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PARTICIPATION OF SOIL NEMATODES IN GRASS LITTER DECOMPOSITION UNDER DIVERSE BIOCENOTIC CONDITIONS OF MEADOWS

ABSTRACT: Decomposition of *Dactylis glomerata* litter was compared in two adjoining ley meadows (aged 2–3 years and 8–9 years), differing in succession phase. The soil nematode density was higher in young meadow than in old one. In young meadow, the numbers of the litter-colonizing nematodes were several times higher. Exposure of litter always promoted an increase in the density of nematodes in the substrate. The species *Panagrolaimus rigidus* was the main dominant in litter.

KEY WORDS: decomposition, age of meadow, nematodes, litter, *Panagrolaimus rigidus*, biocenose richness.

1. INTRODUCTION

Agrarian treatments, including in the first place tillage, change the biocenotic relationships in plant and animal communities, as well as modify soil processes such as decomposition of organic matter, mineralization of elements and humification (S t i n n e r et al. 1984, H e n d r i x et al. 1986). Very recent studies dealing with the relationships between soil microflora and fauna have revealed the regulatory capacity of the fauna in soil processes (C r o s s l e y et al. 1989).

It can be expected that ecosystems with a soil layer remaining intact for a long time may form richer biocenoses. As concerns soil nematodes, it is more often found that tillage contributes to an increase in their numbers (e.g. P a r m e l e e and A l - s t o n 1986), but so far this phenomenon has not been fully elucidated.

The objective of the present studies was to compare litter decomposition in meadows differing in richness of the biocenosis. It was assumed that under conditions of a rich, more stabilized biocenosis the humification processes are enhanced, as compared with the situation when decomposition proceeds under conditions of a newly formed ecosystem. Participation of nematodes in litter decomposition processes was evaluated.

Studies of the numbers of soil mesofauna and macrofauna, rate of exposed litter weight loss, mineralization of elements and humification processes have been reported by K a j a k et al. (1991). On the basis of the same field experiment, this paper presents evaluation of the numbers and composition of soil nematodes in relation to litter decomposition and to participation of soil microflora and soil fauna in this process. It was found of interest, in the first place, to compare colonization of the experimental ecosystems by nematodes (as representatives of soil microfauna) and by larger soil invertebrates.

In these studies the occurrence of differences between new and old meadow in the community structure of the soil nematodes was considered to result from the reaction of these animals to the degree of simplification or richness of the biocenosis.

2. STUDY AREA, SCHEME OF EXPERIMENT AND METHODS

Studies were conducted in the Suwałki Landscape Park in NE Poland, near the Błaskowizna village. Two adjacentley meadows occurring on brown soil formed of light loamy sand of pH 7, were selected. Initially both meadows were sown with the same grass species – *Dactylis glomerata* L.; the succession of vegetation tends towards the Molinio-Arrhenatheretea class (J a n k o w s k i 1991). The meadows differed only in the time elapsed since their having been established; thus, the age of the new meadow (NM) was 2–3 years, and that of the old meadow (OM) was 8–9 years.

The experiment consisted of burying, in soil of both meadows, cages filled with soil from the parent meadow and cages containing sand. The variants with sand were designed to facilitate observation of the increase in elements and humic compounds resulting from litter decomposition, as well as to enable observation of the process of poor substrate penetration by the fauna and microflora from the ecosystem. The cage consisted of steelon screen (1 mm mesh, 100 cm^2 in surface area and 30 cm in length) with open top, containing at soil surface openings for penetration of animals (Fig. 1). In one half of the cages 15-g portions of dried aboveground parts of grass *Dactylis glomerata*, obtained in the first mowing, were exposed. Thus, four experimental variants were formed: cages with sand (Sa), with soil (S), with sand and exposed litter (Sa+L), and with soil and exposed litter (S+L). They were buried in new meadow (NM) and old meadow (OM). Sand (Sa) and soil (S), introduced into the cages, were referred to as substrates, as opposed to meadow soil from the area of the experiment.
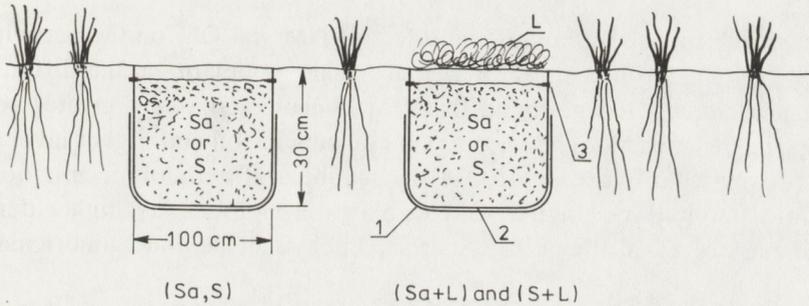
Fig. 1. Scheme of cages

Sa – sand, S – soil, L – litter from *Dactylis glomerata* (15 g dry weight), Sa + L – litter exposed on sand, S + L – litter exposed on soil, 1 – polyethylen foil bag, 2 – steelon screen (1 mm mesh), 3 – openings facilitating access of soil invertebrates

Many cages were used in order to enable analysis or numerous parameters, as reported by K a j a k et al. (1991).

For evaluation of the numbers and structure of the nematode communities, samples were taken from the substrate of selected cages (Sa, S, Sa+L, S+L) and from the meadow in the immediate vicinity of the cages. Steel soil corer with opening surface area of 2.5 cm^2, and 10-cm long, was used. A bulked (mixed) sample comprised 10 cores (1 core each from 10 cages of each experimental variant) or 20 cores of soil of the surrounding meadow. Samples of litter ($\_$) consisted of combined weight portions from several cages. Nematodes were extracted by the modified Baermann method (4 x 25 ml of soil).

The experiment was carried cut from 8 June 1984 until 15 May 1985. Soil samples were taken at the beginning of the experiment, and after 150 and 337 days; also samples of litter were collected at these two dates. For verification of the differences, the nonparametric test, Wilcoxon signed rank test were used (S i e g e l 1956). For evaluation of the generic diversity of nematodes Shannon index was applied (P i e - l o u 1975).

Detailed description of the methods applied in this experiment for: evaluation of the numbers of soil microflora, mesofauna and macrofauna in the substrate, litter and surrounding meadows; assessment of the enzymic activity in the substrate; evaluation weight losses of litter; chemical analysis of litter and substrate; assessment of the content of humic compounds, has been reported by K a j a k et al. (1991).

3. RESULTS

3.1. DENSITY OF NEMATODES IN NEW AND OLD MEADOW ECOSYSTEMS

In the search for the differentiating effect of NM and OM on the participation of nematodes in litter decomposition, it was necessary to determine the differences between these meadows. It was found that OM is characterized by greater abundance of plant species, higher nitrogen and carbon contents in soil and higher level of humic fractions. Likewise, in the case of OM the numbers of cellulolytic microorganisms and enzymic activity were higher. OM displayed a significantly higher density and greater biomass of the Collembola, Acarina, Enchytraeidae and Lumbricidae (Table 1).

