EKOLOGIA POLSKA (Ekol. pol.)	45	3-4	839 – 859	1997

Anna KAJAK, Lucyna WASILEWSKA

Department of Soil Ecology, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny, 05-092 Łomianki

CHANGES IN MEADOW ECOSYSTEMS AS CONSEQUENCE OF SECONDARY SUCCESSION AND PLANT DIVERSITY (SYNTHESIS OF RESEARCH)

ABSTRACT: The decomposition process of *Dactylis glomerata* and the accumulation rate of organic matter was compared in meadows differing in the time since tillage ceased. Over time number of plant species in the sward and the diversity of the majority of analysed invertebrate groups increased.

The youngest meadows were characterized by maximal variability in environmental conditions and variation in the numbers of several dominant invertebrate populations. Litter bags exposed in this meadow were colonized rapidly by bacteria, but slowly by microarthropods, compared to older meadows. The lowest accumulation of total organic carbon and humus fractions was also found in mesocosms inserted in soil profile of these meadows. The community structure of invertebrates colonizing mesocosms was characteristic for ecosystems under stress. Relatively high proportion of small organisms (bacteria, bacteriphagic invertebrates) stimulating the mineralization rate of organic matter were recorded.

KEY WORDS: decomposition, grass litter, secondary succession, carbon accumulation, species diversity, invertebrates, microbes.

1. INTRODUCTION

During the last few decades declining plant species diversity has been recorded in many meadows in Poland, which up till now has not been found on such scale. A decrease of the plant species richness in sward and the high predominance of one or two populations were recorded. One of the most common species has been *Dactylis glomerata*. There are various reasons for these changes, one of the important factors might be a high dozage of fertilizing, especially nitrogen fertilizing (Traczyk and Kotowska 1976, Dąbrowska and Mazur 1987, Kostuch 1987, Michalik 1990a, Kornaś and Dubiel 1990). Impoverished swards have also been observed however in national parks and nature reserves which are excluded from cultivation (Kornaś 1990, Kazimierczakowa 1990, Denisiuk 1990, Michalik 1990b). Mainly the specialized species have declined, whereas mesophyllous, ubiquitous and synanthropic species have expanded (Denisiuk 1990).

Although plant species impoverishment is very common, their effect on ecosystem functioning, primarily on organic matter decomposition is scarcely known.

Our investigations on the influence of uniforming of grassland sward on the diversity of invertebrates, community structure and decomposition were carried out in the Suwałki Landscape Park and in its buffer zone. Plant species richness was strickly related to the successional stage of the meadows. In this region it is quite common that some cultivated fields are converted into leys for several years. These are mown in the spring and grazed by cattle or horses in autumn. Besides there permanent meadows occur, occupying areas where cultivation is difficult. Those meadows are characterized by the highest plant diversity. Plant diversity was related not only to successional age but also inversely related to the intensity of cultivation. Frequent mowing and fertilizing prolong the period of uniform vegetation.

Although the causes of community richness may vary it was hypothesized that their consequences are similar. Suwałki region is a good area for investigating biodiversity, because due to heterogenic relief, in relatively small distance grass monocultures and meadows with diverse plant cover could be found.

Investigations were located in *Arrhenatheretalia* grasslands occurring in outwash plain and in its slopes, on brown soils derived from medium sand (Kusińska and Łakomiec 1997, Jankowski 1997a). 12 study sites formed 4 sequences of meadows varying in successional stage, ranging from new leys (LA) with predominance *Dactylis glomerata* to permanent meadows (P) with rich plant community (Table 1). Over successional age the trends of increasing species richness were coupled with increasing heterogenity of vertical structure, forming of litter layer, increasing organic matter content and sorption capacity in soil (Table 1).

Table 1. Characteristics of study sites

Properties	Grass leys LA	Grass leys LB	Grass leys LC	Permanent meadow P	Author
Meadow age (years)	1–2	5–7	8–10	> 10	
Number of plant species in sward	1–2	21	31	35	Jankowski 1997b
Organic C content % of dry soil in.depth: 0–10 cm	1.1	0.9–1.2	1.3–1.9	1.6–2.7	Kusińska and Łakomiec 1997
10–20 cm	0.2	–	0.7–0.8	0.6–0.8	
Cation exchange capacity (meq $100g^{-1}$) (depth 0–15 cm)	12.3	–	14.6	16.8	Jankowski 1997a

2. METHODS

In the analysis it was difficult to differentiate between the influence of sward species richness and the other parallel ecosystem changes. To limit the effect of these not target factors the experiment in mesocosms was applied (general design in Kajak 1997). Moraine sand filled bags (90 pieces) were inserted into the soil profile of each meadow. In the 45 of such mesocosms sand was covered by litter bags (s + l treatment) containing above-ground parts of *Dactylis glomerata* and in the other half of mesocosms sand was uncovered (s treatment). In the experiment decomposition of the litter derived from the same grass species and exposed on the surface of the similar substrate was compared at every site.

3. SPECIFIC PROPERTIES OF THE YOUNG LEYS

One of the characteristic features of new established leys (LA) were relatively variable environmental conditions, variable numbers of individuals and community structures. Variability of soil moisture was almost twice as high as in several years old meadow (LC) (Table 2). The highest variability of litter weight loss was recored in litter bags exposed on the sand and soil surface in this meadow. Similarly, greater seasonal changes in the density of many invertebrate taxa (nematodes, earthworms and microarthropods) were recorded (Table 3). The variability of the taxonomic diversity indices was also higher in this meadow. The species richness in the community of Collembola in successive periods was also variable in comparison to stable number in the permanent meadow. The greatest seasonal changes were found in this meadow also in the dominance structure of nematodes colonizing grass litter (Stanuszek 1997c).

Certain taxonomic groups of animals that represent high numbers in cultivated fields have remained numerous in the first few years after these fields were converted

Table 2. Mean variability coefficient ($\delta/\bar{x}$ %) of soil moisture and mass of litter residues in litter bags in meadows differentiated by age in 1989 (after Bogdanowicz and Szanser 1997, Stefaniak 1997b)

Parametr	Study sites[1]		
	LA	LC	P
Soil moisture			
10 May –11 Oct. (4 terms)	49	34	27
Litter residues			
24 Jan. –10 Oct. (6 terms)			
on the sand surface	18	18	16
on the soil surface	23	20	16

[1] see Table 1.

Table 3. Variability coefficients (δ/x̄ %) of biotic parameters in meadows differentiated by age (after Kaczmarek and Kajak 1997, Makulec 1997, Petrov 1997, Wasilewska 1994b, Ciesielska unpubl.)

Parameter	Study site LA	Study site LC	Study site P
	Meadow age		
	1–3	6~10	> 20
Nematoda June 1988 – June 1990 (3 sampling terms)			
Density:			
Total community	79	57	57
Bacteriphages	88	81	70
Fungiphages	93	68	70
Facultative phytophages	92	20	53
Obligatory phytophages	83	45	42
Pantophages and predators	52	40	58
Diversity (H') (genera)	14	2.8	2.8
Collembola May 1989 – Feb. 1980 (7 sampling terms)			
Density	54	42	57
Species richness	24	9	0
Species diversity (H')	59	30	41
Acarina May 1989 – Feb. 1990 (7 sampling terms)			
Density:			
Total community	58	48	48
Oribatida June 1988 – Oct. 1990 (9 sampling terms)			
Density	43	46	38
Biomass	42	47	32
Species richness	12	27	15
Species diversity (H')	10	9	9
Lumbricidae August 1988 – Sept.1989 (5 sampling terms)			
Density:			
Total community	40	42	10
Lumbricus rubellus	223	66	26

into meadows. *Oscinella frit* (Diptera) noxious on cereals continued to maintain a dominant position after meadow establishment. They remained dominant for several consecutive years. *Apporectodea caliginosa*, the dominant earthworm species in a plough layer of cultivated fields reached the highest proportion in total earthworm numbers in young leys (Makulec 1997). Above-ground in new established meadows the proportion of herbivorous insects in total arthropod numbers was the highest (Ciesielska unpubl.).

