POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	48	3	209–224	2000

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EFFECT OF SIMPLIFICATION OF GRASS CULTURES AND SOIL CONDITIONS ON COLLEMBOLA (APTERYGOTA) COMMUNITIES IN A LYSIMETRIC EXPERIMENT

ABSTRACT: In 1987–1989 a lysimetric experiment was designed to determine the effect of species composition of grass cultures (mono- and polyculture cultures) on Collembola communities, and to examine correlations between the abundance of Collembola and other soil organisms. Also the dependence of Collembola abundance on plant biomass was examined. Two plant communities were under study: simplified (*Dactylis glomerata* – monoculture) and comprising several species (a mixture of six grass species – polyculture). Plastic 0.16 m² lysimeters were used, filled with alluvial soil made up of coarse sand. The soil was watered and fertilized with earthworm casts.

The simplification of the plant community had an unequivocal effect on the density and species diversity of collembolans. Watering and fertilization accounted for an increase in the density of collembolans only in the upper soil layer of the severalspecies plant community. Fertilization had a shortterm effect, noticeable within 30 days after the introduction of casts.

Cryptopygus bipunctatus, a pioneer species, was the dominant, accounting for over 50% of the community in the upper soil layer and for 30% in the lower layer.

recently been one of the most common subjects of ecological studies. A small number of plant and animal species is typical of human managed ecosystems, mostly agrocoenoses (Heisler 1990, Paoletti et al. 1991, Keiser and Heisler 1994). Impoverishment of the vegetation is also observed in grasslands. Swards rich in species not so long ago are being converted into grassy communities clearly predominated by one species (Kostuch 1987, Kornaś 1990, Kornaś and Dubiel 1990, Bardgett et al. 1993, Kajak and Wasilewska 1997). Although this is a common process, little is known about its effects on basic processes occurring in ecosystems, such as production, matter decomposition, and nutrient cycling. Especially, the consequences of changes in diversity for soil biology are poorly known (Freckman 1994).

The present paper concerns apterous in-

KEY WORDS: Collembola communities, grass culture, diversity, simplified plant community

1. INTRODUCTION

As a consequence of increasing simplification of biocoenoses, species diversity has sects such as Collembola – one of the groups of heterotrophic organisms in soil mesofauna. These insects inhabit spaces among soil particles, litter, mosses, lichens, and tree bark. They live on dead organic matter, fungi, algae, and bacteria (Bødvarsson 1970, Butcher *et al.* 1971, Striganova 1987, Saur and Ponge 1988, Gunn and Cherrett 1993, Zwart *et al.* 1994). By modifying the

species composition and abundance of soil microorganisms, they have an indirect effect on mineralization and humification of organic matter (Cernova et al. 1971, Hanlon and Anderson 1979, 1980, Lusssenhop 1981, Ineson et al. 1982, Seastedt 1984, Anderson et al. 1985, Huhta et al. 1988, Czarnecki 1989, Vitousek et al. 1989, Striganova 1992).

The objectives of the study were: a) to determine the response of collembolan communities (numbers, biomass, and species composition) to experimental changes in the habitat, such as the diversity and biomass of plant communities, watering, and fertilizing and b) to analyse correlations between collembolans and other soil organisms: bacteria, fungi and Acarina (Kajak et al. 1989) and Enchytraeidae (Makulec and Pilipiuk 2000) and c) also between collembolans and plant biomass (Kajak et al. 1989) in simplified and rich plant communities.

mixture of grasses commonly used in agriculture (Table 1). Only grasses were used to ensure similarity in the complexion and requirements of plants in different variants of the experiment. In addition to two plant communities, other sources of variation comprised fertilization with earthworm casts and watering. It was assumed that the control variant, with one grass species neither fertilized nor watered, was the most simplified, whereas the variant with grass mixture fertilized with earthworm casts and watered was the most diverse.

2.1. EXPERIMENTAL DESIGN

The experiment was initiated in June of 1986 at the lysimetric station of the Warsaw

2. STUDY AREA AND DESCRIPTION OF THE EXPERIMENT

Lysimeters were used in experiments designed to analyse differences in the functioning of grass mono- and polyculture. Two communities were compared; a singlespecies community represented by a monoculture of the rougle cock's-foot Dactylis glomerata and a polyculture made up of a

Agriculture University in Warsaw-Ursynów, on two parallel plots: control - not watered (plot I) and watered (plot II) (Fig. 1). Both these plots were watered for several months preceding the experiment to enable the growth of new-sown plants. From 1987, only one plot was watered for three consecutive years.

On each plot, 80 plastic lysimeters 0.16 m² in area and 0.5 m deep were placed in three rows. Each lysimeter was surrounded by 0.9 m² protective microplots, and the distance between lysimeters was 0.2 m. The lysimeters and the two protective microplots were filled with alluvial coarse sandy soil taken from nearby experimental fields of the Warsaw Agriculture University sown with Dactylis glomerata. The soil profile comprised

Table 1. Changes of plant composition (% of yield)¹⁾ in lysimeters with grass mono- and polyculture

Sown gross spacias	Monoculture							
Sown grass species	1986	1987	1988	1989	1986	1987	1988	1989
Dactylis glomerata L.	100	78	95	82	15	5	28	26
Festuca pratensis Huds.	-	-	-	-	20	27	6	6
Festuca rubra L.		-	-	-	15	8	27	31
Lolium perenne L.	-	-	-	-	10	27	12	6
Phleum pratense L.	-	-	-	-	20	22	17	8
Poa pratensis L.	_			-	20	2	3	10

¹⁾after Kajak et al. (1989)



Not watered lysimeters (I)

0.0.0000	• C	0.	0	• 0	• • • • •	0.	0	•	0	•	0	•
	• C	0 •	0	• 0	00000	•	0	•	0	•	0	•
$\circ \circ $	• C	0 •	0	• 0		0 •	0	•	0	•	0	

Watered lysimeters (II)



Fig 1. Scheme of lysimetric experiment

a humus horizon (A1) 0.1 m deep and the underlying horizon (C) 0.4 m deep. The reaction of the soil profile was weakly acid, with pH ber. The yield was removed from the plots. between 6 and 6.5.

did not exceed 1%. The vegetation was mown twice a year: in mid-June and late in Septem-

Lysimeters sown in the same way formed groups of 20. Every second lysimeter was fertilized with earthworm casts. The experiment comprised eight variants:

Monoculture (M):	Polyculture (P):
Control (M)	Control (P)
Watered (W)	Watered (W)
Fertilized (F)	Fertilized (F)
Fertilized + watered (FW)	Fertilized + watered (FW)

The study was conducted in three successive years from April through October of 1987-1989 (the vegetation was examined from April through September), thus it was started one year after the onset of the experiment.