Soil nematodes, as compared with the meso- and macrofauna, exhibited a different character of occurrence. The density of total nematodes and the density of separate trophic groups were greater in NM than in OM (Table 2). In both meadows the group of bacterivores was dominant; the group of obligatory plant parasites came second, having similar density in NM and OM (Table 2).

The composition of the nematode taxa was similar in both meadows, and the same genera were dominant in a given trophic group (if the analysis was based on samples collected on three dates). The dominant genera were: among becteriovores – *Acrobeloides*, *Prismatolaimus* and *Panagrolaimus*; among fungivores – *Aphelenchoides* and *Aphelenchus*; among facultative plant parasites – *Tylenchus* and *Ditylenchus*; among obligatory plant parasites – *Paratylenchus* and *Pratylenchus*; among omnivores – *Eudorylaimus*. In the group of predators different genera were dominant in NM and OM (Table 3).

3.2. LITTER: DECOMPOSITION AND BIOCENOSIS IN MEADOWS DIFFERING IN AGE

In the experiment litter was more rapidly decomposed in OM than in NM, this concerning both kinds of substrate: sand and soil. The litter weight loss rate, litter nitrogen content, nitrogen losses during the decomposition, formation of humic fractions and humification degree were greater in OM, although in the case of some parameters there was no statistical confirmation (Table 4).

The litter – colonizing microflora showed no significant differences between both meadows, except for cellulolytic microorganisms being more numerous in OM (Table 5).

Nematode numbers in litter were definitely greater in NM than in OM (exposed on sand 3.6 times and exposed on soil 3.3 times greater, $p < 0.001$) (Table 5). Litter microarthropods were quantitatively dominant in OM (Table 5). Thus, there was an opposition between the microfauna and mesofauna. The microfauna proved to be more numerous in the meadow with a less rich biocenosis. Thus, the age of meadow exerted an evident effect on the litter weight loss rate and on the composition of the soil-colonizing fauna.

Table 1. Soil and biocenotic parameters making a distinction between soil of new meadow (NM) and old meadow (OM) at the time of setting up the experiment

Number of plant species	NM	OM	Author
	13	39	Jankowski 1991
Nitrogen content in 0 – 10 cm soil layer (% dry wt)	0.137	0.193	Łakomiec (unpublished data)
Humic components in 0 – 10 cm soil layer (g C $\cdot$ 100 g^{-1} dry wt of soil)			Łakomiec (unpublished data)
total	1.397	1.660	
bitumen	0.0581	0.0838	
subst. dissolved in H_2SO_4	0.0760	0.1020	
humic acids	0.300	0.488	
fulvic acids	0.291	0.477	
Sum of extracted C	0.7250	1.1508	
Microflora (number of indiv. $\cdot$ g^{-1} dry wt of soil)			Kajak et al. 1991
Ammonifying bacteria (10^6)	24.7	25.6	
Actinomycetes (10^6)	2.6	1.6	
Fungi (10^5)	3.2	4.2	
Microorg. utilizing mineral N (10^6)	11.3	8.2	
Cellulolytic microorg. (10^3)	10.7*	11.4*	
Enzymes			
Dehydrogenase activity (μl H$_2$ $\cdot$ g^{-1} $\cdot$ d^{-1})	12.4*	14.3*	
Urease activity (mg N-NH$_4$ $\cdot$ 100 g^{-1} soil)	19.7*	31.9*	
Density ($\overline{N} \cdot m^{-2}$) and biomass ($\overline{B}$ in g fresh wt $\cdot$ m^{-2}) of meso- and macrofauna			
Collembola $\dfrac{\overline{N}}{B} \cdot 10^3$	16.4* 0.097*	68.6* 0.597*	
Enchytraeidae $\dfrac{\overline{N}}{B} \cdot 10^3$	2.9* 0.29*	7.6* 0.76*	
Acarina $\dfrac{\overline{N}}{B} \cdot 10^3$	14.5 0.461	20.0 0.149	
Lumbricidae $\dfrac{\overline{N}}{B}$	63.2* 20.2*	133.2* 147.3*	
Total $\overline{B}$	21.0*	148.8*	
Density of microfauna			
Nematoda ($\overline{N} \cdot 10^3 \cdot m^{-2}$)	7842*	4692*	present paper

* NM versus OM: $p < (0.05 - 0.001)$.

Table 2. Density of nematode trophic groups on new meadow (NM) and old meadow (OM) Mean values for 3 collection dates (June 1984, Nov. 1984, May 1985). Significance of differences evaluated by Wilcoxon's test: NM>OM, $N = 6$, $T = 0$, $p<0.05$

Trophic groups	NM		OM	
	$10^3 \cdot m^{-2}$ ± s.e.	%	$10^3 \cdot m^{-2}$ ± s.e.	%
Total community	7932 ± 1266	100.0	6368 ± 921	100.0
Bacterivores	3164 ± 518	39.9	2942 ± 633	46.2
Fungivores	1085 ± 205	13.7	485 ± 103	7.6
Facultative plant parasites	1456 ± 105	18.3	929 ± 236	14.6
Obligatory plant parasites	1647 ± 342	20.8	1697 ± 881	26.6
Omnivores	544 ± 250	7.0	306 ± 83	4.8
Predators	25 ± 14	0.3	9 ± 8	0.2

Decomposing organic matter promotes very substantial reproduction of nematodes. In the presented experiment the nematode number in litter was much higher than in soil; for example, after 150 days of litter exposition on NM there was 3367 nematode individuals per 1 g dry wt of litter and only 61 individuals per 1 g dry wt of soil in NM.

Litter colonization by nematodes was analysed on two dates i. e. after 150 and 337 days from litter exposure . Between the 150th and 337th day of the decomposition of litter the rate of its weight loss significantly decreased (Fig. 2). In this period the numbers of the microflora, as well as of the Acarina and Collembola greatly dropped (K a j a k et al. 1991). During this period the total numbers and biomass of nematodes either increased or showed no significant changes (Fig. 3), although there were differences in the numbers between various genera (Table 6). The higher level of nematoda numbers in NM than in OM persisted throughout the 1-year decomposition period.

3.3. LITTER: DOMINANCE STRUCTURES IN NEMATODE COMMUNITIES IN MEADOWS DIFFERING IN AGE

During the 1-year period of decomposition, litter was almost exclusively colonized by bacterivorous and fungivorous nematodes. *Panagralaimus rigidus* (Schneider 1866, Thorne 1937) was definitely dominant; it was much more numerous and displayed stronger dominance after 150 days than after 337 days of decomposition period (Table 6, Fig. 4). *Plectus* sp. was the second bacterivore in dominance sequence; it was more numerous by the end of the decomposition period. The dominance of two fungivores (*Aphelenchoides* and *Paraphelenchus*) was stronger in the second period of litter decomposition (Fig. 4).

