O) and closed (C) mesocosms for Exp. I (1992), $n = 5$, and Exp. II (1993), $n = 3$, separately. B – bacterivores, F – fungivores, FPF – facultative plant feeders, OPF – obligate plant feeders, Om – omnivores

Trophic groups	Exp. I		Exp. II	
	O	C	O	C
B	1092 (47)	836 (44)	1333 (48)	1893 (47) *
F	256 (11)	184 (10)	387 (14)	447 (11)
FPF	76 (3)	70 (4)	113 (4)	293 (8)
OPF	853 (37)	786 (41)	853 (31)	1247 (31)
Om	52 (2)	20 (1) *	73 (3)	127 (3)
Total ^a	2329 (100)	1896 (100)	2760 (100)	4007 (100)
Ratios (by number):				
1. (B+F+FPF)/OPF	1.67	1.39	2.15	2.11
2. (B+F)/(FPF+OPF)	1.45	1.19	1.78	1.52
3. (B+F+ ½ FPF)/(OPF+ ½ FPF)	1.56	1.28	1.95	1.78

^a Steinernematidae juv. excluded; * $P < 0.05$, Student's t – test.

Table 5. Percentage of taxa of bacterivorous nematodes on the colonizers-persisters (c-p) scale (see text) derived by Bongers (1990) and Bongers *et al.* (1995), and the Maturity Index for bacterivores (Ba MI) in open (O) and closed (C) mesocosms. 100% represents the whole group of bacterivorous nematodes

c-p value	Exp. I		Exp. II	
	O	C	O	C
1	52	36.8	44	40.5
2	47.5	62.7	55.9	59.5
3	0.4	0.2	0	0
4	0.09	0.2	0	0
Ba MI	1.48	1.63	1.56	1.59

case to the grazing food web (No. 2 in Table 4), or halves of it were included to both functional groups (No. 3 in Table 4). In all the three variants, the group of nematodes associated with the detritus food web predominated in open mesocosms (in Exp. I and Exp. II), although absolute numbers of bacterivores alone not always predominated in these mesocosms (Table 4).

The group of bacterivores was further analysed, as it was expected that it can respond to faeces and comminuted plant material formed as a result of macroarthropod activity. In Exp. I and Exp. II, the proportion of bacterivorous nematodes with rank 1 was higher in the open mesocosms (52% and 44%) than in the closed mesocosms (36.8% and 40.5%). Consequently, the index of bacterivore maturity (Ba MI) was lower in the open mesocosms (Table 5).

Rhabditis s.l., one of the dominant taxa also among bacterivores as tested by two-way ANOVA and a nonparametric test (Table 2), was more abundant in the open mesocosms on all sampling dates ($P < 0.03$), except in September 1992 (Fig. 1).

4. DISCUSSION

It is already known that nematode communities living in long-term grasslands reflect differences in soil biological processes and function, and that microbial biomass is positively correlated with nematode abundance (Bardgett *et al.* 1997, Wasilewska 1997, Yeates *et al.* 1997b, Bardgett *et al.* 1998). Nematodes and other soil biota play an important part in releasing nutrients from bacterial biomass. The dominance of bacterivorous nematodes arises from their ability to rapidly colonize resources in the soil. Those nematodes that respond first are enrichment opportunists, and this is primarily the case of Rhabditidae (after Bongers and Bongers 1998, Yeates 1998). It seems that in the present experiment, designed to assess changes in nematofauna caused by patrolling macroarthropods, it was reasonable to look for the response in the group of nematodes taking part in decomposition of organic matter. And so, although most taxa did not show significant changes in abundance between treatments, the numbers of *Rhabditis* s.l. varied (Table 2 and 3, Fig. 1).