Summing up, it should be noted that great variability of environmental conditions and of communities have occurred in the first years after the establishment of new meadows. Simultaneously in comparison to other meadows the high proportion of herbivorous insects occured. Trophic structures and species composition found both in soil and above-ground were characteristic for cultivated areas.

4. DECOMPOSITION OF ORGANIC MATTER

The carbon content in the soil and in the sand exposed in mesocosms was in all study sites related to successional stage, always lower in younger meadows and the highest in permanent grasslands (Kusińska, Łakomiec 1997). There are two reasons for this. Firstly, as many authors show, organic matter content tended to increase along a secondary succession in agricultural land (Juma and McGill 1985, Coleman and Hendrix 1988, Haynes et al. 1991). In the initial stages, before steady state is reached the carbon content in soil is the function of time. Secondly as our experiments showed, the rate of total carbon and humus accumulation was greater in sand filled mesocosms exposed in older meadows over the same period. The greater humus accumulation in the sand inserted in the older, than in the new meadows, unlike litter weight loss, appeared very regularly in the three consecutive experiments (Table 4).

Potential sources of differences between sites in carbon content in sand were:

1. input of carbon derived from exposed litter and from roots ingrowing from surrounding soil,

2. input from the environment deposited by wind and water,

3. humification of exposed grass litter and roots.

Amount of carbon released from the litter exposed on the sand surface in mesocosms did not show significant differences between sites (Table 4). LC : LA ratio was close to 1 in all replicates. Production of roots ingrowing into mesocosms from surrounding soil also did not differ significantly, in 1990 was the lowest in the permanent meadow (Table 4).

If carbon in mesocosms was mainly deposited by percolating water, there should be similar organic matter content in both experimental treatments, in mesocosms with sand covered (s + l) and in those with sand uncovered by litter (s), because the same water percolated through them. It was found however, that C-content in series (s + l) was in all replicates higher than in (s) and increased with meadow age. Also differences in this content between treatments (s + l) – (s) increased regularly in older meadows. The differences in carbon content between treatments (s + l) – (s) were 2.5–7 times greater in meadow LC than LA in the successsive experiments. In the treat-

Table 4. Input and accumulation of total organic carbon (g · m^{-2}) in mesocosms inserted in three meadows differentiated by age during 11 months. Data from three experiments (Ex I – Ex III) and two treatments compared (after Kajak et al. 1991a[1)]), Bogdanowicz and Szanser 1997[2)], Kusińska 1997[3)], Makulec 1997[4)], Makulec and Kusińska 1997[4)]

Experiments	Sites** LA	LC	P	p (A – C)
Treatment (s + l) – sand covered by litter bags				
C released from litter bags				
Ex I[1)]	165.7	167.6	n.a.	
Ex II	179.1	173.7	n.a.	n.s.[a]
Ex III	176.5	151.6	141.8	
C in root production[2)]				
Ex II	64.4	91.8	n.a.	n.s.[a]
Ex III	42.7	44.3	37.1	
C accumulated in top (0–10 cm) sand layer				
Ex I[1)]	57.2	72.8	n.a.	
Ex II[3)]	50.7	80.6	n.a.	T = 2; n = 7; p = 0.025[a]
Ex III[3)]	118.3	248.3	375.7	
Treatment (s) – sand uncovered				
C accumulated in top (0–10 cm) sand layer				
Ex I[1)]	42.9	36.4	n.a.	
Ex II[3)]	45.5	45.5	n.a.	n.s.[a]
Ex III[3)]	98.8	105.3	131.3	
C input with earthworm casts[4)] (in 0–10 cm soil layer)				
Soil (in 1989 year)	78.0	504.0	402.0	

*Experimental periods: Ex I (1984–1985) and Ex III (1989–1990) – 11 months, Ex II (1988–1989) – 8 months; **See Table 1 and text.
[a]Significance of differences tested between young (LA) and older meadows (LC, P) by Wilcoxon signed rank test (one tailed test) basing on all sampling dates.

ment without exposed litter (s) differences between sites were not significant and did not show any trends (Table 4).

It can thus be assumed that a higher increase in C content in mesocosms inserted in the older meadow soil resulted from higher accumulation of C released from plant material, mainly more intense humification of the exposed litter.

The important question is, if differences in the number of individuals and community structure of biota colonizing the litter exposed in every site, might be responsible for different decomposition pattern of the plant material almost identical at the begining of the experiment.

5. GRASS LITTER COLONIZATION

Although differences in litter decomposition rates were observed over several years of study, certain patterns have recurred in all experiments. The maximum mass loss of litter was usually reached in the first 30 days after exposure (Bogdanowicz and Szanser 1997). The bacteria colonized the litter more rapidly than other components of the community. They reached peak abundance one to three months after the exposure. The peah abundance of fungi was reached in most cases after three months (Stefaniak et al. 1997c). The maximum density of soil animals appeared 5 months after litter exposure (Stanuszek 1997b, Kaczmarek and Kajak 1997). Basing on the dynamics of the litter disappearance rate, it can be concluded, that it was primary dependent on the number of bacteria, not on the number of fauna or other groups of microflora.

It was characteristic, that colonization of plant residnes litter by bacteria was more rapid in new grass leys (LA), than in older meadows. The maximum microbial number had appearred there a month earlier than in the other sites (Stefaniak et al. 1997c). In some cases a greater microflora abundance in LA site remained throughout the whole season (Table 5). The biomass of fungi was also found to be the highest there (Stefaniak et al. 1997c). In contrast, the colonization of litter by invertebrates proceeded the slowest in the young meadows. This might be illustrated by the number of nematodes and the biomass of microarthropods colonizing litter, which in most cases were at the begining of the experiments (1–3 months after exposure) higher in older (LC, P) than in young (LA) meadows (Table 5). The results suggest that the influence of invertebrates on the decomposition is less important in young leys than in other meadows.

It was analysed whether differences in taxonomic composition of invertebrates colonizing litter, might be responsible for different pattern of litter decomposition in young meadows. It was found, that the proportion of the Acarina in the total microarthropod was much higher in the permanent meadows (over 80%), than in leys (Table 6). In Oribatida there were two dominant species in all study sites – *Tectocepheus sarackensis* and *Scheloribates leavigatus*. The highest contribution of these species (almost 95%) in total community density was found in the new meadow (Table 6). Whereas, in the species composition of Collembola no characteristic features were found. The species diversity index (H') of collembolans colonizing litter was significantly greater in meadows LA, than in the other sites (Kaczmarek and Kajak 1997). Nematodes comprised mainly one species *Panagrolaimus rigidus*, found in the litter of all the compared meadows (Wasilewska 1992, Stanuszek 1997c) (Table 6).