Table 3. Comparison of the composition and density of nematode taxa in new meadow (NM) and old meadow (OM) (mean values for 3 collection dates)
Significance of differences evaluated by Wilcoxon's test: NM>OM, N = 46, T = 278, $p<0.002$

Trophic groups	Taxon	NM		OM	
		$10^3 \cdot m^{-2}$ ± s.e.	% in trophic group	$10^3 \cdot m^{-2}$ ± s.e.	% in trophic group
Bacterivores	Acrobeloides	1345 ± 228	42.5	1292 ± 224	43.9
	Prismatolaimus	365 ± 157	11.5	244 ± 92	8.3
	Panagrolaimus	349 ± 61	11.0	601 ± 439	20.4
	Plectus	291 ± 37	9.2	175 ± 109	5.9
	Rhabditis	241 ± 41	7.6	182 ± 72	6.2
	Cervidellus	109 ± 9	3.4	15 ± 8	0.5
	Cephalobus	105 ± 73	3.3	103 ± 61	3.5
	Acrobeles	78 ± 46	2.5	37 ± 18	1.2
	Heterocephalobus	75 ± 14	2.4	123 ± 43	4.2
	Eucephalobus	68 ± 32	2.1	17 ± 8	0.6
	Alaimus	62 ± 49	1.9	7 ± 7	0.2
	Monhystera	33 ± 17	1.0	9 ± 9	0.3
	Wilsonema	22 ± 12	0.7	29 ± 20	1.0
	Anaplectus	13 ± 13	0.4	60 ± 60	2.0
	Chiloplacus	9 ± 9	0.3	33 ± 17	1.1
	Teratocephalus			9 ± 9	0.3
	Tripyla			9 ± 9	0.3
Fungivores	Aphelenchoides	592 ± 51	65.5	227 ± 62	51.0
	Aphelenchus	273 ± 129	30.2	209 ± 108	47.0
	Neotylenchus	25 ± 25	2.8	9 ± 9	2.0
	Paraphelenchus	13 ± 13	1.4		
Facultative plant parasites	Tylenchus	649 ± 220	39.7	489 ± 44	50.3
	Ditylenchus	305 ± 154	18.6	149 ± 102	15.3
	Coslenchus	190 ± 94	11.6	29 ± 13	2.9
	Boleodorus	183 ± 133	11.2	41 ± 18	4.2

Table 3, continued

Trophic groups	Taxon	NM		OM	
		$10^3 \cdot m^{-2}$ ± s.e.	% in trophic group	$10^3 \cdot m^{-2}$ ± s.e.	% in trophic group
Facultative plant parasites	*Filenchus*	162 ± 61	9.9	154 ± 49	15.8
	Aglenchus	97 ± 78	5.9	17 ± 17	1.7
	Polenchus	25 ± 25	1.5	9 ± 9	0.9
	Psilenchus	20 ± 20	1.2	59 ± 46	6.1
	Basiria	5 ± 5	0.3		
	Miculenchus			25 ± 25	2.6
Obligatory plant parasites	*Paratylenchus*	737 ± 162	44.7	887 ± 499	52.2
	Pratylenchus	649 ± 204	39.4	685 ± 398	40.3
	Tylenchorhynchus	159 ± 22	9.6	84 ± 51	4.9
	Helicotylenchus	75 ± 75	4.5	33 ± 33	1.9
	Heterodera juv.	28 ± 17	1.7		
	Gracilacus			9 ± 9	0.5
Omnivores	*Eudorylaimus*	383 ± 161	69.0	207 ± 63	67.6
	Diphtherophora	55 ± 43	9.9	25 ± 25	8.2
	Aporcelaimellus	47 ± 47	8.5	35 ± 23	11.4
	Mesodorylaimus	45 ± 10	8.1	9 ± 9	2.9
	Pungentus	17 ± 17	3.1		
	Dorylaimida others	8 ± 8	1.4	15 ± 8	4.9
	Tylencholaimus			15 ± 8	4.9
Predators	*Mononchus*	8 ± 8	100.0		
	Tripyla			9 ± 9	100.0

The taxons composition was much poorer in litter than in meadow soil. Nematodes colonized litter selectively. In litter the above-mentioned *Panagrolaimus rigidus* was the dominant occurring in evident character of the "colonizer", whereas in meadow soil *Acrobeloides* was the main bacterivore dominant (Tables 3 and 6). Among fungivores, *Aphelenchus* did not occur in litter, but was numerous in meadow soil. Also plant parasites facultatively feeding on fungal hyphae, were absent from litter.

Table 4. Characterization of litter decomposition on new meadow (NM) and old meadow (OM) (sign + denotes the higher value, *NS* – not significant, according to K a j a k et al. 1991)

Parameters	Litter exposed on:					
	sand			soil		
	NM	OM	significance of differences between meadows	NM	OM	significance of differences between meadows
Litter weight loss rate		+	*NS*		+	*NS*
Half-life of litter disappearance	+			+		
Amount of nitrogen lost during litter decomposition		+	$p = 0.05$		+	$p = 0.05$
Humic fractions: (bitumen, subst. dissolved in H_2SO_4, humic acids, fulvic acids, humins)		+	*NS*		+	*NS*
Humification degree		+	$p < 0.001$		+	$p < 0.001$

Different substrate (Sa, S) influenced the nematode composition and number in litter to a lesser extent, as compared with differences in meadow age. Litter exposed in NM, both on sand and soil, displayed – as compared with litter exposed in OM – a several times more numerous *Panagrolaimus rigidus* population (Table 6). In litter exposed in OM the dominance of *Plectus* sp. was stronger (Table 6). Thus, the effect of meadow age on the nature of litter colonization by nematodes became manifest.

3.4. THE EFFECT OF LITTER ON THE SUBSTRATE

In the experiment it has been proved that the density of soil mesofauna (Collembola, Acarina and Enchytraeidae) and the numbers of the microflora were greater in the variants with exposed litter; moreover, the exposure of litter caused a significant increase in the contents of carbon, nitrogen and humic compounds in sand (K a j a k et al. 1991).

Similarly as in the case of the mesofauna, litter was found to cause a significant increase in the density of the whole nematode community (Fig. 5). The significance of the differences was evaluated by Wilcoxon test for two last dates of sample collection:

(Sa + L) > Sa, $N=8$, $T=0$, $p<0.01$; (S + L) > S, $N = 8$, $T = 0$, $p<0.01$

A similar effect was found for both main trophic groups of nematodes, i.e. for bacterivores:

Table 5. Numbers of the litter-colonizing organisms on new meadow (NM) and old meadow (OM) (according to K a j a k et al. 1991, except for the Nematoda)

Groups of organisms			Litter exposed on:	
			sand	soil
Microflora (indiv. $\cdot$ g^{-1} dry wt of litter)	ammonifying bacteria ($\cdot$ 10^8)	NM	132.6	122.3
		OM	148.6	93.6
	Actinomycetes ($\cdot$ 10^7)	NM	9.6	8.3
		OM	7.8	1.9
	fungi ($\cdot$ 10^7)	NM	17.5	18.6
		OM	14.0	10.1
	microorganisms utilizing mineral N ($\cdot$ 10^8)	NM	54.3	44.3
		OM	97.5	66.3
	cellulolytic microorganisms ($\cdot$ 10^4)	NM	62.8	31.3
		OM	84.2*	92.1*
Nematoda (indiv. $\cdot$ g^{-1} dry wt of litter)		NM	3106 ± 412	3314 ± 54
		OM	857 ± 236**	1003 ± 20***
Microarthropods (number of indiv. per 1 cage)	Collembola	NM	25.0	27.2
		OM	54.4	93.1
	Folsomia quadrioculata	NM	0.1	0.2
		OM	33.6*	66.5*
	Acarina	NM	192.7	191.4
		OM	211.5	143.6

* $p<0.05$. ** $p<0.01$. *** $p<0.001$ – NM versus OM.

