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THE ROLE OF EARTHWORMS (LUMBRICIDAE) IN TRANSFORMATIONS OF ORGANIC MATTER AND IN THE NUTRIENT CYCLING IN THE SOILS OF LEY MEADOWS AND PERMANENT MEADOWS

ABSTRACT: Analysis concerned the carbon content, main fractions of soil humus, total nitrogen content and contents of selected exchangeable elements (P-PO_4, K, Ca, Mg and Mn) in the casts produced by earthworms, and in the upper layers of the soil, on several leys and permanent meadows. The percentage contents of C, fulvic acids and humic acids are always higher in casts than in the soil and rise along the sequence from younger to older meadows. The content of total nitrogen is also clearly greater in earthworm casts than in the soil and the C/N ratio rises along the sequence to older meadows. Exchangeable elements other than manganese show similar trends. It is shown that these trends probably result from changes in the proportions of two dominant species of Lumbricidae with alternate feeding specializations, namely the geophagous *Aporrectodea caliginosa* (Sav.) and the detritivorous *Lumbricus rubellus* Hoffm.

KEY WORDs: casts, Lumbricidae, meadows, humus, exchangeable elements

1. INTRODUCTION

The amounts of casts excreted by Lumbricidae can be assessed directly or on the basis of laboratory data to amount to between several and tens tonnes per ha in the course of a season. These characteristic soil formations have a rich and active microflora, are rich in exchangeable elements, have a low C/N ratio and contain a large amount of organic matter at various stages of decomposition, mixed with the mineral soil fraction.

To date little is known of the qualitative composition of organic matter in earthworm casts. Given most often is the elemental composition, particularly the total carbon content (L u n t and J a c o b -

son 1944, Graff 1971, Czerwiński et al. 1974).

The aim of this study was therefore to trace the changes occurring in the humus fractions and in the composition of elements in the soil and in casts, against the background of successional changes in the meadow biocoenosis.

2. STUDY AREA AND METHODS

In north-eastern Poland, meadows constitute a normal element of rotation. They are established by ploughing and by subsequent sowing with a single species of grass (*Dactylis glomerata* or *Phleum pratense*), or else with a mixture of grasses and clover. After 8–10 years of use they are ploughed again and converted into cultivated fields. However, in areas that are too steep, stony or wet, permanent meadows of the *Anthylli-Trifolietum* type occur (Jankowski 1997).

Selected for research were 6 sites located within Suwałki Landscape Park (north-eastern Poland). Three of these were located on an outwash plain and the remainder in the edge zone of a river valley. A detailed characterization of the soil and vegetation cover has been given by Kusińska and Łakomiec (1997), as well as by Jankowski (1997). Some basic features of the these meadows are given in Table 1.

The meadows studied created three successional sequences identified as series II and series III (see Kajak 1997). Successive age stages were defined by the symbols LB_2 and LB_3 – 3–5-year-old

Table 1. Site characteristics

Site	Series II			Series III		
	LB_2	LC_2	P_2	LB_3	LC_3	P_3
Age (years after tillage)	4	12	not tilled	6	8	not tilled
Utilization	mown	mown-grazed	grazed	mown-grazed	mown-grazed	grazed
Number of plant species in sward*	10	< 30	> 30	6	20	30
Soil**	Brown soils from loamy sand					
depth (cm) of horizon A1	40	52	38	40	43	50
% C in horizon A1	1.2	1.6	2.4	1.0	1.2	1.8
pH_{H2O}	7.3	5.5	5.4	7.0	5.9	5.8
Enzymatic activity***						
cellulase (µg glucose g^{-1} $24h^{-1}$)	74.4	87.7	161.9	73.4	85.3	84.9
protease (mg glicine g^{-1} $24h^{-1}$)	0.65	0.92	1.36	0.84	0.91	0.63

* Jankowski (1997), ** Kusińska and Łakomiec (1997), *** Stefaniak et al. (1997); LB_2, LC_2 – ley meadows and P_2 – permanent meadow on successional sequence II, LB_3, LC_3 – ley meadows and P_3 – permanent meadow on successional sequence III.

meadows, LC_2 and LC_3 – 6–8-year-old meadows and P_2 and P_3 for permanent meadows. Ley meadows (LB and LC) were managed by cutting and autumn grazing of cattle or horses, while permanent meadows were either wastelands or permanent pastures (P_3).