So, the main differences found in the community composition of the litter which could influence lower organic matter accumulation in the new meadows were: – rapid litter colonization by bacteria, – the highest fungi biomass, – slow litter colonization by microarthropods and nematodes, – simplified species composition of Oribatida.

Table 5. Number (N) or biomass (B) ratios, between old (LC, P) and new (LA) meadows, of organisms colonizing litter bags in the experiment II (1988) and III* (1989)

Months after start of the experiment	Number Ratio				
	Bacteria			Nematoda	
	$N_{LC} : N_{LA}$		$N_P : N_{LA}$	$N_{LC} : N_{LA}$	$N_P : N_{LA}$
	1988	1989	1989	1989	1989
1	1.2	0.4	0.1	1.2	1.3
3	0.7	0.9	0.3	1.8	1.2
5–8	0.5	0.4	0.1	1.4	1.2

Months after start of the experiment	Biomass Ratio					
	Acarina			Collembola		
	$B_{LC} : B_{LA}$		$B_P : B_{LA}$	$B_{LC} : B_{LA}$		$B_P : B_{LA}$
	1988	1989	1989	1988	1989	1989
1	–	7.8	2.5	–	52.2	0.1
3	1.9	0.5	0.5	8.6	5.5	5.7
5	1.4	0.6	0.9	0.2	0.5	0.1
8	0.1	1.1	0.1	3.4	7.6	0.8

*after Kaczmarek and Kajak (1997), Stefaniak et al. (1997c), Stanuszek (1997c).

Table 6. Biomass (mean over season) (mg dry wt m^{-2}) of invertebrates in litter bags and percentage – of predominating species in the taxon density (1989)

Taxa	Sites		
	Leys		Permanent
	LA	LC	P
Nematoda (bacteriphagic)[1]	**630.6**	**966.9**	**970.7**
Panagrolaimus rigidus	100	100	100
Acarina[2]	**148.1**	**11.0**	**126.2**
Tectocepheus sareckensis[3]	67.3	52.3	23.4
Scheloribates laevigatus	26.6	29.2	41.3
Collembola[2]	**80.3**	**127.5**	**25.3**
Mesaphorura sp.	36.0	33.2	26.6
Onychiurus variabilis	35.5	55.5	0.0
Isotoma notabilis	5.5	0.5	24.1

[1]after Stanuszek (1997c), [2]Kaczmarek and Kajak (1997), [3]Petrov (1996).

6. SPECIES DIVERSITY, DENSITY AND BIOMASS OF INVERTEBRATES ABOVE- AND BELOW-GROUND

The important questions arised, if unified plant community is associated with low animal diversity and, if changes in the fauna diversity might affect humification processes.

Almost all the invertebrate groups examined were richer in respect to species number below- and aboveground as well, in older meadows (LC, P). Exceptional were only bacteriphagic nematodes (Table 7) and large predatory arthropods (ground beetles and spiders) (Kajak and Łukasiewicz 1991). Whereas the Shannon-Wiener diversity index (H') was significantly higher in older meadows only in 4 out of 8 examined taxa (Nematoda, Diptera, Oribatida and Lumbricidae) (Table 8). In the remining taxa differences between compared meadows were either not significant (predatory arthropods) or they were significantly more diverse in the young meadows (bacteriphagic Nematoda, Collembola).

Lack of relation between plant and animal diversity in predatory arthropods was a consequence of mobility of these animals, they are not restricted to any particular plot (Kajak and Łukasiewicz 1991). The common feature of the two other groups more diverse in uniform habitats (Collembola, bacteriphagic Nematoda) is that they can inhabit relatively rapidly new terains, disturbed areas such as cultivated fields and new meadows. It seems, that succession proceeded in these groups rapidly, community structure is formed quicker than in the other taxa.

Table 7. Number of species (or genera*) communities in soil and sward in age differentiated meadows

Taxa	Sites (meadow age in years): Leys LA (1–3)	Leys LC (8–10)	Permanent P > 10	Author
Microfauna				
Nematoda – total community*	10–23	24–31	23–31	Wasilewska (1994b)
Nematoda-bacteriphages* soil layer (0–25 cm)	14	17	7	Wasilewska (1994b)
Nematoda-bacteriophagous colonizers sward and soil (0–5cm)	8	5	5	Stanuszek (1997a)
Mesofauna				
Collembola	20	21	29	Kaczmarek and Kajak (1997)
Oribatida (Acarina) imagines	16	29	32	Petrov (1997)
Diptera (imagines)	12	20	28	Ciesielska (unpubl.)
Lumbricidae	2	5	5	Makulec (1997)

Table 8. Shannon-Wiener diversity index (H') for soil and sward communities in age differentiated meadows

Taxa	Leys LA (1–3)	Leys LB (4–7)	Leys LC (8–10)	Permanent P (> 10)	p**	Author
Nematoda – total community* soil depht 0–25 cm	4.2		4.4	4.3	n.s.	Wasilewska (1994b)
Nematoda-bacteriphagous colonizers sward and soil (0–5cm)	0.9		0.6	0.5	< 0.001	Stanuszek (1997a)
Collembola	3.7		3.0	2.8	< 0.001	Kaczmarek and Kajak (1997)
Oribatida (imagines)	2.4		3.3	3.5	0.001	Petrov (1997)
Diptera (imagines)	2.2		2.3	3.2	< 0.001	Ciesielska (unpubl.)
Lumbricidae	0.2		1.4	1.5	0.001	Makulec (1997)
Araneae (range)	–	1.3–1.7	–	1.4–1.5	n.s.	Kajak and Łukasiewicz (1991)
Carabidae (range)	–	1.6–1.8	–	1.2–1.4	n.s.	Kajak and Łukasiewicz (1991)

*diversity based on genera; **significance testet between LA and P meadows.

The total biomass of soil fauna was in general the highest in several years old leys (LC) and the lowest in the young meadows (LA) (Table 9). Several faunal groups – earthworms, springtails and nematodes reached the highest number and biomass in the soil of several years old meadows, the biomass of other animal taxa increased with meadow age (Acarina and Diptera). Very rarely the maximum biomass of any one group occured in the youngest meadow (LA). It was found only in one series in respect to nematodes (Wasilewska 1992). The microbial abundance was frequently the lowest in permanent meadows (P). The highest values occurred, as in the analysis of animal biomass, in several years old meadows (LB and LC) (Stefaniak et al. 1997b)

7. THE NUMBER AND BIOMASS OF ORGANISMS COLONIZING SAND IN MESOCOSMS

In the mesocosms containing sand inserted into the meadow all the invertebrate and microbial groups were less numerous than in the surrounding soil. Some groups showed different trends in sand than in soil. The highest microbial abundance and enzymatic activity in sand were reached in youngest meadow, whereas in soil in several years old meadows. Significant differences were found between LA and LC meadows in the number of bacteria and protease activity

Table 9. Annual density (ind. m^{-2} $\pm$ SE) and biomass (mg dry wt m^{-2}) of invertebrates in soil in relation to meadow age. Data from 1989. Density and biomass of microarthropods (Collembola, Acarina total, Oribatida) compared in two consecutive years (after Kaczmarek and Kajak 1997, Makulec 1997, Petrov 1997, Wasilewska 1997, Ciesielska unpubl.)