(Sa + L)>Sa, $N = 8$, $T = 0$, $p<0.01$; (S + L)>S, $N = 8$, $T = 0$, $p<0.01$
and for fungivores:
(Sa + L)>Sa, $N = 8$, $T = 0$, $p<0.01$; (S + L)>S, $N = 8$, $T = 3$, $p<0.01$
(Figs. 6 and 7). This seems to be well-founded, as both these groups are associated with litter decomposition by bacteria and fungi. The numbers of the dominant genera of these two groups (*Rhabditis, Panagrolaimus, Aphelenchus* and *Aphelenchoides*) significantly increased in the case of exposed litter (Table 7). A positive reaction to litter exposure was displayed also by other genera of the group of bacterivores, by obligatory plant parasite – *Tylenchorhynchus*, and by omnivore – *Eudorylaimus* (Table 7).

3.5. KIND OF SUBSTRATE, AND NEMATODE DENSITY AND COMPOSITION

Introduction of a poor substrate (Sa) was aimed at facilitating observation of litter decomposition products; moreover, it offered an opportunity to observe nema-
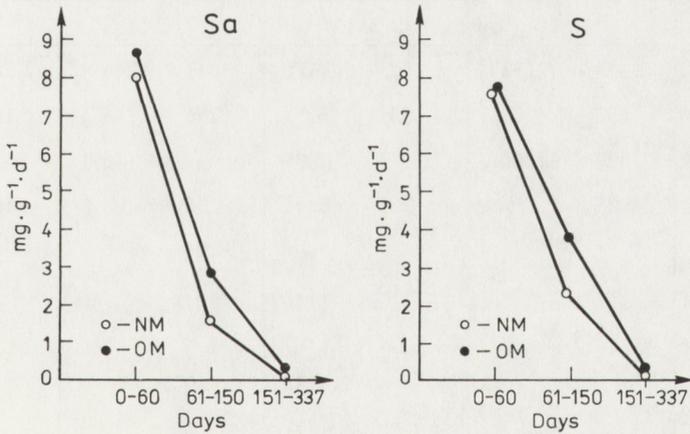
Fig. 2. The weight loss rate of litter exposed on sand (Sa) and on soil (S) of new meadow (NM) and old meadow (OM); according to K a j a k et al. 1991
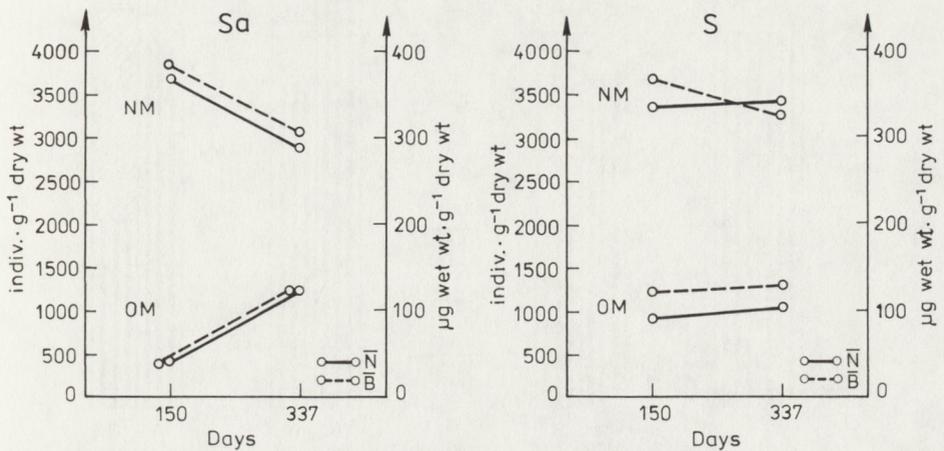

Fig. 3. Numbers ($\overline{N}$) and biomass ($\overline{B}$) of nematodes colonizing litter exposed on sand – Sa and on soil – S of new meadow (NM) and old meadow (OM) after 150 and 337 days

Table 6. Numbers of nematode genera colonizing litter on new meadow (NM) and old meadow (OM) (indiv. $\cdot$ g^{-1} dry wt of litter)
First number – after 150 days, the number in brackets – after 337 days from litter exposure

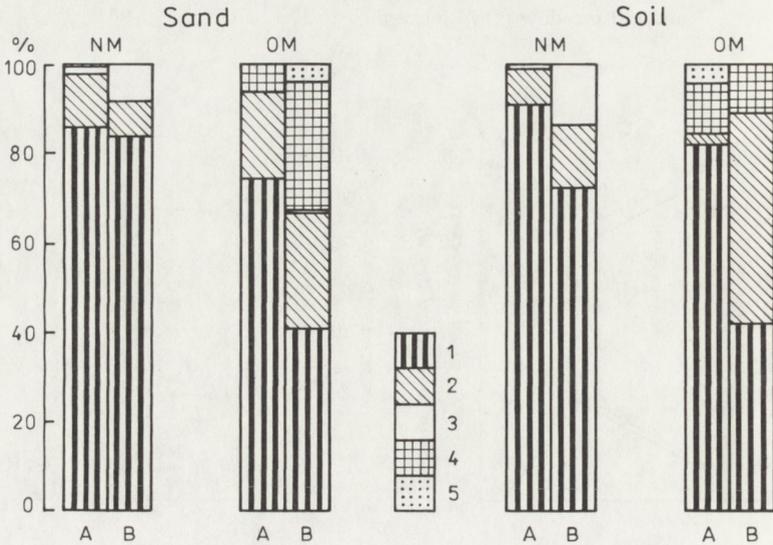| Genus	Sand				Soil			
	NM		OM		NM		OM	
Panagrolaimus	3318	(2133)	323	(367)	3043	(2467)	782	(440)
Aphelenchoides	452	(200)	83	(317)	256	(467)	100	(480)
Paraphelenchus	79	(200)		(3.3)		(467)		
Plectus	23		28	(367)	36		105	(113)
Rhabditis					44			
Heterocephalobus				(17)				
Mesodorylaimus				(10)	9			
Cephalobus				(3)	9			
Wilsonema				(7)				
Acrobeloides				(7)				
Tylenchorhynchus				(3)				