Samples were taken at the end of September 1987. Populations were assessed using the formalin method, which involves the extraction of earthworms using a c. 0.3% solution of formaldehyde (Raw 1959). 10 samples with a surface area of 0.3 × 0.3 m were taken at each site. Earthworm casts were collected at the same time. Casts were collected from demarcated areas cleared of vegetation, with the quantities removed being sufficient to allow for chemical analysis. Control samples of soil were taken from the same places at the two levels 0–5 cm and 5–10 cm.

Humic substances from soils and casts were divided with the aid of a mixture of sodium pyrophosphate ($Na_4P_2O_7 \cdot 10H_2O$) and soda lye. The prepared solution had a pH of about 13. The method is known widely as that of Kononova and Bielczikowa (Kononowa 1968). Total nitrogen was determined by the Kjeldahl method.

Exchangeable elements were extracted with a mixture of 0.5 n CH_3COOH and 0.5 n CH_3COONH_4, at a pH of 4.65 (Lakanen 1962). The cations K, Ca, Mg and Mn were determined by the flame photometery method on a Varian 1200 machine, while P-PO_4 was determined colorimetrically at a wavelength of 690 nm.

3. RESULTS

3.1. CARBON AND NITROGEN CONTENTS IN CASTS AND IN SOIL

The content of total carbon in earthworm casts always exceeded the level noted in soil. This was true of both series II and series III. The average proportion of carbon in earthworm casts was twice as high as the content in the 0–5 cm layer of soil and three times higher than in the 5–10 cm layer (Table 2).

These relations have a certain regularity, in that the ratio of the C content in casts to that in the soil at a depth of 5–10 cm shows a tendency to rise along the series from the youngest to the oldest meadows. Thus it would seem that, as the meadow biocoenosis develops, there is an increase in the significance of Lumbricidae in the shaping of organic matter resources in the surface layer of the soil. This was true of both successional sequences.

Such a regularity was not recorded in the case of the upper (0–5 cm) layer. This is probably largely the result of the significantly greater differentiations in concentrations of this element as the result of the diversity of the vegetation cover, the degree of sodding and the amount of litter and roots. These made it impossible for the methods used to detect a similar regularity.

In general, the content of organic matter in earthworm casts is greater on older meadows. This is noted at the stage moving from several-year-old to many-year-old meadows (series III), or only when these meadows are compared to permanent meadows (series II).

The meadow ecosystems of the two successional sequences are clearly different from the point of view of the richness

Table 2. Content of organic matter (%C) and nitrogen (%) in casts of Lumbricidae and in the soil

Site and source			% C	C_{casts} : C_{soil}	% N	N_{casts} : N_{soil}	C : N
LB_2	casts		4.8		0.39		12.3
	soil:	0–5 cm	2.2	2.2	0.20	1.9	11.0
		5–10 cm	1.6	3.0	0.14	2.8	11.4
LC_2	casts		4.7		0.37		12.7
	soil:	0–5 cm	2.4	2.0	0.23	1.6	10.4
		5–10 cm	1.5	3.1	0.17	2.2	8.8
P_2	casts		7.2		0.49		14.7
	soil:	0–5 cm	3.3	2.2	0.28	1.7	11.8
		5–10 cm	2.3	3.2	0.21	2.3	10.9
LB_3	casts		3.0		0.23		13.0
	soil:	0–5 cm	1.5	2.0	0.16	1.4	9.4
		5–10 cm	1.3	2.3	0.10	2.3	13.0
LC_3	casts		3.9		0.27		14.4
	soil:	0–5 cm	1.6	2.4	0.17	1.6	9.4
		5–10 cm	1.3	3.0	0.14	1.9	9.3
P_3	casts		2.9		0.17		17.0
	soil:	0–5 cm	1.7	1.7	0.16	1.0	10.6
		5–10 cm	0.9	3.2	0.13	1.3	6.9

For sites characteristics see Table 1.

of the upper layers of the soil in carbon. Higher concentrations were recorded on the meadows of series II. When this series is compared with series III, the percentage content of carbon on similarly-aged meadows is always higher. The most marked differences are between permanent meadows, probably as a result of the different mmanagement, with meadow P_3 being a permanent pasture and meadow P_2 a wasteland area grazed only sporadically.