2.2. VEGETATION

The composition of plant communities in the cultures of both types was subject to changes from year to year. In the monoculture, however, D. glomerata always contributed more than 70% of the total yield. In the several-species community, the proportion of different grass species varied in successive years but always two-three species predominated, accounting for 20-40% of the total yield. In addition to the sown species, also other grasses emerged, but their proportions

2.3. WATERING

The water content of plot I, which was not watered, was dependent on atmospheric precipitation, thus it was insufficient from time to time. The functioning of this system is described by Pawłat (1982). The total input of water from April to September averaged about 165 mm each year. In the periods of high water deficiency, the two plots were supplied with 15 mm of water at a time to prevent the drying of plants (Kajak et al.1989).

2.4. FERTILIZATION

Fertilization with earthworm casts was applied on the soil surface once a year at the beginning of June. Earthworm casts were collected from urban lawns. A dose of 300 g d.w. per lysimeter was used. The content of nutrients supplied in this way in kg ha⁻¹ was: carbon – 106, nitrogen – 41, phosphorus – 8, potassium – 10, sodium – 0.5, magnesium – 13, and calcium – 117. These amounts of nitrogen, phosphorus, and potassium corresponded to low doses used in meadow (Kajak et al. 1989).

3. METHODS

Soil samples were taken in 1987–1989 at depths of 0-5 cm and 5-10 cm, three times per season: in June, August, and October. A soil sampler 10 cm² in surface area was used. On each occasion samples were taken from six lysimeters of each variant of the experiment (see schema of the experiment above -2.1. Experimental design), that is, from 48 lysimeters (from 24 lysimeters with monoculture and from 24 lysimeters with polyculture). Each year they were taken from a different group of lysimeters. Soil samples were taken from central parts of lysimeters to avoid the edge effect. In total, 864 samples were taken, from which 16156 individual insects were extracted. Collembolan biomass was calculated from the length of individuals by using the Dunger's (1968) table. About half of the individuals selected at random were measured (a total of 7000). The mean biomass of different species was calculated from their mean length and abundance in the samples.

where a - is the number of individuals of a given species in the community A, b - is the number of individuals of a given species in the community B, and w - is the number of individuals of common species for the communities A and B.

Author's own scale was used to describe similarity:

below 25%no similarityfrom 25% to less than 50%weak similarityfrom 50% to less than 75%high similarityfrom 75%very high similarity

The species diversity of collembolan communities was calculated from the Shannon-Wiener (1963) formula:

The significance of differences in the density and biomass of Collembola was analysed by using nonparametric tests (Siegel 1956, Blalock 1974) because the frequency distributions were not normal even after logarithmic transformation.

Correlations of collembolan numbers with root biomass and crop and with Acarina (Kajak *et al.*1989) and Enchytraeidae (Makulec and Pilipiuk 2000) were tested by using the coefficients of multiple correlation (Enlandt 1964). To evaluate the correlation between collembolan numbers and bacteria or fungi numbers (Kajak *et al.*1989) a simple, nonparametric Kendall correlation was used (Siegel 1956).

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where S – is the number of species, $p_i = n_i/n$, n_i – is the numerical abundance of different species, and n – is the total number of individuals.

Statistical significant of differences among the values of H' was estimated by using the Hutcheson (1970) test.

Moreover, author's own scale was used to describe the dominance structure:

more than 30%	dominant
from 10% to 30%	subdominant
from 5% to less than 30%	recedent
less than 5%	accessory

The collected material was divided into ecological groups, that is, groups of species were distinguished with respect to moisture preferences (hygrophilous, mesophilous, and xerophilous, after Stach 1960); distribution and preferred habitat type (eurytopic, open areas, forests, and others, after Stach 1964, Christian and Thibaud 1988, Sterzyńska 1989a, b); preference for soil layer: litter (after Christiansen 1964), epigeic species – occurring on the surface of soil and plants, that can move rapidly (Christiansen 1964, Stebaeva 1970), hemiedaphic species – dwelling the litter, top soil layer under the lit-

Species similarity of collembolan communities in different variants and lysimeters was calculated from Marczewski and Steinhaus (1959) formula:

$$s = \frac{w}{a+b-w}$$

ter, mosses and lichens, and occurring on water surface, euedaphic species - inhabiting the soil, nests of insects, and caves.

4. RESULTS

4.1. DENSITY OF COLLEMBOLA

The effect of the simplification of plant species composition on collembolan densities was relatively low. Only in the watered variant, the density of insects in the upper soil layer (0–5 cm) was significantly higher in the several-species community as compared with the simplified community (Table 2). At the same time, in the control lysimeters, the density of springtails in the lower layer (5-10 cm) was lower in the several-species community than in the monoculture (Table 2).

an effect of fertilization on their densities (Table 3). Only one month after this treatment, collembolan densities in the upper soil layer of the variant with the several-species community were significantly different in both cultures (Table 3).

4.2. BIOMASS OF COLLEMBOLA

Springtail biomass varied depending on the variant. In the control (M and P), a higher biomass was noted for the monoculture than for the polyculture (Fig. 2, P < 0.05). Springtail biomass was lower in the deeper soil layer as compared with the upper layer, but the difference was significant only in two cases - in the control variant with the monoculture, and in the fertilized and watered variants with both types of grass communities (Fig. 2, P < 0.05).

Watering had a positive effect on springtail density only in the upper soil layer with the mixture of grasses (Table 2). No significant differences in insect densities were found between the other variants in relation to watering (Table 2).

Based on the whole material, the analysis of numbers of collembolans did not show

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4.3. SPECIES COMPOSITION AND SIMILARITY OF COLLEMBOLA COMMUNITIES

Over the study period, 16 collembolan species were noted in the lysimeters (Table 4). Among them, 10 occurred in all variants of the experiment (Table 4). Their communities showed a very high or a high similarity of

Table 2. Density of collembolan communities (in 10^3 ind. m^{-2}) of different experimental variants in the grass mono- and polyculture. Mean ± SD for all data 1986-89 is given.