Fig. 4. Dominance structure of nematode genera colonizing exposed litter after 150 days (A) and 337 days (B) in new meadow (NM) and old meadow (OM)
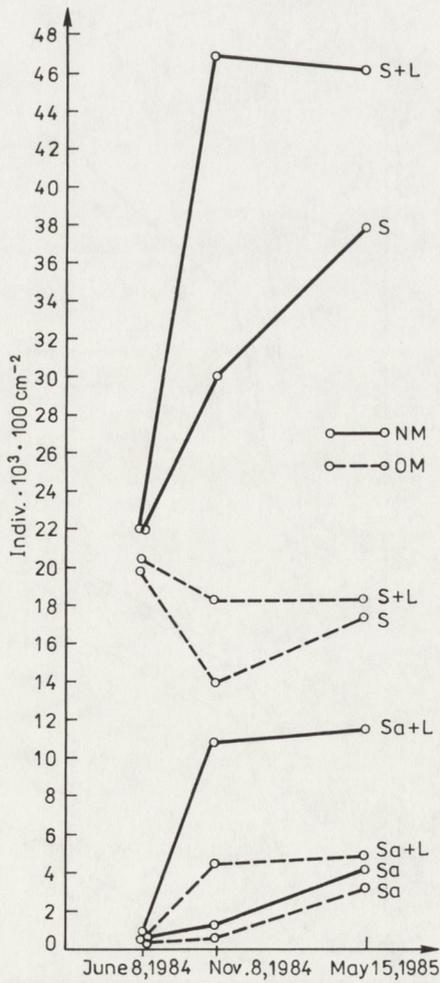1 – Panagrolaimus, 2 – Aphelenchoides, 3 – Paraphelenchus, 4 – Plectus, 5 – others

Fig. 5. Density of the whole nematode community in experimental variants dealing with new meadow (NM) and old meadow (OM) on three dates of sample collection
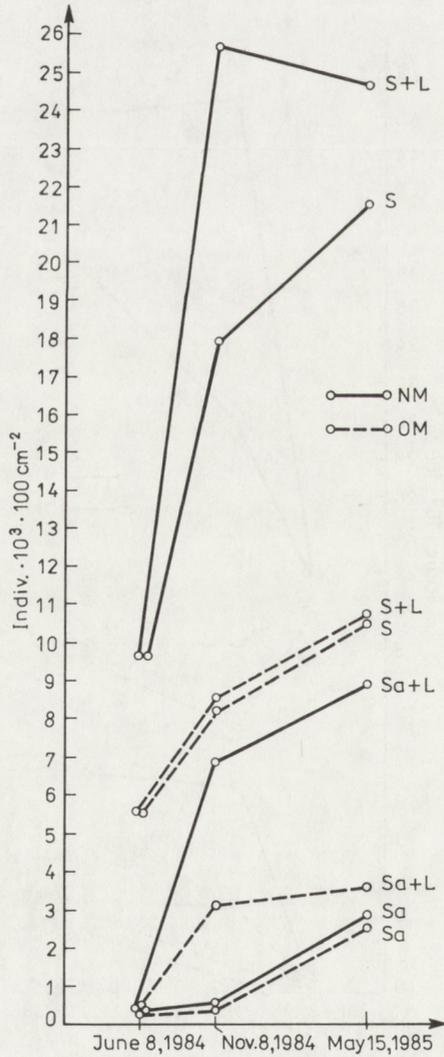Sa – sand, Sa + L – sand with exposed litter, S – soil, S +L – soil with exposed litter

Fig. 6. Density of bacterivorous nematodes in experimental variants dealing with new meadow (NM) and old meadow (OM) on three dates of sample collection
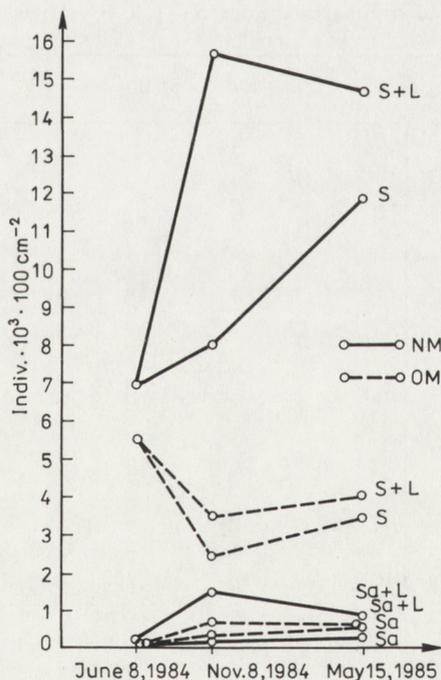Explanations as in Figure 5

Fig. 7. Density of fungivorous nematodes, jointly with facultative plant parasites, in experimental variants dealing with new meadow (NM) and old meadow (OM) on three dates of sample collection
Explanations as in Figure 5

tode penetration from the meadow soil and colonization of the new substrate. The total nematode density as well as the density of the bacterivorous and fungivorous groups was definitely higher in cages with soil (S) than in those with sand (Sa), on two dates of analyses (Figs. 5, 6 and 7). This also concerned the group of obligatory plant parasites (the range of density amounted for soil to 1360–3200 indiv. · 100 cm^{-2}, and for sand to 40–1400 indiv. · 100 cm^{-2}), and the group of omnivores, including predators (700–3016 and 0–1130 indiv. · 100 cm^{-2}, respectively).

Sand (Sa) is easily and rapidly colonized by nematodes; after 1 year it showed the presence of 37 taxons, whereas at this time soil (S) contained 46 taxons. The effect of litter exposed on sand (Sa + L), as compared with that exposed on soil (S

Table 7. List of nematode genera in cage substrate, whose reaction was related to the presence of exposed litter

(The samples with and without litter were placed in opposition, irrespective whether they originated from new meadow (NM) or old meadow (OM). The percentage of samples in which the numbers of the given species increased by more than a half (+) or dropped by more than a half (–) was accepted as the measure.)

Sa – sand, Sa + L – sand with exposed litter, S – soil, S + L – soil with exposed litter

Genus	$Sa + L_{(NM + OM)} > Sa_{(NM + OM)}$	$S + L_{(NM + OM)} > S_{(NM + OM)}$
Rhabditis	+	+
Panagrolaimus	+	+
Aphelenchus	+	+
Aphelenchoides	+	+
Tylenchus	+	+
Eudorylaimus	+	+
Tylenchorhynchus	+	+
Plectus	+	+
Chiloplacus	+	+
Heterocephalobus	+	+
Acrobeles	+	+
Cephalobus	+	–
Acrobeloides	+	–
Wilsonema	+	–
Prismatolaimus	+	–
Cervidellus	+	–
Pratylenchus	+	–
Paratylenchus	+	–
Number of all genera in substrate	(Sa) (Sa + L) 37	(S) (S + L) 46

+ L), stronger promoted an increase in the number of genera (Table 7). The genera: *Acrobeloides, Cephalobus, Acrobeles, Wilsonema, Prismatolaimus* and *Cervidellus* (bacterivores), as well as *Pratylenchus* and *Paratylenchus* (obligatory plant parasites) displayed a smaller or greater drop in the density in the case of litter exposed on soil (Table 7). Meadow soil was in the first place richer in omnivores and predators, e.g. *Pungentus, Dorylaimellus, Nygolaimus* and *Discolaimus*, and in obligatory plant parasites, e.g. *Meloidogyne, Heterodera* and *Criconemoides* (not indicated in Table 7).