Taxa	Sites LA	Sites LC	Sites P
	Meadow age in years: 1–2	8–9	> 10
Nematoda			
Density (10^5)	26.7 ± 11.7^a	73.5 ± 24.3^a	52.7 ± 20.7^a
Biomass*	147^a	364^a	261^a
Microarthropoda			
Density (10^3)	54.0 ± 8.0^a	62.1 ± 6.3^a	60.6 ± 7.4^a
Biomass	691.7^a	1312.4^b	859.7^{**}
Diptera larvae			
Density	163.5 ± 17.7^a	143.6 ± 22.4^a	156.1 ± 96.2^a
Biomass	244.9 ± 41^a	362.5 ± 53^b	936.0 ± 101^c
Lumbricidae			
Density	24.7 ± 4.2^a	114.2 ± 19.2^b	$70 \pm 9.0^{**}$
Biomass	1540 ± 364^a	6440 ± 1225^b	$3450 \pm 891^{**}$
Biomass total	2624^a	8479^b	5507^c
Collembola			
Density (10^3) in 1988	9.3 ± 1.9^a	40.4 ± 9.6^b	8.6 ± 1.0^a
Biomass	35.7^a	279.9^b	54.9^a
Density (10^3) in 1989	21.4 ± 5.0^a	32.7 ± 3.9^b	18.0 ± 2.6^a
Biomass	192.0^a	545.1^b	172.5^a
Acarina			
Density (10^3) in 1988	38.8 ± 5.6^a	34.9 ± 4.7^a	54.9 ± 6.9^a
Biomass	600.7^a	930.2^b	984.2^b
Density (10^3) in 1989	32.6 ± 3.0^a	29.4 ± 2.4^a	42.5 ± 4.8^b
Biomass	499.7^a	767.3^b	687.2^b
Oribatida			
Density (10^3) in 1988	7.8 ± 1.2^a	7.5 ± 1.3^a	16.1 ± 2.9^b
Biomass	44 ± 0.4^a	72 ± 2^b	152 ± 3.6^c
Density (10^3) in 1989	9.1 ± 1.7^a	9.2 ± 2.1^a	15.2 ± 2.2^b
Biomass	60 ± 0.8^a	52 ± 1.6^b	136 ± 4^c

* it was assumed after Wasilewska (1979), that mean weight of individual Nematoda = 0.459 µg, f. wt corresponds to 0.1 µg dry wt. **Data for permanent meadows analysed in 1987 were used Significance of differences estimated using t-Student test and Wilcoxon matched-pairs signed rang test. The figure followed by the different letter means significant difference between sites, $p < 0.05$.

Table 10. Abundance (mean over season) of microflora and microfauna and enzymatic activity in sand filled mesocosms inserted in meadow soil (treatment s + l) (1989–1990)

Parameter	Sites LA	LC	P	p LA–P
Microflora[a)] (N ind. 10^6 g dry wt^{-2})				
Bacteria	7.70	6.40	5.40	< 0.01
Actinomycetes	0.56	0.28	0.24	< 0.01
Fungi	0.01	0.02	0.01	n.s.
Nematoda[b)] total (N ind. 10^3 m^{-2})	1000	1350	650	n.s
Bacteri- and fungiphages	850	1100	500	n.s
Obligatory plant parasites	100	50	0	n.s.
Pantophages and predators	0	200	150	n.s
Enzymatic activity[c)]				
Dehydrogenase (mg TTC/g of sand 24h)	0.002	0.001	0.001	n.s.
Protease (mg glycine/g of sand 24h)	0.45	0.35	0.30	< 0.05
Cellulase (µg glucose/g of sand 24h)	25.30	30.10	26.50	n.s.

Data after: [a)]Stefaniak et al. 1997b; [b)]Wasilewska unpubl.; [c)]Stefaniak et al. 1997b

Table 11. Biomass (mean over season) (mg dry wt m^{-2}) of microarthropods and earthworms colonizing sand in mesocosms inserted in meadows soil (after Kaczmarek and Kajak 1997, Makulec unpubl.)

Taxa	Years	Sites LA	LC	P
Collembola	1988	37.7	117.1	n.a.
	1989	123.6	756.0	96.9
Acarina	1988	409.0	260.5	n.a.
	1989	181.2	165.0	249.3
Lumbricidae	1989	0.0	710.0	180.0
Total biomass	1989	304.8	1631.0	526.2

Wilcoxon signed rank test applied; n.a. – not analysed.

(Table 10). Abundance of microflora and microfauna was the lowest in the permanent meadow. In nematode community density of plant parasites and contribution of microbivores decreased with secondary succession. The total invertebrate biomass was similarly as in soil the highest in the eight years old meadow, the lowest in the new grass ley (Table 11).

8. DISCUSSION

8.1. CHANGES IN COMMUNITIES UNDER THE INFLUENCE OF STRESS

In our studies we tried to answer two questions: 1. whether the decrease in plant species richness affects diversity of invertebrates and 2. if changes in the diversity influence decomposition pattern. In many studies species diversity of animal taxa is measured, but there have been only a few studies in which the role of diversity in ecosystem function has been studied. Until now, attention was mainly focused on stabilizing effect of the diversity on the number of individuals.These studies has lead to controversial conclusions (Elton 1958, Goodman 1975, Pimm 1984, McNaughton 1993, Schulze and Mooney 1993). Declining species richness is an important community response for environmental stress (Pętal 1983,. Odum 1985, Kajak et al. 1985, Rapport et al. 1986). Most vulnerable species are mainly affected (Howarth 1989). As a result structure of communities changes. Transformation depends on increasing proportion of r-strategists with intensive energy dissipation and decreasing proportion of organisms of relatively large sizes and long life cycles (Odum 1985, Rapport et. al. 1986, Wasilewska 1994 b). The matter mineralization in these stressed ecosystems is accellerated and occurs mainly by bacteria and bacteriphagous animals, less important are fungi and mycophagous invertebrates (Hendrix et al. 1987). It is often coupled with decline of the number of large saprophages, the group stimulating humification. Number of polyphagous predatory animals, mainly animals of relatively large sizes and long life cycles declines (Pętal 1983, Kajak et al. 1985, Hill and McKevan 1987, Kajak 1989). Such changes proceeded primarily in the ecosystems where as an effect of disturbance soil moisture decreases e.g. after ploughing or drainage.

The occurence of this syndrome characteristic for stressed ecosystems was found most clearly in the community colonizing mesocosms inserted in the new grass ley. In this meadow significantly higher number of bacteria and actinomycetes was recorded than in older ones. Microbiphagic and obligatory phytophagic nematodes also occured numerously, whereas earthworms were absent.

8.2. DIVERSITY AND FUNCTION OF SOIL FAUNA IN HUMIFICATION

Little is known about the functional role of particular species of soil fauna. It is clear however, that certain groups stimulate humus formation and that invertebrate biomass is positively correlated with humus content in soil (Gilarov 1975, Ryszkowski 1985, Edwards 1984, Kajak 1989, Coleman and Hendrix 1988). It is also known, that in ecosystems with different humus types, differences in proportions between microarthropods and earthworms in the total biomass of soil fauna were found (Macfadyen 1963, Gilarov 1965, Arpin et al. 1984). Informations on significance of soil fauna diversity are scarce.