N. ·	Soil laye	Statistical significance		
Variants	Monoculture	Polyculture	between M and P	
Control	27.6 ± 30.4	20.8 ± 12.0	n.s.	
Fertilized (F)	22.5 ± 14.1	$20.0 \pm 13.5^{(b)}$	n.s.	
Watered (W)	17.6 ± 8.1	$28.9 \pm 14.9^{(a)}$	+	
Fortilized + watered (FW)	195 ± 109	30 2 + 23 7	nc	

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	Soil layer	5–10 cm	
Control	21.0 ± 22.3	$12.1 \pm 12.6^{(c)}$	++
Fertilized (F)	17.3 ± 19.0	15.7 ± 15.9	n.s.
Watered (W)	13.7 ± 14.4	17.2 ± 17.3	n.s.
Fertilized + watered (FW)	15.0 ± 17.4	11.4 ± 10.7	n.s.

(a - statistical significance (+) between variants control-watered in polyculture, ^{(b} - statistical significance (+) between variants fertilized - fertilized + watered, (c - statistical significance (+) between upper and lower soil layer in control of polyculture ++P < 0.01, +P < 0.05, n.s. P > 0.05.

Table 3. The effect of fertilization with earthworm casts on collembolan density (in 10^3 ind. m⁻²) after days fertilization (means SD for all data 1987–89, N = 9)

	Monod	culture	
	Not fertilized	Fertilized	Statistical significance
Soil layer 0-5 cm			
Control (M)	11.7 ± 9.3	18.3 ± 18.4	n.s.
Watered	24.4 ± 19.9	23.7 ± 19.9	n.s.
Soil layer 5-10 cm			
Control (M)	12.0 ± 19.2	7.4 ± 9.7	n.s.
Watered	7.1 ± 7.3	11.0 ± 21.1	n.s.
	Polyc	ulture	
	Not fertilized	Fertilized	Statistical significance
Soil layer 0-5 cm			
Control (P)	20.1 ± 22.6	38.2 ± 27.4	++
Watered	17.9 ± 16.6	37.0 ± 16.6	+

Son layer 5-10 cm	60.02	120 ± 154	
Control (P)	0.9 ± 0.3	12.9 ± 13.4	11.5.
Watered	11.2 ± 21.4	14.9 ± 22.9	n.s.

Statistical significance: ++ P < 0.01, + P < 0.05, n.s. - no significance





monoculture soil layer 5-10 cm

mg fresh weight m ⁻²			
1400 7			
1000			

polyculture soil laver 5-10 cm

mg fresh weight m⁻² 1400

Fig. 2. Mean (of all data 1987–98) biomass (mg fresh weight m^{-2}) of collembolan communities of different experimental variants (M or P – control, F – fertilized, W – watered, FW – fertilized+watered)

Table 4. Composition and number of species (from all data 1987-89) among Collembola of different experimental variants (M or P - control, F - fertilized, W - watered, FW - fertilized+watered)

	Monoculture				Polyculture			
Species		F	W	FW	Р	F	W	FW
1. Cryptopygus bipunctatus (Axels.)	+	+	+	+	+	+	+	+
2. Crypopygus thermophilus (Axels.)		+						
3. Proisotoma minuta (Tullb.)	+		+		+		+	+
4. Isotoma notabilis (Schaff.)	+	+	+	+	+	+	+	+
5. Isotoma viridis Bourl.	+	+	+	+	+	+	+	+
6. Isotomodes productus (Axels.)	+	+	+	+	+	+	+	+
7. Folsomia fimetaria (L.)	+		+	+			+	+
8. Folsomia quadrioculata (Tullb.)	+	+	+	+	+	+	+	+
9. Folsomides parvulus Stach.		+						
10. Mesaphorura spp.	+	+	+	+	+	+	+	+
11. Metaphorura affinis (Born.)	+	+	+	+	+	+	+	+
12. Brachystomella parvula (Schaff.)	+	+	+	+	+	+	+	+
13. Schoetella ununguiculata (Tullb.)	+	+	+	+	+	+	+	+
14 Lepidocyrtus lanuginosus (Gmel.)	+	+	+	+	+	+	+	+
15. Pseudosinella alba (Pack.)						+	+	
16. Sminthurinus aureus (Lubb.)	+	+	+	+	+	+	+	+
Number of species	13	13	13	12	12	12	14	13

the species composition in different variants. In the monoculture, the similarity ranged from almost 92 to 100% in the upper soil layer and from a little more than 57 to almost 77% in the lower layer. In the poluculture, the similarity of the species composition in the upper soil layer of different variants was lower, and it ranged from almost 65 to 85%, whereas in the deeper soil layer from 50 to almost 82%. It can thus be concluded that the species composition of Collembola in different lysimeters was more similar for the monoculture than for the mixture of grasses.

nities, the highest similarity in Collembola ture than in monoculture but only in control

was noted between lysimeters with the monoculture and mixture of grasses (Table 5). A little lower similarity was found between watered and not watered variants, and between fertilized and unfertilized variants (Table 5).

4.4. DIVERSITY OF COLLEMBOLA COMMUNITIES

The effect of simplification of grass cultures on collembolan communities was ambiguous.

In the upper soil layer the collembolan When comparing the two grass commuspecies diversity was higher in grass polycul-

Table 5. The influence of type of grass culture, watering and fertilizing on species similarity(% values of Marczewski and Steinhaus index (1959) for all data 1986-89) of Collembola of different experimental variants

Similarity between:	Soil layer 0-5 cm	Soil layer 5-10 cm
Variants with monoculture and polyculture	84	73
Variants: watered and not watered	71	71
Variants: fertilized and not fertilized	79	71

and fertilized variations. In the lower soil layer, however the collembolan species diversity was higher in grass monoculture than in polyculture (Table 6).

The species diversity of Collembola was usually higher in the upper soil layer than in the lower soil layer in both grass cultures. nearly 38% (in the lower soil layer of the several-species community) (Table 7).

In the lower soil layer, the group of dominants also comprised species of the genus *Mesaphoura* (Table 7).