3.6. THE EFFECT OF NEW AND OLD MEADOW ON NEMATODES IN THE SUBSTRATE

Old meadow (OM) is characterized by greater increases in substrate nitrogen and carbon contents, resulting from *D. glomerata* decomposition; likewise, the levels of

different humic fractions are higher (K a j a k et al. 1991). This indicates that in the OM substrate the humification process is more intensive and the element retention ability is higher. The authors of this finding (K a j a k et al. 1991) relate this fact to greater abundance of the mesofauna (particularly of the Collembola) in OM. The microflora displayed no significant differences between meadows, except for the Actinomycetes and microorganisms utilizing mineral N, whose numbers are significantly greater in NM (K a j a k et al . 1991).

According to the present results, similarly as nematodes in litter, the Nematoda colonizing the substrate proved to be significantly more abundant in the cages buried in NM. This took place for the whole nematode community irrespective of the experimental variant (the significance of the differences was verified by Wilcoxon test for 2 dates of sample collection: 8 November 1984 and 15 May 1985):

$$NM_{(Sa), (Sa + L)} > OM_{(Sa), (Sa + L)}, N=8, T=0, p<0.01;$$
$$NM_{(S), (S + L)} > OM_{(S), (S + L)}, N=8, T=0, p<0.01 \text{ (Fig. 5)};$$

for the group of bacterivores:

$$NM_{(Sa), (Sa + L)} > OM_{(Sa), (Sa + L)}, N=8, T=0, p<0.01$$
$$NM_{(S), (S + L)} > OM_{(S), (S +L)}, N=8, T=0, p<0.01 \text{ (Fig. 6)};$$

for the group of fungivores:

$$NM_{(Sa), (Sa + L)} > OM_{(Sa), (Sa + L)}, N=8, T=2, p<0.02$$
$$NM_{(S), (S + L)} > OM_{(S), (S + L)}, N=8, T=0, p<0.01 \text{ (Fig. 7)};$$

and for the group of omnivores including predators (density ranges in sand: in NM: 260–1000 indiv. $\cdot$ 100 cm^{-2}, in OM: 0–204 indiv. $\cdot$ 100 cm^{-2}; density ranges in soil: in NM: 2480–3392 indiv. $\cdot$ 100 cm^{-2}, in OM: 600–1128 indiv. $\cdot$ 100 cm^{-2}). The density of the obligatory plant parasites was drastically reduced after placing of soil in the cages; they did not exceed 3000 indiv. $\cdot$ 100 cm^{-2}, probably because of a lack of host plants.

Nematode communities comprised more taxa in NM than in OM (Table 8). Several genera displayed greater density in NM than in OM. This concerned 8 genera in the case of a poor substrate (Sa, Sa + L) and 17 genera for a rich substrate (S, S + L) (Table 8). They were mainly bacterivores and fungivores. In contrast, the obligatory plant parasites were more abundant in OM (Table 8), except for the genus *Tylenchorhynchus* being more numerous in NM.

Higher density of nematodes, in the situation when the meso- and macrofauna were less numerous, was found both in litter and substrate. The exception was variant S or S + L, where the Acarina and Enchytraeidae follow the same pattern like Nematoda, being more abundant in NM than OM (Table 9).

3.7. DIVERSITY INDEX OF NEMATODES IN NEW AND OLD MEADOW

The present results testified to significant taxonomic differentiation of in the case of both – the experimental meadows and the experiment itself. Shannon's generic diversity index (H') was higher for the NM than OM ecosystem. The eveness index

Table 8. List of nematode genera in cage substrate, whose reaction was related to the age of meadow (The samples from new meadow (NM) and old meadow (OM) were placed in opposition, irrespective whether they originated from a substrate with or without litter. The percentage of samples in which the numbers of the given species increased by more than a half (+) or dropped by more than a half (−) was accepted as the measure.)
Explanations as in Table 7

Genus	$NM_{(Sa)\ (Sa+L)} > OM_{(Sa)\ (Sa+L)}$	$NM_{(S)\ (S+L)} > OM_{(S)\ (S+L)}$
Rhabditis	+	+
Panagrolaimus	+	+
Aphelenchus	+	+
Aphelenchoides	+	+
Acrobeloides	+	+
Acrobeles	+	+
Tylenchorhynchus	+	+
Eudorylaimus	+	+
Tylenchus		+
Aglenchus		+
Filenchus		+
Cervidellus		+
Wilsonema		+
Boleodorus		+
Alaimus		+
Tylencholaimus		+
Prismatolaimus		+
Paratylenchus		−
Pratylenchus		−
Number of all genera in substrate of:	(Sa) (Sa + L)	(S) (S + L)
NM	33	42
OM	30	39

pointed to greater differentiation of the nematode community in the NM ecosystem (Table 10).

In a case of nematodes colonizing litter, the situation was different. The diversity index of nematodes in litter exposed for decomposition was higher for OM than for NM; this concerned both kinds of substrate on which litter was exposed. Between the 150th and 337th day of litter decomposition, the generic diversity index increased (Fig. 8).

Table 9. Colonization of litter and substrate by soil invertebrates in the experiment on new meadow (NM) and old meadow (OM) (samples collected in Nov. 1984) (according to K a j a k et al. 1991, except for the Nematoda)

Sa – sand, Sa + L – sand with exposed litter, S – soil, S + L – soil with exposed litter

Taxa		Litter (indiv. · g^{-1} dry wt) exposed on:		Substrate (indiv. · 100 cm^{-2})			
		Sa	S	Sa	Sa + L	S	S + L
Nematoda	NM	3754	3335	1080	10840	29760	41248
	OM	433	947	180	4390	13760	12060
Acarina	NM	24.3	26.6	1	62	29	305
	OM	30.9	22.8	1	78	89	129
Collembola	NM	3.2	3.8	5	32	67	324
	OM	7.9	14.8	21	357	283	980
Enchytraeidae	NM			10	24	130	135
	OM			19	70	65	73

Table 10. Shannon's generic diversity index (H') and evennes index (e) for nematode communities in the new meadow (NM) and old meadow (OM) environments

Date of collection	NM		OM		NM versus OM
	H'	e	H'	e	
June 1984 (beginning of experiment)	4.21	0.86	3.90	0.80	$p<0.001$
Nov. 1984 (after 150 d)	4.15	0.85	3.37	0.72	$p<0.001$
May 1985 (after 337 d)	4.06	0.84	3.85	0.81	$p<0.001$

The diversity index of nematodes in the substrate of the cages assumed, inversely as in litter and similarly as in the experiment-surrounding meadows, higher values for NM than for OM (with one exception). The Shannon's index was lower for all experimental variants involving sand and was higher for all combinations with soil (Table 11).

The positive effect of litter on the Shannon's index became manifest only during the early part of the decomposition period (Table 11).