The earthworms are the only soil taxon of temperate region well known in terms of functional significance. The production of earthworm casts is dependent on their biomass. In the present study in the mesocosms with sand and in the surrounding soil the earthworm biomass gradually increased over years in ley meadows and underwent a decrease in the permanent meadow. In the new leys there occured almost exclusively one endogeic species – *Apporrectodea caliginosa.* After a lapse of years species richness increased, proportion of the litter feeding species, penetrating soil surface was greater. It was suggested, that high propotion of the surface dwelling species – *Lumbricus rubellus* (half of the total earthworm biomass) in the permanent meadows was an important reason of relatively high carbon content of earthworm casts found there compared to leys. The ratio between carbon content in casts and in soil, especially in deeper layer (5–10 cm) was also the highest in this meadow (Makulec and Kusińska 1997). So, in meadows with diverse earthworm community more carbon is deposited in soil. In respect to this animal group there was strict relationship between species richness and humification.

The other group with significant increase in diversity with successional age were Diptera (Table 8). The main components of this community were phytophagic and phytosaprophagic larvae belonging to Tipulidae and Bibionidae (70–93% of total dipterans biomass). The biomass of these taxa increased with meadow age, and was 5 times higher in permanent than in the new meadow (Table 12). These two Diptera families are considered, similarly as earthworms, as humificators, because in their excrements higher content of humic and fulvic acids were found than in consumed plant residues (Kozlovskaja 1976, Striganova 1980). In the permanent meadow considerable increase of the biomass of predatory Diptera was also noted (9 times more compared to the new ley) (Table 12). More intense was also soil surface patrolling by predatory, polyphagic macroarthropods (Kajak and Łukasiewicz 1994). Based on the previous results (Kajak and Jakubczyk 1976, Kajak et al. 1991) it might be stated, that such patrolling contribute to matter mineralization retard by decreasing number of mesofauna and microflora.

The role of mesofauna in humification processes is poorly known. In the laboratory experiments, it was shown that excrements of Collembola and Acarina contain humus components (Gilarov 1970, Butcher et al. 1971, Striganova 1980). Dunger (1968, 1991) had also determined that in the initial successive stages when mesofauna is the main community component humifica-

Table 12. Trophic structure of *Diptera* larvae biomass (mg dry wt m^{-2}) based on data from January 1989 (after Ciesielska, unpubl)

Trophic groups	Sites[1)]		
	LA	LC	P
Saprophages	31.4	44.9	102.6
Phytophages and phytosaprophages	236.8	633.6	1277.1
Tipulidae + Bibionidae (% of phytophages)	79.9	92.9	50.4
Coprophages	–	–	176.3
Predators	26.2	2.8	278.1

1) see Table 1.

tion proceeded and mor or moder type humus is formed. So Acarina and Collembola have been included among microhumiphages. It was found that microflora of alimentary tracts of Oribatida may digest substrates resistant for decomposition (Seniczak 1978, Striganova 1980). It may suggests that oribatids could also be categorized to humiphages. In our studies biomass and diversity of this taxon was the greatest in soil of permanent meadows.

Summing up the biomass and the diversity of several animal groups which might be included into category of humiphages increase along time gradient of meadows.

The results simultaneously provide evidence that in the new grass leys intesive mineralization of dead plant material might be expected. In the mesocosms inserted there the highest microbial abundance and activity of certain enzymes were found. Among nematodes microbiphagic and plant parasitic species prevailed in both ley meadows. The new leys were characterized by the highest proportion of r-strategic species among bacteriphagous nematodes (Wasilewska 1994b) and oribatid mites (Petrov 1996). The data of microcosm experiments indicate that such species stimulate mineralization rate of organic matter, enhance microbial activity and nutrient turnover (Coleman et al. 1977, Ingham et al. 1985, Freckman 1988).

8.3. HUMIFICATION AND SWARD SPECIES RICHNESS

The species richness of plant communities is considered by certain soil scientists as the best indicator of soil fertility (Puchalski and Prusinkiewicz 1975). In the present study the maximum accumulation of carbon was found in soil of the most complicated, permanent meadow. The recorded in our experiments increase in the carbon content had exceeded the input derived from decomposed litter and roots. But on the other hand, the assessed increase was lower than the amount of carbon deposited in the surrounding soil by earthworm casts (Kusińska and Makulec 1997). The comparison of the two treatments, with and without litter bags suggests, that the main reason of higher carbon accumulation in the older meadows were different pattern of litter decomposition. High carbon accumulation in soils of older meadows seems to be an effect of two interactions – the slowing down of mineralization processes and the increasing importance of humiphages in faunal communities (Lumbricidae, Collembola, Oribatida, Diptera).

The assessment if the community structure found in the new leys is an effect of tillage, which proceeded meadow formation, or is the response for impoverished species richness of vegetation, is difficult. Similar trends to those observed in the secondary succession in meadows were observed in agroecosystems in experiments with no-tillage or integrated farming in comparison with conventional farming systems (Hendrix et al. 1987, House et al. 1984, Stinner and House 1990, Lee and Pankhurst 1992). Management allowing the succession of soil communities leads to an increase in the diversity of animal communities and in the proportion of K-type strategists. The biomass of taxa stimulating humification and of predators increases. In some experiments an increase in the ratio between fungal and bacterial biomass was found (Beare et al. 1992). An increase in the content of soil organic matter in comparison with conventional farming systems occurred in spite of the fact that vegetation remains monospecific (House et al. 1986, Lee and Pankhurst 1992), even in long-term monocultures (Juma and McGill 1985).

However in the monocultures under conventional management syndrome characteristic for stressed ecosystems proceeded more strongly than in the crop rotation practice, although in both cropping systems soil is disturbed in the similar way (Ryszkowski and Karg 1990, Karg et al. 1990, Łoginow et al. 1990). Edaphon structure was similar to this found in mesocosms inserted in the new ley.

To conclude, community structure characteristic for stressed systems may be found in those cases where succession of soil biota is disturbed. This effect is exaggerated in monocultures. Secondary succession of soil communities may attenuate disturbance effects, even though one species vegetation is maintained. The results of our experiments suggest, that the time factor is very important in the formation of humus. In the permanent meadows and old leys relatively high proportion of the carbon released in decomposition is retained in soil, compared to younger meadows. The above data enable us to conclude that the area of such meadows should be extended for regeneration of humus content in cultivated soil.

9. SUMMARY

The present study compares decomposition pattern as well as community structure of decomposers in Arrhenatheretalia meadows differentiated by the plant species richness, increasing along successional gradient.

The field experiment in mesocosms was carried out to analyse decomposition rate of the same at every site plant material (above-ground parts of Dactylis glomerata) exposed on the similar substrate in each study site. Steelon bags (200 cm^2 · 30 cm) were filled with moraine sand and inserted into the meadow soil profile. 90 such mesocosms were inserted in each site. Destructive sampling was applied. The sand surface in every second mesocosm was covered by 10g dry wt. of grass litter (treatment s+l), the rest was uncovered (treatment s).

Investigations were carried out in north-eastern Poland, in the Suwałki Landscape Park and in its buffer zone, in meadows on brown soils derived from medium sand (Kusińska and Łakomiec 1997, Jankowski 1997 a). The study sites were located in grass leys differentiated by the time since establishment (leys: young 1-2 years old (LA), 3–5 years old (LB), more than six years old (LC) and in permanent meadows (P). The sward of youngest meadows was almost monoculture of *Dactylis glomerata*. Along the secondary succession sward and soil complexity increased (Table 1).

Characteristic features of the youngest meadows were high variability in space and time of environmental conditions, as well as of biotic parameters (density of individuals, taxonomic diversity, litter disappearance rate) (Table 2 and 3).