Among other species, the following had a high contribution: *Isotoma notabilis* and

Table 6. Diversity of collembolan communities by reference to value for Shannon-Weaver H' index of different experimental variants (all data 1987-89)

Variant	Monoculture	Polyculture	Statistical significance		
	(M)	(P)	between M and P		
	Soil layer	r 0–5 cm			
Control	1.34 ^{(a,c}	1.55 ^{(a,d}	+++		
Fertilized (F)	1.38 ^{(c}	1.48 ^{(d}	+		
Watered (W)	1.47 ^{(b}	1.47 ^{(b,d}	n.s.		
Fertilized+watered (FW)	1.52 ^{(c}	1.37 ^{(d}	+++		
	Soil layer	5–10 cm			
Control	1.29 ^{(a}	1.29 ^{(a}	n.s.		
Fertilized (F)	1.28	1.23	+		
Watered (W)	1.46 ^{(b}	1.31 ^{(b}	++		
Fertilized+watered (FW)	1.41	1.49	+++		

(a - statistical significance between variants: control and fertilized: in monoculture, in upper and lower layer P < 0.01; in polyculture, in upper and lower soil layer P < 0.05

^{(b} – statistical significance between variants: watered and fertilized+watered: in monoculture in upper and lower soil layer P < 0.001; in polyculture, in upper soil layer P < 0.01 and in lower soil layer P < 0.001

(c – statistical significance between upper and lower soil layers in monoculture P < 0.01

^{(d} – statistical significance between upper and lower soil layer in polyculture P < 0.001statistical significance: +++ P < 0.001, ++ P < 0.001, + P < 0.05

4.5. DOMINANCE STRUCTURE OF COLLEMBOLA COMMUNITIES

Springtail communities were highly predominated by *Cryptopygus bipunctatus*. It contributed to 53–62% of the community in the upper soil layer, and to 34–55% in the lower layer (Table 7). Typically its proportion in the community was lower in the several-species community as compared with the monoculture (Table 7). Brachystomella parvula in the upper soil layer, and Metaphorura affinis in the lower layer (Table 7). The proportion of I. notabilis was higher in the watered variant, where it was one of the dominants (Table 7). M. affinis was more abundant in the mixed culture, where it was in the groups of subdominants or dominants (Table 7).

The second dominant was *Isotomodes* productus and its proportion was the highest in the fertilized and watered variant in lower soil layer, and depending on the layer and plant community it ranged from 18% (in the upper soil layer of the two communities) to

4.6. PROPORTIONS OF ECOLOGICAL GROUPS OF COLLEMBOLA

Based on the whole material collected, it has been found that mesophilous species and species characteristic of open habitats predominated in all variants of the experiment (Fig. 3). In the upper soil layer, the species of Table 7. Dominance structure (% of all individuals 1987–89) among Collembola of different experimental variants (M or P – control, F – fertilized, W – watered, FW – fertilized+watered)

Species	Monoculture			Polyculture				
	М	F	W	FW	Р	F	W	FW
		Soil	layer 0-5	5 cm				
Cryptopygus bipunctatus	62	59	58	53	55	56	57	57
Isitimina thermophila	-	-	-	-	-	< 1	< 1	< 1
Proisotoma minuta	-	-	-	-	-	-	< 1	-
Isotoma notabilis	7	4	13	11	9	5	13	12
Isotoma viridis	3	2	4	2	3	2	1	2
Isotomodes productus	14	19	11	18	13	18	11	19
Folsomia fimetaria	< 1	-	< 1	< 1	-	-	< 1	< 1
Folsomia quadrioculata	2	2	2	2	4	1	< 1	-
Mesaphorura spp.	5	7	5	4	5	4	5	3
Metaphorura affinis	1	2	1	2	1	2	4	1
Brachystomella parvula	6	4	3	6	8	8	6	4
Schoetella ununguiculata	< 1	< 1	1	1	1	1	< 1	< 1
Lepidocyrtus lanuginosus	< 1	1	< 1	< 1	< 1	< 1	< 1	< 1
Pseudosinella alba	-	-	-	-	-	< 1	< 1	-
Sminthurinus aureus	< 1	< 1	1	1	< 1	1	2	< 1
		Soil	layer 5-1	0 cm				
Cryptopygus bipunctatus	51	51	50	43	55	55	54	34
Isotoma thermophila	-	< 1	-	-	-	-	-	-
Proisotoma minuta	< 1	-	< 1	-	< 1	-	< 1	< 1
Isotoma notabilis	2	1	3	4	3	< 1	1	5
Isotoma viridis	1	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Isotomodes productus	25	24	21	29	21	27	20	37
Folsomia fimetaria	-	-	< 1	1	-	-	-	< 1
Folsomia quadrioculata	< 1	< 1	< 1	< 1	-	< 1	-	< 1
Folsomides parvulus	-	0.4	-	-	-	-	-	-
Mesaphorura spp.	17	18	13	19	11.8	9	10	13
Metaphorura affinis	2	4	9	3	7	6	12	9
Brachystomella parvula	< 1	< 1	1	1	1	1	1	1
Schoetella ununguiculata	-	-	. 1	< 1	< 1	-	< 1	-
Lepidocyrtus lanuginosus	< 1	-	-	< 1	_	< 1	< 1	-
Pseudosinella alba	-	-	-	_	-	-	-	-
Sminthurinus aureus	< 1	< 1	1	-	_	< 1	1	< 1

hemiedaphon were dominants. In the lower layer, they were only a little more abundant than the species of euedaphon (Fig. 3). The highest proportion of euedaphon was found in the lower soil layer of the watered and fertilized variant (Fig. 3). 4.7. INFLUENCE OF SOME SOIL ORGANISMS AND THE BIOMASS OF YIELD ON COLLEMBOLA ABUNDANCE

Using a multiple correlation between densities of Collembola, Acarina, and Enchytraeidae over the whole study period, it was

Fig. 3. Proportion (% of total numbers of individuals) of ecological species groups, determined by environmental preferences (H – hemiedaphic, E – euedaphic, Hy – hygrophilous species, Me – mesophilous species, X – xerophilous species, Eu – eurytopic species, O – species of open areas, Fo – forest species) of collembolan communities of different experimental variants (M or P – control, F – fertilized, W – watered, FW – fertilized+watered)

found that Collembola were positively correlated with Acarina in the two soil layers, and in the lower soil layer, they were also positively correlated with Enchytraeidae (Table 8).

No significant relationships were found between numbers of springtails and bacteria or fungi neither in the whole material nor in separate analyses of the two types of culture (Table 8). and springtail numbers estimated at the same time, that is, in June and October of each study year. Based on 3-year materials, a negative correlation was found between springtail numbers and crop biomass.