As with carbon, the total nitrogen content in casts is clearly higher than in soils. However, the relative degree of richness is lower. At the same time, along the sequence between younger and older meadows there is a gradual decline in the ratio of nitrogen in casts to nitrogen in soil, especially in the 5–10 cm layer (Table 2). The predominant proportion of the organic nitrogen taken in by earthworms with food undergoes metabolic changes and is excreted through the integument as urea and ammonia. Casts therefore contain non-available or mineral forms of nitrogen.

The changes in the C : N ratio are interesting. In both successional series, the ratio is higher in casts than in soils, and is greater on older meadows. At the same time, in series III – which is clearly poorer in both carbon and nitrogen – the index is higher than on meadow series II (Table 2). This points to the significant role of Lumbricidae in the shaping of the feeding conditions for the cast microflora in a direction favouring the processes of humification of organic matter.

3.2. FRACTIONAL COMPOSITION OF THE HUMUS OF CASTS AND SOIL

Like those of total carbon, the amounts of humic acids, fulvic acids and humins are higher in casts than in soil (Table 3). The differences are of a similar order and point to similar regularities, i.e. an increase in amounts on many-year-old meadows (LC) in relation to several-year-old meadows on series III, and a clear prevalence of site P_2 in relation to both of the younger meadows in the sequence.

The percentage shares of the fractions vary. In general, casts are poorer than soils in both fulvic and humic acids (Table 3), while the humin fraction shows the reverse trend, with casts having

Table 3. Humus fractions in earthworm casts and in the soil

Site and source		mg · 100g^{-1} of soil			$C_{humic} : C_{fulvic}$	% in total C		
		humic acids	fulvic acids	humins		humic acids	fulvic acids	humins
LB_2	casts	778	946	3046	0.82	16	20	64
	soil: 0–5 cm	282	422	1546	0.67	12	19	69
	5–10 cm	241	389	1020	0.62	15	24	62
LC_2	casts	708	1127	2844	0.63	15	24	61
	soil: 0–5 cm	471	697	1232	0.67	20	29	51
	5–10 cm	331	486	744	0.68	21	31	48
P_2	casts	1228	1812	4290	0.62	16	25	59
	soil: 0–5 cm	534	819	1947	0.65	16	25	59
	5–10 cm	426	649	1205	0.65	19	28	53
LB_3	casts	423	513	2094	0.82	14	17	69
	soil: 0–5 cm	222	297	981	0.75	15	20	65
	5–10 cm	159	202	939	0.79	12	16	72
LC_3	casts	626	966	2308	0.65	16	25	59
	soil: 0–5 cm	352	565	732	0.62	21	34	45
	5–10 cm	252	360	648	0.70	20	29	51
P_3	casts	523	858	1529	0.61	18	30	52
	soil: 0–5 cm	308	582	791	0.53	18	35	47
	5–10 cm	159	323	388	0.49	18	37	45

For sites characteristics see Table 1

higher concentrations, particularly in the earlier stages of meadow succession.

The proportions of both basic constituents of humus (humic and fulvic acids) are greater on older meadows, but the trend is clearer for the latter. At the same time, the disproportions in both types of acid increase with the development and transformation of the meadow biocoenosis.

The changes in the mutual relations of carbon in humic to carbon in fulvic acids in casts and soil are interesting. In both successional series, the $C_{HA} : C_{FA}$ ratio in casts on similarly-aged meadows is very similar and shows a downward trend between the several-year-old and permanent meadows. This is to a great extent due to the aforementioned disproportion in changes in the contents of the two humus constituents along the successional sequence. Thus the casts of earthworms on progressively older meadows have greater proportions of fulvic acids – the youngest and least permanent humus fraction.