4. DISCUSSION

The no-tillage agroecosystem bears a similarity to the natural system in which nutrient cycling is more conservative, decomposition of organic debris is slower, soil
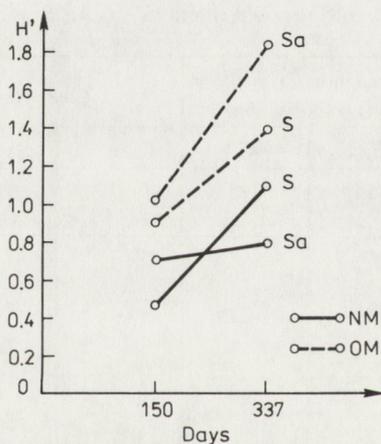
Fig. 8. Shannon' generic diversity index (H') of nematode communities colonizing litter in experimental variants dealing with new meadow (NM) and old meadow (OM) after 150 and 337 days of exposure

Sa – litter exposed on sand, S – litter exposed on soil

Table 11. Comparison of the Shannon's diversity index (H') obtained for nematode communities in the substrate of cages located in new meadow (NM) and old meadow (OM)

Sa – sand, Sa + L – sand with exposed litter, S– soil, S + L – soil with exposed litter

Date	Meadow	Sa	Sa + L	S	S + L
June 1984	NM	2.96		4.05	
	OM	2.96		3.83**	
Nov. 1984	NM	3.37	3.88	3.77	4.02
	OM	2.84*	3.67	3.50	3.85*
May 1985	NM	3.42	3.35	3.77	3.92
	OM	3.27	2.84**	4.04**	3.78*

* $p = 0.05$. ** $p = 0.01$ – NM versus OM.

biota are numerous and their activity is high (H o u s e and B r u s t 1989) . Tillage creates conditions for the development of saprophages – grazers, with a high metabolic rate and rapid ontogenesis.

C o l e m a n et al. (1988) single out two different types of trophic webb, in dependence on the agrosystem: tillage system dominated by bacteria, and no-tillage system dominated by fungi and – correspondingly – by their grazers.

It is possible to perceive in NM the model resulting from the tillage system and in OM the no-tillage model displaying many properties of the natural system (attaining stabilization during 8 years). In general outline a picture consistent with the model of the tillage system and natural system was obtained. In the first place this became manifest in that in OM the numbers of the macrofauna and mesofauna were greater, and the processes of humification and element retention were predominant. In NM the microfauna proved to be definitely more numerous. Grass litter weight loss was in the experiment more rapid in OM than in NM. It cannot be ruled out that in OM the litter was mechanically pulled into soil by the more numerous soil meso- and macrofauna. It is also probable that the regulatory processes among soil invertebrates are responsible for the state observed in the experiment.

Grazing is a process which both reduces soil microflora and stimulates its turnover (H a n l o n and A n d e r s o n 1979). Nematodes grazing on bacteria and fungi reduce the number of the microorganisms responsible for the decomposition. On the other hand, the indirect role of nematodes in the element mineralization process is known (F r e c k m a n 1988); this second function is most often demonstrated in simple systems of the microcosmos type. Under natural conditions it is difficult to draw a distinction between both these functions , because many processes and interactions occur in soil simultaneously. The present results are at most sufficient for putting forward hypotheses.

In the present experiment the litter was almost exclusively colonized by bacterivorous and fungivorous nematodes, whereas in the substrate of the cages these nematodes accounted for 77–85% of the whole community. It is justified to assume that bacterivorous and fungivorous nematodes grazing on the microflora active in decomposition contribute to slowing down of the decomposition rate. This takes place in NM where their numbers exceed those of nematodes in OM.

Some microflora groups, e.g. cellulolytic microorganisms (in meadow soil, litter and substrate) and microorganisms utilizing mineral N (in litter), display in fact smaller numbers in NM than in OM. Indeed, an increase in the number of nematodes grazing on the microflora in the system being in time closer to the moment of tillage (NM), as compared with the no-tillage system (OM), is confirmed in the literature (P a r m e l e e and A l s t o n 1986, S o h l e n i u s and S a n d o r 1989, E l T i t i and I p a c h 1989). In the present studies author did not succeed in providing a univocal explanation of the microflora – grazers relationships.

The ecosystem of the recently ploughed meadow (NM), as compared with that of the meadow ploughed long ago (OM), was characterized by significantly greater numbers of the fungal feeding Tylenchida (denoted as the group of fungivores and facultative plant parasites in Table 2 and Fig. 7). This is inconsistent with the model presented by H e n d r i x et al. (1986), whereas it is in agreement with the results

of S o h l e n i u s and S a n d o r (1989). This indicates that the problem is still
"young" and calls for further studies.

The much richer meso- and macrofauna in OM comprises the animals doubtless
responsible for the reduction of nematodes. Examples from the literature prove that
experimental reduction of the numbers of nematodes (grazing on bacteria and fungi)
as a result of predatory pressure of mites has promoted litter decomposition under
desert conditions (S a n t o s et al. 1981, W h i t f o r d et al. 1982, P a r k e r et al.
1984). In general it is evaluated that organic matter decomposition is reduced by
40%, if there is no pressure of predatory mites on nemetodes grazing on bacteria
(Y e a t e s and C o l e m a n 1982). Various mesostigmatid, astigmatid, crypto-
stigmatid and endeostigmatid mites feed on nematodes (M u r a o k a and I s h i -
b a s i 1976, K a r g 1983, W a l t e r et al. 1986, W a l t e r 1988a, W a l t e r
1988b). There is also the reduction of nematode numbers by earthworms in grass
ecosystems and experiments (D a s h et al. 1980, Y e a t e s 1980, 1981,
R ö s s n e r 1981). In the present experiment and in meadow soil surrounding the
cages, the earthworms were more numerous in OM and thus the pressure on nema-
todes was higher. Nematodes stronger reduce the microflora active in litter decompo-
sition if the level of their numbers is higher and the impact of predators is less strong.
S e t ä l ä and H u h t a (1990) are of a similar opinion.

Apart from predation – caused reduction of nematodes, reduction resulting from
interspecies competition for food cannot be ruled out. This assumption arises from
the fact that the lower numbers of fungi in OM may be due to grazing by the strongly
represented fungivorous Collembola species, particularly *Falsomia quadrioculata*
Tullb. The latter species, being the dominant among the Collembola in OM, does not
occur in NM; this could lead to a higher level of the numbers of fungivorous nema-
todes. The fact of microbial grazing by one of the species of *Folsomia* sp.
(A n d r é n and S c h n ü r e r 1985) allows for perceiving similar relationships
of competition for food between bacterivorous nematode species and Collembola
strongly represented in OM.