To analyse relationships between springtail numbers and root biomass, the data from the last two study years were used. Data on root biomass were from October, as this analysis could be made only after the termination of soil sampling. No correlation was found between springtail numbers and root biomass in the two soil layers (Table 8).

It should be noted, however, that the correlation between springtails and fungi tended to be negative, whereas the correlation between springtails and bacteria tended to be positive (the simplified community was an exception).

For the analysis of multiple correlation, the crop biomass at two harvests was used

5. DISCUSSION

Collembola abundantly occur mainly in soils of forest ecosystems (Petersen 1982).

Table 8. Correlations (by using multiple correlation index – r and simple correlation – τ) of collembolan and *Cryptopygus bipunctatus* numbers with numbers of Acarina¹⁾, Enchytraeidae²⁾, numbers of bacteria and fungi¹⁾ and with root biomass and yield¹⁾

Multiple correlation	n index (r)				
Correlation of Collembola numbers and:	Soil layer 0-5 cm	Statistical significance	Soil layer 5–10 cm	Statistical significance	
Acarina numbers	0.34	P < 0.001	0.48	P < 0.001	
Enchytraeidae numbers	-0.06	n.s.	0.44	P < 0.001	
Yield biomass of grass culture (mg fresh weight m ⁻²)	-0.54	P < 0.001	-0.45	P < 0.001	
Correlation of Cryptopygus bipunctatus numbers and:					
Yield biomass of grass culture (mg fresh weight m^{-2})	-0.49	P < 0.001	-0.36	P < 0.001	
Root biomass (mg fresh weight m ⁻²)	-0.02	n.s.	-0.06	n.s.	
Simple correlat	ion (τ)				
Correlation of Collembola numbers and:	Soil layer 0-10 cm		Statistical significance		
Bacteria $(10^7 \text{ g}^{-1} \text{ dry weight of soil})$	0	.06	n.s.		

Fungi $(10^5 \text{ g}^{-1} \text{ dry weight of soil})$

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    after Kajak et al.(1989)
    after Makulec and Pilipiuk (2000)
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However, they are also relatively abundant in meadow soils. Mean collembolan densities in meadows vary from one thousand to 100 10³ ind. m^{-2} , and fresh mass from 250 to 650 mg m⁻² (Petersen and Luxton 1982). Persson and Lohm (1977) found mean densities of these insects in meadows of the order of 110 10^3 ind. m⁻² and biomass of the order of 400 mg m⁻². Densities of springtails in managed peat meadows ranged from 7.7 to 17.2 10³ ind. m⁻², depending on soil moisture and time after drainage, whereas biomass from 170 to 728.9 mg m⁻² (Kajak et al. 1985, Kajak et al. 1991, Kaczmarek 1991). In meadows of the order Arrenatheretalia located in north-eastern Poland (Suwalszczyzna), that differed in age and species richness, Collembola densities varied from 16.4 to 68.8 10^3 ind. m⁻² and their densities from 97 to 595 mg fresh wt m^{-2} (Kaczmarek and Kajak 1997). According to Sterzyńska (1990), collembolan densities in Arrhenatheretum medioeuropeum meadows were lower, of the order of $8.33 \, 10^3$ ind. m^{-2} , in pastures 6.57 10³ ind. m^{-2} , and in arable land from 1.53 to 6.88 10^3 ind. m⁻².

Curry and Momen (1988) found on average over 73 10^3 ind. m⁻² in a two-year- old meadow. Bardgett *et al.* (1993) noted densities from 23.0 to 49.0 10^3 ind. m⁻² in a pasture grazed by sheep. For comparison, mean springtail densities in urban lawns were much lower than in meadows, and they varied from 1.37 to 7.64 10^3 ind. m⁻² (Sterzyńska 1990). All these data refer to the soil layer 0–10 cm deep. They show that densities and biomass of springtails in meadow soils can largely differ, even within very similar soil types.

n.s.

-0.13

In the lysimetric experiment, springtail densities in the same soil layer varied from 32.9 to $48.6 \ 10^3$ ind. m⁻² and biomass from 403.2 to 856.2 mg fresh wt m⁻². These densities were within the range known for meadows, and they were close to maximum values. Biomass was a little higher than known from the literature cited above. These data show that the experimental conditions did not reduce live potentiality of Collembola.

In this experiment, simplification of the plant community had little effect on the den-

sity and biomass of Collembola, although Kaczmarek and Kajak (1997) have found that in new-established meadows, with small plant species richness (two species), springtail numbers and biomass were significantly lower than in a multi-year meadow, with a relatively high species richness of the sward (30 species). The total collembolan biomass in the youngest meadow comprised mostly small species (less than 0.5 mm), so that differences in biomass between meadows were even higher than differences in densities of collembolans (Kaczmarek and Kajak 1997).

Vegetation has an indirect effect on collembolan densities – through humus formation, and soil moisture or insolation (Dunger 1963, Christiansen 1964, Ponge 1993), thus the type of vegetation and soil cover are important to the population size of these insects (Czarnecki 1989, Diekrüger and Röske 1995). According to Czarnecki (1989), springtail densities in mineral soils are dependent on the content of organic matter and on plant production. In the present experiment, a negative correlation was found between the yield and collembolan numbers. This was probably due to the fact that crop removal impaired trophic conditions of the soil. Organic matter removed with the crop was not replenished and, consequently, the soil was gradually impoverished. The impoverishment of the soil proceeded at a higher rate in the several-species culture (grass mixture). This is evidenced, for example, by a reduced content of some nutrients (N, P, K, Mg, Ca) in dry plant mass in the mixture of grasses and in the soil (Kajak et al. 1989). Collembolan abundance depends on soil fertility, as stated by Hågvar (1982), who analysed large materials from forests of different trophy. Fertilization by the application of earthworm casts was likely compensate for this effect to some extent. Thus, the effect of fertilization on Collembola densities was short-lasting, noticeable only for one month after the application of earthworm casts.

Watering had a positive effect on collembolan density in some variants of the experiment. Many authors indicated that soil moisture was important to the development and activity of these insects, thus it influenced their numbers (Christiansen 1964, Butcher *et al.* 1971, Kaczmarek 1975; Sterzyńska 1989a)

Many authors found significant correlations between microflora and Collembola abundance (Christiansen 1964, Usher *et al.* 1982, Barret *et al.* 1993). In the present experiment no significant correlation was found between numbers of bacteria or fungi and springtail abundance.