In the experimental mesocosms the highest carbon accumulation was found in sand inserted in old leys and permanent meadows, the lowest in the young leys with simplified vegetation (Table 4). We tried to find if differences in the community structure and species diversity of decomposers were responsible for differences found between young and older meadows in carbon retention.

In the most of analysed invertebrate taxa species richness increased along the time gradient (Table 7). Species diversity however, proceeded differently. In some taxa the greatest species diversity (H') was found in the young, uniform meadow (bacteriphagic Nematoda, Collembola) (Table 8). In earthworm community only, it was possible to show relationship between the species richness and the intensity of organic matter humification. In this taxon diversity is coupled with increasing proportion of species feeding near soil surface, in the humus rich layer. As a result carbon content in their

casts is higher and in the consequence the amount of carbon deposited in soil (Table 4). Functional meaning of the diversity of the other taxa is not clear. It was found however, that community of organisms colonizing grass litter exposed in the young ley differed compared to the other meadows. This litter was colonized rapidly by microflora, mainly bacteria, but colonization by microarthropods was retarded. (Table 5).

Density and biomass of fauna in sand and soil was the lowest in the young meadow. (Table 9, 11). Structure of the community colonizing sand in mesocosms inserted there was characteristic for ecosystems under stress. Significantly more abundant were two groups od microflora – Bacteria and Actinomycetes (Table 5 and 10). In contrary the biomass of fauna, particularly of large humiphages (Tipulidae, Bibionidae, Lumbricidae) and predatory macroarthropods was scarce. (Table 10, 11 and 12). No clear and recuring in successive years differences in species composition of litter colonizers were found between the young and old meadows (Table 6).

It seems reasonable for organic matter regeneration in cultivated soils to increase an area of old leys and permanent meadows.

10. POLISH SUMMARY

Celem przeprowadzonych badań było porównanie przebiegu rozkładu materii oraz porównanie zespołów organizmów uczestniczących w tym rozkładzie, na łąkach różniących się bogactwem gatunkowym runi. Bogactwo runi było zależne od zaawansowania sukcesji wtórnej na porównywanych łąkach.

Dla śledzenia rozkładu posłużono się eksperymentem terenowym, który polegał na rozmieszczeniu na każdej z łąk 90 dołków (200 cm^2, głębokości 30 cm) wypełnionych piaskiem o tym samym wszędzie pochodzeniu. Na powierzchni dołków umieszczono naważki powietrznie suchej ściółki *Dactylis glomerata* (po 10 g s.m.) w woreczkach z siatki stilonowej. Co drugi dołek pozostawał odkryty, służył jako kontrola (Kajak 1997). Dzięki takiemu eksperymentowi można było porównać przebieg rozkładu na jednakowym podłożu na wszystkich stanowiskach, oraz ocenić wielkość akumulacji węgla w ciągu roku.

Łąki znajdowały się na glebach brunatnych wytworzonych z piasków gliniastych, zaliczone zostały do rzędu Arrhenatheretalia (Kusińska, Łakomiec 1997, Jankowski 1997b). Były to łąki przemienne różniące się głównie pod względem długości okresu od ich założenia (LA – 1–2 lata od założenia, LB – 3–5 lat, LC – ponad 6 lat) i łąki trwałe (P). Ruń najmłodszych łąk była niemal monokulturą kupkówki. Wraz z sukcesją wtórną zwiększała się liczba gatunków roślin w runi (od 3 do ponad 30) i różnicowały się w jej obrębie warstwy (tab. 1).

Łąki najmłodsze, o najmniej zróżnicowanej runi cechowała największa zmienność zarówno warunków siedliskowych jak i liczebności i różnorodności zwierząt glebowych (tab. 2 i 3). W eksperymencie z wprowadzonym piaskiem stwierdzono, że największa akumulacja węgla organicznego w podłożu zachodzi na łąkach wieloletnich, o urozmaiconej runi, najmniejsza na łąkach najmłodszych, gdzie dominuje w runi jeden gatunek trawy (tab. 4).

Poszukiwano różnic w liczebności i składzie organizmów, które mogły decydować o stwierdzonych różnicach w akumulacji węgla. U większości grup fauny stwierdza się występowanie mniejszej liczby gatunków na nowych łąkach (tab. 7). Nie zawsze jednak pokrywa się to z ich różnorodnością (H' Shannona-Wienera). W zespołach bakteriofagicznych Nematoda i Collembola, które szybko formują zespoły po zaburzeniach w środowisku, największa różnorodność gatunkowa występowała na najmłodszych łąkach (tab. 8).

Tylko w odniesieniu do dżdżownic wykazano bezpośrednią zależność między bogactwem gatunkowym zespołu, a ilością przetwarzanego węgla. Wzrost różnorodności polega bowiem w tej grupie na rosnącym udziale gatunków żerujących w pobliżu powierzchni gleby, w warstwie zasobnej w materię organiczną. Taki sposób żerowania powoduje wysoką zawartość węgla w koprolitach i zwiększenie ilości węgla wprowadzanego przez te zwierzęta do gleby (tab. 4).

Znaczenie funkcjonalne różnorodności innych zespołów nie jest wyjasnione. Stwierdzono jednak, że ściółka wyłożona na nowozałożonej łące zostaje szybciej w porównaniu z innymi łąkami opanowana przez mikroflorę, głównie przez bakterie, podczas gdy kolonizacja przez zwierzęta (głównie mikrostawonogi) jest opóźniona (tab. 5). Liczebność i biomasa zwierząt w glebie jest również na nowej łące mniejsza niż na pozostałych łąkach (tab. 9a i 9b).

Struktura liczebności i biomasy organizmów zasiedlajacych wprowadzone na łąki substraty (ściółka, piasek) przybiera na nowej łące wartości charakterystyczne dla ekosystemów poddanych stresom. Jest tam mianowicie istotnie większa liczebność bakterii i promieniowców, a więc organizmów o strategii r, najmniej zaś zwierząt o strategii typu K, a więc o stosunkowo dużych rozmiarach i długich cyklach życiowych, których przykładem mogą być zaliczane do humifikatorów Tipulidae, Bibionidae, Lumbricidae, oraz stawonogi drapieżne (tab. 10, 11 i 12). Nie stwierdzono natomiast w składzie gatunkowym poszczególnych grup zwierząt zasiedlających ściółkę (Collembola, Oribatida, Nematoda) wyraźnych i powtarzających się w kolejnych latach różnic między łąkami, które mogłyby tłumaczyć odmienny przebieg rozkładu na tych łąkach (tab. 6).

Dla regeneracji próchnicy w glebach uprawnych wydaje się celowe poszerzenie areału kilkuletnich łąk przemiennych i trwałych.