The ability of bacteri- and fungivorous nematodes to colonize new habitats, par-
ticularly those enriched in decomposing organic matter, is well known (W a s i l e -
w s k a et al. 1981, S o h l e n i u s and B o s t r ö m 1984, W a s i l e w s k a and
B i e ń k o w s k i 1985); this explains the great numbers of nematodes in decompo-
sing litter. *Panagrolaimus rigidus*, being the most important dominant in litter, found
better developmental conditions in NM, irrespective whether litter was exposed on a
poor substrate (sand) or on a richer one (soil). It may be assumed that there are
involved, apart from trophic conditions, also other factors (perhaps the absence of
competing species). These facts suggest that *P. rigidus* is a species of the nature of
"colonizer". Earlier literature data indicate that *P. rigidus* stronger colonizes litter than
soil (W a s i l e w s k a and B i e ń k o w s k i 1985); its occurrence beyond litter
is in the first place associated with the upper and near–surface layer of meadow soil
(W a s i l e w s k a 1974), and it displays plant penetration ability (W a s i l e w s k a
1967).

The composition of nematode dominants colonizing the investigated litter originating from *Dactylis glomerata* and litter derived from spring barley (in another experiment – W a s i l e w s k a and B i e ń k o w s k i 1985) was closely similar. In both cases the genera *Panagrolaimus* and *Aphelenchoides* were dominant. In barley litter exposed in a potato culture also *Rhabditis* sp. was dominant, this being related to earlier fertilization of the field with manure (other situation than in a meadow). The consistence of the composition of dominants in both litters concerns also the dynamics of their numbers. During the 1-year decomposition period the dominance and numbers of *Panagrolaimus* sp. dropped, whereas those of *Aphelenchoides* sp. increased (in the case of the meadow ecosystem, this concerned soil). Therefore, neither the type of eeosystem (crop field, meadow) nor the age of meadow (NM, OM) changed the fact of dominance of the same nematode taxa. The age of meadow was only decisive of the population density. This problem calls for closer investigations, as suggested by e.g. the fact that *Panagrolaimus* sp. has not been strongly represented in barley litter in a decomposition experiment performed in Sweden (S o h l e n i u s and B o s t r ö m 1984).

N o r t o n (1989) has stressed that species diversity is an important biocenotic parameter of the nematode community. As concerns conventional and no-tillage cultivation, literature data claim either that tillage promotes an increase in the diversity index in nematode communities (S t i n n e r and C r o s s l e y 1982, N o r t o n 1989), or that the effect of tillage is of low importance (S o h l e n i u s and S a n - d o r 1989). The present results concerning meadow ecosystems testify to a similar relationship (index *H*' is higher for NM than for OM). It remains unclear why in the case of litter colonized by nematodes the situation is opposite (index *H*' is higher for OM than for NM). Similar tendencies in nema'ode colonization, making a distinction between NM and OM, are observed irrespective whether at the time of setting up the experiment the substrate is different (soil) or identical (litter, sand).

5. CONCLUSIONS

(1) There are differences between new meadow (2–3 years after establishment) and old meadow (8–9 years after establishment) in soil nematode colonization of grass litter exposed for decomposition. (2) In the ecosystem of new meadow and in litter exposed on new meadow soil nematode numbers are always greater than in the case of old meadow. (3) The richer meso- and macrofauna of old meadow and the higher level of the humification processes, displayed by this meadow, are consistent with less abundant nematodes microfauna representing. (4) Litter exposure always promotes an increase in substrate content of nematodes, mainly of the groups of bacterivores and fungivores. (5) The nematode species *Panagrolaimus rigidus* is the main dominant (80–90%) among nematodes colonizing grass litter. It is considered to be the "colonizer" in decomposing plant material.

6. SUMMARY

The present experiment was aimed at evaluation of nematode participation in the process of grass litter decomposition in two ley meadow ecosystems differing in the time elapsed from their establishment and consequently differing in the meadow succession phase. New meadow (2–3 years after establishment, was characterized by a seven times smaller biomass of the soil meso- and macrofauna, lower enzymic activity in soil (Table 1), greater nematode numbers and higher diversity index of nematode communities, as compared with old meadow (8–9 years after establishment) (Tables 2, 3, 10).

The present experiment consisted at of cages filled either with soil from the parent meadow or with sand, which were dug into the soil of both meadows (Fig. 1). The experimental variants with sand were intended to faciliate observation of the course of the decomposition and humification processes, and the differences could be attributed to the dissimilar biocenosis state in both meadows. In old meadow the litter exposed for decomposition was mineralized more rapidly and the substrate displayed higher retention of the elements released from litter as well as a higher level of humic fractions (Fig. 1, Table 4).

In this biocenotic and habitat situation, the numbers of nematodes colonizing litter and the nematode density in substrate were several times greater in new meadow than in the old one (Figs. 3, 5, 6, 7, Tables 6, 8, 9). The richer meso- and macrofauna of old meadow and the higher level of the humification processes, typical of this meadow, were consistent with lower levels of the numbers of nematodes which represent microfauna. Litter exposure always promoted an increase in nematode density in the substrate (Table 7). Nematode species *Panagrolaimus rigidus* was the main dominant (80–90%) among litter-colonizing nematodes (Fig. 4). It is regarded as the "colonizer" in decomposing plant material.

7. POLISH SUMMARY

Celem przeprowadzonego eksperymentu była ocena udziału nicieni w procesie rozkładu ściółki trawiastej w dwóch ekosystemach łąkowych zróżnicowanych czasem od zagospodarowania, a co za tym idzie – fazą sukcesji łąki. Łąka nowa (2–3 lata od zagospodarowania) charakteryzowała się siedmiokrotnie mniejszą biomasą mezo- i makrofauny glebowej, mniejszą aktywnością enzymatyczną w glebie (tab. 1) oraz wyższą liczebnością nicieni i wyższym wskaźnikiem różnorodności w zespołach nicieni niż łąka wieloletnia (8–9 lat od zagospodarowania) (tab. 2, 3, 10).

Założono eksperyment polegający na wkopaniu w powierzchnię każdej z łąk izolatorów, wypełnionych glebą z łąki macierzystej lub wypełnionych piaskiem (rys. 1). Kombinacje z piaskiem miały ułatwić śledzenie przebiegu procesu rozkładu i humifikacji, zaś różnice można było przypisać odmiennemu na obu łąkach stanowi biocenozy. Wyłożona do rozkładu ściółka ulegała szybszej mineralizacji na łące wieloletniej, a w podłożu nastąpiła większa retencja pierwiastków uwolnionych ze ściółki i tam też był wyższy poziom frakcji próchnicznych (rys. 2, tab. 4).

W takiej sytuacji biocenotycznej i siedliskowej stwierdzono, iż liczebność nicieni zasiedlających ściółkę oraz podłoże była kilkakrotnie wyższa na łące nowej niż na łące wieloletniej (rys. 3, 5, 6, 7, tab. 6, 8, 9). Bogatsza mezo- i makrofauna łąki wieloletniej i wyższy na niej poziom procesów humifikacji były więc zbieżne z niższym poziomem liczebności mikrofauny – nicieni. Stwierdzono, iż wyłożenie ściółki zawsze sprzyjało wzrostowi liczebności nicieni w podłożu (tab. 7). Gatunek nicienia *Panagrolaimus rigidus* jest głównym dominantem (80–90%) wśród nicieni zasiedlających ściółkę (rys. 4). Uznano go za "zasiedlacza" w rozkładającym się materiale roślinnym.

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