In this experiment, a positive correlation

was found between numbers of Collembola, Acarina and Enchytraeidae. It seems that Collembola as a pioneers stimulated to growth these soil organisms.

The number of springtail species largely varies in meadows. It depends on the type of soil, age of the meadow, surrounding habitats, etc. Kaczmarek (1973) recorded 47 species from meadows in the Kampinoski National Park. In mown meadows of the order Arrhenatheretalia near Warsaw, 16–36 species were found (Sterzyńska 1989a, 1990), and in the Suwalszczyzna region 20–29 species (Kaczmarek and Kajak 1997). Persson and Lohm (1977) noted 24 springtail species in a management meadow.

In the present lysimetric experiment, 16 springtail species were recorded. A similar number of 17 species was found in another lysimetric experiment dealing with the functioning of plant communities (Byzova *et al.*

1989). Thus, the number of species in the present experiment was close to the lowest values known from natural meadows, and was also similar to that observed in analogical experiments. The soil used in the experiment was poor, and this could account for a small number of species. As found by Hågvar (1982), using coniferous forests as an example, species richness of Collembola increases with soil fertility.

Anderson (1978) and Sagrdelis and Margaris (1993) have found that habitat diversity determines not only the density of Collembola but also the species diversity of these insects. In the present experiment, the simplification of the grass community influenced the species diversity of these insects (typically, a higher diversity was noted in the mixture of grasses than in the *Dactylis glomerata* monoculture), and this was the case despite the fact that the plant diversity increased with time.

The dominant species of Collembola such as Cryptopygus bipunctatus occurs near human setIments (Stach 1947) and is abundance in areas with excessive nutrient content (liquid manure) (Melicis 1987) This species and Isotomodes productus, other dominant, belong to pioneer species (Dunger 1968, 1991), appearing in the initial stages of succession, and rapidly colonizing the area. 3. The other soil mesofauna groups (Acarina and Enchytraeidae) responded like Collembola.

4. The simplification of plant community affected the species diversity of Collembola communities. Typically, it was lower in the simplified community as compared with the several-species community.

6. SUMMARY

In 1987–1989, an experiment was designed at the lysimetric station of the Warsaw Agriculture Academy to determine the effect of simplification of grass culture on Collembola communities. The experiment was set up in plastic lysimeters 0.16 m² in surface area, filled with alluvial soil made up of coarse sand. Half of the lysimeters were sown with Dactylis glomerata and the other half with a mixture of grasses typically used in meadow management (Table 1). To differentiate habitat conditions, some lysimeters were watered, or fertilized, or watered and fertilized (Fig. 1). Earthworm casts were used as fertilizer in a dose of 300 g dry wt per lysimeter. Watering was automatically applicated. Thus, four variants of the experiment were run: control, watered, fertilized, and watered plus fertilized. Habitat conditions in lysimeters varied with time as the number of plant species was increasing and soil fertility was altering during the experiment. To estimate densities and species composition of springtails, soil samples were taken with a soil corer 10 cm² in area at depths of 0-5 cm and 5-10 cm. A total of 864 soil samples contained 16 156 insects. Almost 7 000 individuals were measured to estimate the biomass of the community. The effect of the simplification of grass culture on springtail densities was not obvious (Table 2). Watering and fertilization enhanced the densities of insects only in the upper soil layer of the several-species culture (Tables 2 and 3). The effect of fertilization was noticeable only for one month after the treatment (Table 3). Nor vegetation simplification clearly influenced the biomass of collembolans (Fig. 2). There were noted 16 species of springtails in the lysimeters and among them, 10 occurred in all variants of experiment (Table 4).

Pioneer species are usually eurytopic, most rapidly colonising the area after stress, r-strategists (Odum 1985). Presumably, the presence of this species may be indicative of a small sensitivity of Collembola to experimental conditions.

To sum up:

1. The simplification of plant communities has little effect on numbers and biomass of Collembola. This is a consequence of predominance of pioneer species in insect communities, little sensitive to environmental variation. The watering and fertilization slightly modified the effect of simplification on Collembola numbers.

2. Decreasing soil fertility over the experiment had a large effect on the results obtained. The impoverishment of soil proceeded at a higher rate in the severalspecies culture. The reason was that the crop was higher in this culture, thus more organic matter was removed. Because of that a negative correlation was found between the crop and springtail numbers.

Similarity of Collembola of all experimental variants was high (Table 5).

Species diversity of springtails was dependent on the variant of the experiment, and typically it was reduced in the lower as compared with the upper soil layer (Table 6).

Cryptopygus bipunctatus was the absolute dominant in all the variants. It accounted for over 50% of the springtail community in the upper soil layer (0–5 cm) and for almost 30% in the lower layer (5–10 cm). This species belongs to the group of r-strategists and is characteristic of early stages of succession. Another dominant species in the springtail community was *Iso-tomodes productus*, also a pioneer species (Table 7).

There has been found that mesophilous species characteristic of open habitats predominated in all experimental variants (Fig. 3).

Relationships between numbers of Collembola and other soil organisms were analysed in the experiment as well. It has been shown that the response of Acarina was similar to that of Collembola (Table 8).

A negative correlation was found between the plant crop/production and Collembola numbers, as the removal of the crop had a negative effect on soil fertility. The removed organic matter was not replenished.

It is suggested that the low responsiveness of springtail communities to the experimental treatments (diversity of plant communities, soil moisture, fertilization with earthworm casts) and to the progressive impoverishment of the soil with time arose from the fact that they were predominated by early-successional species. lysimeters with differen plant cover] (In: Ekologia mikroarthropod lesnych pocv [Ecology of microarthropods of forest soils] Ed. J. M. Cernova) – Nauka: pp. 101–114. (in Russian).

- Cernova N. M., Byzova Ju. B., Cernova A. I. 1971 – Relationship of number, biomass and gaseus exchange rate indices in microarthropods in substrates with various organic contents – Pedobiologia, 11: 306–314.
- Christian E., Thibud J. 1988 Terrestrsch-interstitielle Collembola aus osterreichen und ungarischen Sanden – Pedobiologia, 31: 229–237.
- Christiansen K. 1964 Bionomics of Collembola Ann. Rev. of Entom. 9: 147–178.
- Curry J. P., Momen F. M. 1988 The arthropod fauna of grassland on reclaimed cutaway peat in Central Ireland – Pedobiologia, 32: 99–109.
- Czarnecki A. 1989 Collembola jako element biologicznego systemu na obszarach podlegajacych silnej antropopresji [Collembola as a component of biological system in antropogenic area] – UMK, Torun, 156 pp.