11. REFERENCES

1. Arpin P., Ponge J. F., Dabin B., Mori A. 1984 – Utilisation des nematodes Mononchida et des Collemboles pour caractériser des phénomenes pédobiologiques – Rev. Ecol. Biol. Sol. 21(2): 243–268.
2. Bogdanowicz L., Szanser M. 1997 – The decomposition of grass litter in grasslands differenciated by age and management – Ekol. pol. 45: 647–663.
3. Butcher J. W., Snider R., Snider S. J. 1971 – Bioecology of edaphic Collembola and Acarina – Ann. Rev. Ent. 16: 249–281.
4. Coleman D. C., Hendrix P. F. 1988 – Agroecosystems processes (In: Concepts of ecosystem ecology. Eds. L. R. Pomeroy, J. J. Alberts) – Springer-Verlag, New York, Berlin, Heidelberg, 149–170.
5. Coleman D. C., Cole C. V., Anderson R. V., Blaha M., Campion M. C., Clarholm M., Elliot E. T., Hunt H. W., Shaefer B., Sinclair J. 1977 – Analysis of rhizosphere – saprophage interactions in terrestrial ecosystems – Ecol. Bull. 25: 299–309.
6. Dąbrowska L., Mazur K. 1987 – Dynamics of changes in floristic composition of montane meadow during 11 year of experimental fertilizing. – Zesz. probl. Post. Nauk roln. 300: 115–123. (in Polish)
7. Denisiuk Z. (Ed) 1990 – Nature conservation in Poland, actual state and developmental tendencies – Stud. Naturae A, 35: 1–70. (in Polish)
8. Dunger W. 1968 – Die Entwicklung der Bodenfauna auf rekultivieren Kippen und Halden des Braunkohlentagebares – Abh. Berichte Naturkund, 256 pp.
9. Dunger W. 1991 – Zur Primar-Sukzession humiphager Tiergruppen auf Bergbauflächen – Zool. Jb. Syst. 118: 423–448.
10. Edwards C. A. 1984 – Changes in agricultural practice and their impact on soil organisms (In: Agriculture and the environment. Ed. D. Jenkins) – Institute of Terrestrial Ecology, Banchory, 56–65.
11. Elton C. S. 1958 – The ecology of invasions by animals and plants – Methuen, London.
12. Freckman D. 1988 – Bacterivorous nematodes and organic-matter decomposition – Agriculture, Ecosystems and Environment, 24: 195–217.
13. Gilarov M. S. 1965 – Zoologcheskij metod diagnostiki pochv – Nauka, Moskva, 275 pp.
14. Gilarov M. S. 1970 – Bespozvonochnye razrusiteli podstilki i puti povysenija ikh poleznoj dejatelnosti – Ekologija, 2: 8–21.
15. Gilarov M. S. 1975 – General trends of changes in soil animal populations of arable land (In: Progress in soil zoology. Ed. J. Vanek) – Academia, Praque, 31–39.
16. Goodman D. 1975 – The theory of diversity-stability relationships in ecology – Q. Rev. Biol. 50: 237–266.
17. Haynes R. J., Swift R. S., Stephen R. C. 1991 – Influence of mixed cropping rotations (pasture – arable) on organic matter content, water stable aggregation and clod porosity in a group of soils – Soil and Tillage Research, 1a: 77–87.
18. Hendrix P. F., Crossley D. A., Coleman D. C., Parmelee R. W., Beare M. H. 1987 – Carbon dynamics in soil microbes and fauna in conventional and no-tillage agroecosystems – Intecol. Bull. 15: 59–63.

19. Hill S. B., McKevan D. K. 1987 – The soil fauna and agriculture: past finding and future priorities (In: Soil fauna and soil fertility. Ed. B. R. Striganova) – Nauka, Moskva, 49–56.
20. House G. J., Stinner B. R., Crossley D. A., Odum E. P. 1984 – Nitrogen cycling in conventional and no-tillage agroecosystems analysis of pathways and processes – J. appl. Ecol. 21: 991–1012.
21. Howarth R. W. 1989 – Comparative responses of aquatic ecosystems to toxic chemical stress (In: Comparative analysis of ecosystems. Eds. J. Cole, G. Lorett, S. Findlay) – Springer, Berlin, 169–195.
22. Ingham R. E., Trofymov J. A., Ingham E. R., Coleman D. C. 1985 – Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth – Ecol. Mon. 55: 119–140.
23. Jankowski W.1997 – Floristic diversity of grassland sward in Suwalki landscape Park (NE Poland) in relation to use and age – Ekol. pol. 45: 619–632.
24. Juma H. G., McGill W. B. 1985 – Decomposition and nutrient cycling in agroecosystems (In: Microfloral and faunal interactions in natural and agroecosystems. Eds. M. J. Mitchell, J. P. Nakas) – Junk, Dordrecht, Boston, Lancaster, 74–136.
25. Kaczmarek M., Kajak A.1997 – Microarthropods and decomposition processes in meadows of various plant species richness – Ekol. pol. 45: 795–813.
26. Kajak A. 1989 – Czy ubożenie fauny może wpływać na zawartość próchnicy w glebach uprawnych? [Can fauna impoverishment affect humus content in cultivated soils] – Wiad. ekol. 35: 235–249.
27. Kajak A. 1997 – Preface. Scope of studies, experimental design, study area – Ekol. pol. 45: 581–585.
28. Kajak A., Jakubczyk H. 1976 – Experiments on the influence of predatory arthropods on the number of saprophages and disappearance rate of dead plant material – Pol. ecol. Stud. 2: 219–229.
29. Kajak A., Łukasiewicz J. 1991 – Intensywność penetrowania łąk i ich otoczenia przez zespóły drapieżnych stawonogów (Araneae, Carabidae, Formicidae) [Intensity of area patrolling in meadows and adjacent habitats by predatory arthropods (Araneae, Carabidae, Formicidae)] – CPBP 04.10.80 SGGW-AR: 286–309.
30. Kajak A., Łukasiewicz J. 1994 – Do semi-natural patches enrich crop fields with predatory epigean arthropods – Agriculture, Ecosystems and Environment, 49: 149–161.
31. Kajak A., Andrzejewska L., Chmielewski K., Ciesielska Z., Kaczmarek M., Makulec G., Wasilewska L. 1985 – Long-term changes in grassland communities of heterotrophic organisms on drained fens – Pol. ecol. Stud. 11: 21–52.
32. Kajak A., Chmielewski K., Kaczmarek M., Rembiałkowska E. 1991 – Experimental studies on the effect of epigean predators on matter decomposition processes in managed peat grasslands – Pol. ecol. Stud. 11: 289–310.
33. Kajak A., Makulec G., Bogdanowicz L., Chmielewski K., Kaczmarek M., Kusinska A., Łakomiec J. 1991 – Experimental studies on the decomposition of *Dactylis glomerata* L. grass litter on meadows varying in the complexity of vegetation – Ekol. pol. 39: 113–134.
34. Karg J., Czarnecki A., Paprocki R., 1986 – Edaphon of rye field in monoculture and crop rotation (In: Ecological effects of applying monoculture in areals) – IUNG, Puławy, 113–133. (in Polish)
35. Karg J., Czarnecki A., Witkowski T., Paprocki T. 1990 – Edaphon density and biomass in fields with monoculture and crop rotation (In: Ecological processes in monocultures of cereals. Eds. L. L. Ryszkowski., J. Karg., J. Pudełko) – Wydawnictwo Naukowe Uniwersytetu A. Mickiewicza, Poznań, 187–195. (in Polish)
36. Kazimierczakowa R. 1990 – The effect of sheep grazing on the biotop and community of clearings in Tatras – Prace Muz.Szafera, Prądnik, 2: 127–136. (in Polish)
37. Kornaś J. 1990 – Why and how do our plant communities extinct – Wiad. Bot. 32: 7–16. (in Polish)
38. Kornaś J., Dubiel E. 1990 – Changes in meadow associations in last 30 years in Ojcov National Park – Prace Muz. Szafera, Prądnik, 2: 97–106. (in Polish)
39. Kostuch R. 1987 – Floristical changes in the sward of montane grasslands as an effect of N – fertilizing – Zesz. Probl. Post. Nauk roln. 308: 209–218. (in Polish)
40. Kozlovskaja L. S. 1976 – Rol bespozvonochnykh v transformacji organicheskogo vezhchestva bolotnych pochv – Nauka, Leningrad, 212 pp.