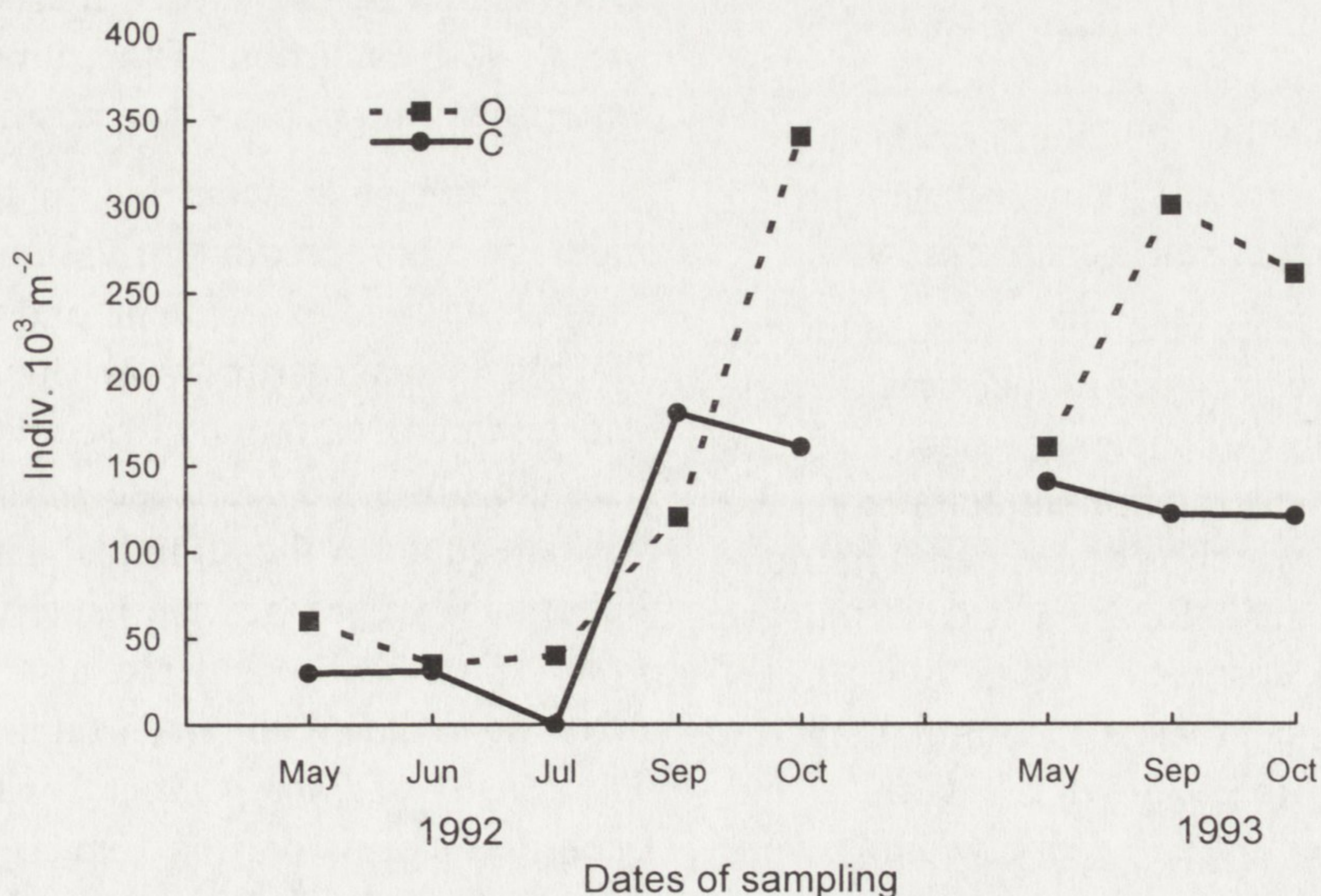


Fig. 1. Density of *Rhabditis* s.l. in open (O) and closed (C) mesocosms over the duration of Experiment I (1992) and Experiment II (1993) (O > C, Friedman test, $P < 0.03$)

Tendency to a higher abundance of nematodes associated with the detrital food web than in the grazing food web was observed in open mesocosms. This tendency occurred no matter to what group facultative plant feeders were assigned (Table 4). Bongers and Bongers (1998) tend to classify FPF rather as phytophages, in which case the ratio 2 from Table 4 would be closer to reality.

The group of bacterivores, the mean density of which was not significantly higher in open mesocosms (in Exp. I it was higher but not significantly, and in Exp. II, $C > O$), showed a characteristic feature. The proportion of taxa with rank 1 (*Rhabditis* s.l. and *Panagrolaimus*) was higher in open than in closed mesocosms. Moreover, the value of Ba MI was lower in open mesocosms in both experiments (Table 5), providing evidence for better food conditions in O than in C mesocosms. Examples of such responses, measured in the same way, are given by Wasilewska (1998). A similar response of bacterivorous nematodes was observed in the soil of pot experiments with plants subjected to grazing by orthopterans and sucking by aphids (Wasilewska 1998). The response depends only on the intensity of the stimulus.

Densities of *Rhabditis* s.l. were higher in open mesocosms in Exp. I and Exp. II (Fig. 1). Higher densities in open mesocosms in autumn coincided with higher carbon content in the soil to a depth of 3 cm, and were probably due to a higher soil moisture in 1993.