7. REFERENCES

- Anderson J. M. 1978 Inter- and intra- habitat relationship between Woodland Cryptostigmata species diversity and the diversity of soil and litter microhabitats – Oecologia, 32: 341 – 348.
- Anderson J. M., Huish S. A., Ineson P., Leonard M. A., Splatt P. R. 1985 – Interactions of invertebrates, microorganisms and tree roots in nitrogen and mineral element fluxes in deciduous woodland soils (In: Ecological interactions in soil. Plants, microbes and animals. Eds. A. H. Fitter, D. Atkinson, D. J. Read, M. B. Usher) – Blackwell Scientific Publications, Oxford, London, Edinburgh, Boston, Palo Alto, Melbourne, pp. 377–391.
- Bardgett R. D., Frankland J. C., Whittaker J. B. 1993 – The effects of agricultural managment on the soil biota of some upland grasslands – Agric. Ecosystem Environ. 45: 25–45.

- Diekkrüger B., Röske H. 1995 Modelling the population dynamics of *Isotoma notabilis* (Collembola) of sites of different agricultural usage – Pedobiologia, 39: 58–73.
- Dunger W. 1963 Leistungsspezifitat bei Streuzersetzern (In: Soil organisms. Eds. J. Doeksen, J. Van der Drift) – North-Holland Publ. Comp. Amsterdam, pp. 92–102.
- Dunger W. 1968 Die Entwicklung der Bodenfauna auf rekultievierten Kippen und Halden des Braunkohlentagebaues – Abh. Ber. Natur., Gorlitz, 43: 1–256.
- Dunger W. 1991 Zur Primarsukzession humiphager Tiergruppen auf Bergbauflachen – Zool. Jb. Syst. 118: 423–447.
- Elandt R. 1964 Statystyka matematyczna w zastosowaniu do doswiadczalnictwa rolniczego [Mathematical statistic in agriculture experiments]– PWN, Warszawa, 400 pp. (in Polsish).
- Freckman D. W. 1994 Life in the soil. Soil biodiversity: its importance to ecosystem processes. Report of a Workshop Held at The Natural History Museum, London, England, August 30–September 1, 1994, 20 pp
- Gunn A., Cherrett J. M. 1993 The exploitation of

Blalock H. M. 1974 – Statystyka dla socjologów [Statistic for sociologists] – PWN, Warszawa, 400 pp. (in Polish).

Bødvarsson H. 1970 – Alimentary studies of seven common soil-inhabiting Collembola of Southern Sweden – Ent. Scand. 1: 74–80.

Butcher J. W., Snider R., Snider J. 1971 – Biocenology of edaphic Collembola and Acarina – Ann. Rev. of Entom. 16: 249–287.

Byzova J. W., Uvarov A. V., Lobutev A. P. 1988

- Pocvennye bezpozvonocnye lizymetrov s raznym rastitelnym pokrovom [Soil invertebrates in food resources by soil meso- and macro invertebrates – Pedobiologia, 37: 303–320.
Hågvar S. 1982 – Collembola in Norwegian coniferous forest soils. I. Relations to plant communities and soil fertility – Pedobiologia, 24: 255–296.
Hanlon R. D., Anderson J. M. 1979 – The effects of Collembola grazing on microbial activity in decomposing leaf litter – Oecologia, 38: 93–99.
Hanlon R. D., Anderson J. M. 1980 – Influence of macroarthropod feeding activities on microflora in decomposing oak leaves – Soil Biol. Biochem. 12: 255–261.

- Heisler C. 1990 Collembolen und Raubmilben auf Unterschiedlich Verdichteten Ackerflachen unter Getreide - Verhandlung der Geselschaft für Ökologie, 19: 262-267
- Heisler C. 1994 Auswirkungen von Bodenverdichtungen auf die Bodenmesofauna: Collembola und Gamasina - ein dreijahriger Feldersuch - Pedobiologia, 38: 566-576.
- Huhta V., Setala H., Haimi J. 1988 Leaching of N and C from birch leaf litter and raw humus with special emphasis on the influence of soil fauna – Soil. Biol. Biochem. 20: 875-878.
- Hutcheson K. 1970 A test for comparing diversities based on the Shannon formula - J. Theor. Biol. 29: 151–154.
- Ineson P., Leonard M. A., Anderson J. M. 1982 -Effect of collembolan grazing upon nitrogen and cation leaching from decomposing leaf litter -Soil Biol. Biochem. 14: 601-605.
- Kaczmarek M. 1973 Collembola in biotopes of the Kampinos National Park distinguished according to the natural succession - Pedobiologia, 13: 257-272.

netwicklung, Collembolenfauna, Denitrifikation und Mineralisation in einem Agrarstandort - Mit-Dt. Bodenkundl. Gesellsch. teilungen 66: 531-534.

- Kornaś J. 1990 Jak i dlaczego giną zespoły roślinne? [How and why do plant communities disappear?] – Wiad. Bot. 32: 7–16. (in Polish).
- Kornaś J., Dubiel E. 1990 Przemiany zbiorowisk łąkowych w Ojcowskim Parku Narodowym w ostatnim trzydziestoleciu [Changes of grasslands in Ojcowski National Park during last period of thirty years] - Prace Muz. Szafera, Prądnik 2: 97-106. (in Polish).
- Kostuch R. 1987 Zmiany florystyczne zachodzące pod wpływem zróżnicowanego nawożenia azotowego [Changes due to different doses of nitrogen fertilization] – Zesz. Probl. Post. Nauk roln. 308: 209-218.
- Lussenhop J. 1981 Microbial and microarthropod detrital processing in a prairie soil - Ecology, 62: 964-972.