41. Kusińska A. 1997 – Humification of grass litter on age-differentiated meadows in the Suwałki Landscape Park (north-eastern of Poland) – Ekol. pol. 45: 665–671.
42. Kusińska A., Łakomiec I. 1997 – Contents of humus fractions in the soil of meadows situated in the Suwałki Landscape Park (north-eastern Poland), depending on the time of management – Ekol. pol. 45: 609–618
43. Lee K. E., Pankhurst C. E. 1992 – Soil organisms and sustainable productivity – Aust. J. Soil Res. 30: 855–892.
44. Loginow W., Andrzejewski J., Wiśniewski W., Kusińska A., Cieścińska B., Karlik B., Janowiak J. 1990 – Influence of monocultural cereal cultivation on transformations of organic matter and Nitrogen in soil (In: Ecological processes in monocultures of cereals. Eds. L. Ryszkowski, J. Karg, J. Pudełko) – UAM-Poznan, 111–132. (in Polish)
45. Macfadyen A. 1963 – The contribution of the microfauna to total soil metabolism (In: Soil organisms. Eds. J. Doeksen, J. van der Drift) – North Holland Publishing Co., Amsterdam, 3–16.
46. Makulec G. 1997 — Density and biomass of earthworms (Lumbricidae) on leys and permanent meadows – Ekol. pol. 45: 815–823.
47. Makulec G., Kusińska A. 1997 – The significance of earthworms (Lumbricidae) in transformations of organic matter and in the economy of elements in the soils of ley meadows and permanent meadows – Ekol. pol. 45: 825–837.
48. McNaughton S. J. 1993 –Biodiversity and function of grazing ecosystems (In: Biodiversity and Ecosystem Function. Eds. E. D. Schulze, H. A. Mooney) – Springer, Berlin, 361–383.
49. Michalik S. 1990a – Plant succession of the clearing during 20 years after grazing ceased in Gorce National Park – Prace Muz. Szafera, Pradnik, 2: 137–148. (in Polish)
50. Michalik S. 1990b – Secondary succession and problems of active conservation of seminatural communities in national parks and nature reservations – Prace Muz. Szafera, Prądnik, 2: 175–198. (in Polish)
51. Odum E. P. 1985 – Trends expected in stressed ecosystems – Bio Science, 35: 419–422.
52. Petrov P. 1997 – The reactions of communities of Oribatid mites to vegetational succession on meadows – Ekol. pol. 45: 781–793.
53. Petrov P. 1996 – Changes in mite communities (Acari: Oribatida) colonizing soil and litter during secondary succession in grasslands – Ph. d. thesis, Institute of Ecology PAN.
54. Pętal J. 1983 – The effect of mineral fertilization on biocenotic structure and matter economy on meadows – Ekol. pol. 31: 913–929.
55. Pianka E. R. 1970 – On r- and K- selection – Am. Nat. 104: 592–597.
56. Pimm S. L. 1984 – The complexity and stability of ecosystems – Nature, 307: 321–326.
57. Puchalski T., Prusinkiewicz Z. 1975 – Ekological bases for fores habitat studies – Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa, 463 pp. (in Polish)
58. Rapport D. J., Rigier H. A., Hutchinson T. C. 1986 – Ecosystem behaviour under stress – Am. Nat. 125: 617–640.
59. Ryszkowski L. 1985 – Impoverishment of soil fauna due to agriculture – Intecol Bull. 7–17.
60. Ryszkowski L., Karg J. 1990 – Main results of interdisciplinary studies of monocultures (in: Ekological processes in monocultures of cereals. Eds. L. Ryszkowski, J. Karg) – UAM-Poznań, 232–238. (in Polish)
61. Schulze E. D., Mooney H. A. 1993 – Ecosystem function of biodiversity: A summary – Ecol. Stud. 99: 497–510.
62. Seniczak S. 1978 – Juvenile stages of moss mites (Acarina, Oribatei) as an essential component of agglomerations of these mites transforming the organic matter of soil – Ph. d. thesis UMK-Toruń, 171 pp.
63. Stanuszek S. 1997a – Species composition, functional and age nematode community structure of variously aged meadows in a postglacial region (Suwałki Landscape Park, north-eastern Poland) – Ekol. pol. 45: 733–754.
64. Stanuszek S.1997b – Abundance and biomass of saprophagic nematodes in variously aged meadows in Suwałki Landscape Park (north-eastern Poland) – Ekol. pol. 45: 755–763.
65. Stanuszek S. 1997c – The role of saprophagic nematodes in the decomposition of grass litter in variously aged meadows of the postglacial region of Suwałki Landscape Park (north-eastern Poland) – Ekol. pol. 45: 765–780.

66. Stefaniak O., Ślizak W., Maniewska R., Gorlach K. 1997a – Numbers of microflora and enzymatic activity of grassland soils in the Suwałki Landscape Park in relation to landscape heterogeneity and management – Ekol. pol. 45: 673–682.
67. Stefaniak O., Ślizak W., Maniewska R., Gorlach K. 1997b – Relationships between the age of grasslands and soil microflora – Ekol. pol. 45: 683–694.
68. Stefaniak O., Ślizak W., Gorlach K. 1997c – Microflora colonizing grass litter exposed in bags on differently-aged meadows – Ekol. pol. 45: 695–708.
69. Stefaniak O., Ślizak W., Maniewska R., Gorlach K. 1997d – The effect of grass litter on the development of microorganisms in the substrate – Ekol. pol. 45: 709–717.
70. Stinner B. R., House G. J. 1990 – Arthropods and other invertebrates in conservation – tillage agriculture – Ann. Rev. Entomol. 35: 299–318.
71. Striganova B. R. 1980 – Pitanie pochvennych saprofagov – Nauka, Moskva, 1–243.
72. Szanser M. 1997 – Below ground plant production and biomass of Arrhenatheretalia meadows of different age – Ekol. pol. 45: 633–646.
73. Traczyk T., Kotowska J. 1976 – The effect of mineral fertilization on plant succession of a meadow – Pol. ecol. Stud. 2: 75–84.
74. Wasilewska L. 1979 – The structure and function of soil nematode communities in natural ecosystems and agrocenoses – Pol. ecol. Stud. 5: 97–145.
75. Wasilewska L. 1981 – Function assessment of soil nematodes in forest, grassland and arable ecosystems – Zesz. Probl. Post. Nauk roln. 249: 53–68 (in Polish).
76. Wasilewska L. 1992 – Participation of soil nematodes in grass litter decomposition under diverse biocenotic conditions of meadows – Ekol. pol. 40: 75–100.
77. Wasilewska L. 1995a – Direction of changes in communities of soil nematodes in man-disturbed ecosystems – Acta zool. Fenn., 196: 271–274.
78. Wasilewska L. 1994b – The effect of meadows age on succession and diversity in soil nematode communities – Pedobiologia, 38: 1–11.
79. Wasilewska L. 1997 – Meadow plant diversity versus diversity of soil nematode communities – Ekol. pol. 45: 719–732.