Thus, the main changes caused in the experiment by the presence of macroarthropods in the meadow concerned bacterivorous nematodes called enrichment colonizers, the occurrence of which is associated with transient conditions (Bongers and Bongers 1998). In mesocosms accessible to macroarthropods, the contents of comminuted organic matter (38.9 g dry wt m⁻²) and arthropod faeces (12.9 g dry wt m⁻²) were higher than in inaccessible (closed) mesocosms (17.1 g dry wt m⁻² and 2.1 g dry wt m⁻², respectively). As a result, in accessible

(open) mesocosms total bacteria, ammonifying bacteria, cellulolytic bacteria, Actinomycetes, and fungi were more abundant in Exp. I, and total bacteria, ammonifying bacteria, and cellulolytic bacteria in Exp. II. Moreover, the activity of enzymes: dehydrogenase, protease, and cellulase (Exp. I) and dehydrogenase and cellulase (Exp. II) was higher in open mesocosms (Stefaniak *et al.* 2000).

In this experiment, the regulation of nematode numbers by macroarthropods was likely to go not only through changes in trophic conditions in the belowground detrital food web, but also through predation by invertebrate fauna and nematophagous fungi. In the field experiment it was not possible to assess these interactions. Nor was it possible to estimate the regulatory role of entomopathogenic nematodes. If the numerical preponderance of nematodes of the group of insect parasites (free-living stage of the nematodes of the family Steinernematidae) in mesocosms accessible to macroarthropods were statistically documented, then it should be considered as a factor important to this biocoenosis. However, no statistical support was found for insect parasites whose numbers in open mesocosms were two-three times higher than in closed mesocosms (Table 3). The extension of the duration of the experiment might provide a positive answer.

The changes occurring in this experiment were observed by a five-month period. This was a field experiment, and the activity of epigeic macroarthropods showed spatial and temporal variation. It seems, however, that the observed response of Rhabditidae was adequate to the stimulus. This analysis intentionally excludes the bacterivore taxon *Panagrolaimus*, considered also as a colonizer, up to date with rank 1 on the c-p scale. The density of *Panagrolaimus* was higher in open mesocosms only in Exp. I, whereas in Exp. II it was more abundant in closed mesocosms. Bongers and Bongers (1998) expect to verify its position on the c-p scale.

This paper provides evidence that soil nematodes as a community or, like in this paper, as a functional group, are sensitive to environmental changes. This is indicative of their regulatory role in microbial communities and nutrient dynamics in the soil, as earlier shown in a more comprehensive way by Bardgett and Cook (1998), Bardgett *et al.* (1998), Ferris *et al.* (1998), and Huhta *et al.* (1998).

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5. SUMMARY

A field experiment in Arrhenatheretalia permanent meadow (peripheries of the Kampinos Forest, Central Poland) was carried out to estimate the effect of soil surface patrolling by macroarthropods on organic matter content in soil. The complete description of the experiment is given by Kajak (2000).

One of the components of this experiment was the soil nematode community (density, trophic structure, dominance, and also the diversity and maturity indices) which were compared between two types of mesocosms: accessible (open – O) and inaccessible (closed – C) to macroarthropods. The intensity of the penetration of the open mesocosms by macroarthropods (Formicidae, Carabidae, Araneae) was over 100 times higher than in closed mesocosms. Mesocosms contained meadow soil cores in isolators (bags), made up of a steelon screen with 24 mm meshes. Open mesocosms had holes cut at the soil interface.

To estimate nematodes, 100 mesocosms were established in 1992 and 60 mesocosms in 1993. Nematodes were sampled to a depth of 10 cm with a soil corer on 5 (1992) and 3 (1993) occasions. Ten soil cores were combined and processed according to Wasilewska (1979). Nematodes were identified to genus.

The experimental meadow was characterized by a low density of total nematodes (like another meadow located near Warsaw) (Table 1).

The following parameters were established: the density of nematode taxa (Table 3), the density of trophic groups (Table 4), ratios (by numbers) between groups (Table 4), the number of taxa, Shannon diversity index, maturity indices (MI, Σ MI, MINO MI, Σ MINO MI, Ba MI and PPI). Two-way ANOVA was used to compare above mentioned parameters between open and closed mesocosms (Table 2). Most parameters of nematodes did not vary significantly between mesocosms (Table 2 and Table 3).

The densities of the taxon *Rhabditis* s.l. were statistically higher in the mesocosms accessible to macroarthropods (Table 2, 3, and Fig. 1). The groups associated with the detritus food web (bacterial-, fungal- and facultative fungal feeding nematodes) predominated in open mesocosms (Table 4). The proportion of bacterivorous nematodes with rank 1 was higher and index of bacterivore maturity (Ba MI) was lower in open mesocosms (Table 5).

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