- Kaczmarek M. 1991 Communities of Collembola in reclaimed organic soil formed of various types of peat - Pol. ecol. Stud. 17: 221-247.
- Kaczmarek M., Kajak A. 1997 Microarthropods and decomposition processes in meadows of various plant species richness - Ekol. pol. 45: 795-813.
- 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.
- Kajak A., Andrzejewska L., Ciesielska Z., Chmielewski K., Kaczmarek M., Makulec G., Pętal J., Ryszkowska J., Stopnicki J., Szanser M., Wasilewska L. 1991 - Ekologiczna analiza przemian zachodzących na torfowiskach pod wpływem gospodarki [The ecological analycal analysis of the changes in the peatlands following the management] - Zesz. Probl. Post. Nauk rol. 372: 436-454.
- Kajak A., Kusińska A., Makulec G., Olejniczak I., Pawłat H., Stefaniak O., Szanser M., Wasilewska L.1989 – Baza danych uproszczonych

- Makulec G., Pilipiuk I. 2000 Influence of plant diversity and earthworm casts on the abundance and species composition of enchytraeids (Oligochaeta: Enchytraeidae) in a lysimeter experiment - Pol. J. Ecol. 48: 185-193.
- Marczewski E., Steinhaus H. 1959 Odległość systematyczna biotopów [On the taxonomic distance of biotop] - Zast. Matem. 4: 195-203. (in Polish).
- Melecis V. 1987 Springtails (Collembola) as bioindicators of soil pollution (In: Soil fauna and soil fertility. Ed. B. R. Striganova) - Proc. 9th Int. Col. Zool., Moscow pp. 123–124.
- Moore J. C., Walter D. E., Hunt H. W. 1988 Arthropod regulation of micro- and mesobiota in below-ground detrital food webs - Ann.Rev. Entomol. 33: 419-439.
- Odum E. P. 1985 Trends expected in stressed ecosystems - BioScience, 35: 419-422.
- Paoletti M. G., Favretto M. R., Stinner B. R., Purrington F. F., Bater J. E. 1991 - Invertebrates as bioindicators of soil use - Agric. Ecosystem Environ. 34: 341-362.
- Pawłat H. 1982 Granice produktywności nawadnianych zbiorowisk trawiastych w warunkach zróżni-

zbiorowisk trawiastych Zakładu Krajobrazu (poprzednio Zakład Ekologii Gleby) IE PAN [Data base of grass communities simplification in the Department of Landscape Ecology (f. Department of Soil Ecology) IE PAS]. Kajak A., Wasilewska L. 1997 - Changes in meadow ecosystems as a consequence of secondary succession and plant diversity (synthesis of research) - Ekol. pol. 45: 839-859. Keiser E.A., Heisler C., Walenzik G., Heimemeyer O. 1991 - Einflüsse von mechanischen Bodenbelastungen auf mikrobiele Biomassecowania nawożenia [The productivity of the watered grass communities in different conditions of fertilization] - SGGW, Warszawa, 20 pp. (in Polish).

Persson T., Lohm V. 1977 – Energetical significance of the annelids and arthropods in a Swedish grassland soil - Ecol. Bull. (Stockholm) 23. Petersen H. 1982 – The total soil fauna biomass and its composition - Oikos, 39: 245-264. Petersen H., Luxton M. 1982 - A comparative analysis of soil fauna populations and their role in the composition processes - Oikos, 39: 265-388.

- Pielou E. C. 1966 Shannon's formula as a measure of specific diversity. Its use and measure - Am. Nat. 100: 463-465.
- Ponge J. F. 1993 Biocenoses of Collembola in atlantic temperate grass-woodland ecosystems - Pedobiologia, 37: 223-244.
- Saur E., Ponge J., F. 1988 Paratullbergia callipygos using transmission electron microscopy - Pedobiologia, 31: 355-379.
- Seasted T. R. 1984 The role of microarthropods in decomposition and mineralization processes -Ann. Rev. of Entom. 29: 25-46.
- Sgardelis S. P., Margaris N. S. 1993 Effects of fire on soil microarthropods of phryganic ecosystem – Pedobiologia, 37: 83–94.
- Shannon C. E., Wiener W. 1963 The mathematical theory of communication - Univ. of Illionois Press, Urbana, 117 pp.
- Siegel S. 1956 Nonparametric statistics for the behavioral sciences - Mc Graw-Hill Book Comp. New York, Toronto, London, 559 pp.

- Sterzyńska M. 1989b Collembola from urban areas. 3rd International Seminar on Apterygota, University of Siena, Siena, Italy: 347-354.
- Sterzyńska M. 1990 Communities of Collembola in natural and transformed soils of the linden-oak-hornbean sites of Mazovian Lowland - Frag. fau. 34: 165-262.
- Striganova B. R. 1987 Soil animals in detrite food webs (In: Soil fauna and soil fertility. Ed. B. R. Striganova) - Proc. 9th Int. Col. on Soil Zool. 1985, Moscow, pp. 18-23.
- Striganova B. R. 1992 Trophic relations in soil animal communities and decomposition rates -Pol. ecol. Stud. 16: 119-130.
- Tilman D., Downing J. A. 1994 Biodiversity and stability in grasslands - Nature, 367: 363-366.
- Tramer E. 1969 Bird species diversity: Component of Shannon's formula – Ecology, 50: 927–929.
- Usher M. B., Booth R. G., Sparkes K. E. 1982 A review of progress in understanding the organiza-

- Stach J. 1947 The Apterygotan fauna of Poland in relation to the world - fauna of this group of insects. Family: Isotomidae - Acta monogr. Cracoviae, Kraków, 488 pp.
- Stach J. 1964 Owady bezskrzydłe. Apterygota. Katalog Fauny Polski [Wingless insects. Aperygota. Catalogue of Polish Fauna] - PWN, Warszawa cz.15, 214 pp. (in Polish).
- Stebaeva S. K. 1970 Zyznennye formy nogochwostok (Collembola) [Biological forms of springtails (Collembola)] - Zoologiceskij Zurnal XLIX, 10: 1437-1454. (in Russian).
- Sterzyńska M. 1989a Springtails (Collembola) of moist meadows on the Mazovian Lowland - Memorabilia Zool. 43: 61-81.

tion of communities of soil arthropods - Pedobiologia, 23: 126-144.

- Vitousek P. M., Matson P. A., van Cleve K. 1989 - Nitrogen availability and nitrification during succession: Primary, secondary, and old-field seres (In: Ecology of Arable Land, Perspectives and Challenges. Eds. M. Clarholm, L. Bergstrom) - Kluwer Acad. Publ. pp. 161-171.
- Zwart K. B., Burges S. L. G. E., Bloem J., Bouwman L. A., Brussard G., Didden W. A. M., Marinissen J. C. Y., Vreeken-Buijs M. J., de Ruite P. C. 1994 – Population dynamics in the below ground food webs in the different agricultural system - Agric. Ecosystem Environ. 51: 187-198.

(Received after revising September1999)