3.3. CONTENTS OF EXCHANGEABLE ELEMENTS IN CASTS AND IN THE SOIL

The contents of exchangeable phosphorus in casts and in soil show similar directions of change to those described previously for total carbon, but the trends are much more distinct (Table 4). In both successional series of ley meadows, the relative richness of casts in exchangeable phosphorus is clearly greater on older meadows. This is clear for the upper layer and even more marked in the case of the deeper (5–10 cm) layer of the profile. On permanent meadows (P), the ratios described do not reach such high values but still maintain the same trend. On average, casts are 3–16 times richer in exchangeable phosphorus than soils of the 5–10 cm layer. This points to the significant role of earthworms in providing easily-available phosphorus compounds for plants and microflora.

The analyzed exchangeable cations in general repeat the regularities described earlier. This is very clear in the case of potassium, calcium and magnesium (Table 5). On many-year-old meadows (LC), the relative increase in the contents in casts is always greater than on younger (several-year-old) meadows (LB). Permanent meadows rarely constitute a continuation of the sequence, but

Table 4. Concentrations of exchangeable phosphorus (ppm $P\text{-}PO_4$) in earthworm casts and in the soils of leys and permanent meadows

Site and source			$P\text{-}PO_4$	$P_{casts} : P_{soil}$
LB_2	casts		24.2	
	soil:	0–5 cm	6.3	3.8
		5–10 cm	4.2	5.8
LC_2	casts		32.6	
	soil:	0–5 cm	4.2	7.8
		5–10 cm	2.0	16.3
P_2	casts		19.2	
	soil:	0–5 cm	7.0	2.7
		5–10 cm	4.3	4.5
LB_3	casts		23.4	
	soil:	0–5 cm	14.2	1.6
		5–10 cm	6.9	3.4
LC_3	casts		17.8	
	soil:	0–5 cm	5.0	3.6
		5–10 cm	2.1	8.5
P_3	casts		12.2	
	soil:	0–5 cm	3.6	3.4
		5–10 cm	1.6	7.6

For sites characteristics see Table 1

the relative rise in the contents of elements is always greater than on the youngest, 3–5-year-old meadows (LB).

Manganese behaves variably. This microelement occurs in trace quantities in plant material and passes to the alimentary tract of earthworms together with the mineral fraction of the soil. On the meadows studied, the greatest increase in the content of this element in casts is observed at the youngest sites along the successional sequence (Table 5). This would suggest that the Lumbricidae occurring there take large amounts of the mineral fraction as well as organic matter.

Table 5. Concentrations of exchangeable cations (ppm) in earthworm casts and in soil

Site and source			K	$K_{casts} : K_{soil}$	Mg	$Mg_{casts} : Mg_{soil}$	Ca	$Ca_{casts} : Ca_{soil}$	Mn	$Mn_{casts} : Mn_{soil}$
LB_2	casts		304		345		3500		85	
	soil:	0–5 cm	139	2.2	225	1.5	3000	1.2	69	1.2
		5–10 cm	79	3.8	255	1.3	3200	1.1	53	1.6
LC_2	casts		494		360		4400		83	
	soil:	0–5 cm	144	3.4	120	3.0	1450	3.0	84	1.0
		5–10 cm	64	7.7	45	8.0	1250	3.5	77	1.1
P_2	casts		509		400		4800		86	
	soil:	0–5 cm	159	3.2	170	2.3	2200	2.2	80	1.1
		5–10 cm	64	7.9	110	3.6	1600	3.0	75	1.1
LB_3	casts		189		450		4300		77	
	soil:	0–5 cm	99	1.9	300	1.5	3800	1.1	67	1.1
		5–10 cm	51	3.7	350	1.3	4250	1.0	42	1.8
LC_3	casts		219		190		2300		85	
	soil:	0–5 cm	118	1.8	75	2.5	1100	2.1	77	1.1
		5–10 cm	64	3.4	40	4.7	1050	2.2	75	1.1
P_3	casts		246		175		2150		84	
	soil:	0–5 cm	114	2.2	110	1.6	1050	2.0	80	1.0
		5–10 cm	62	4.0	90	1.9	1000	2.1	72	1.1

For sites characteristics see Table 1.

3.4. THE INFLUENCE OF CHANGES IN THE SPECIES COMPOSITION, ABUNDANCE AND BIOMASS OF LUMBRICIDAE ON THE PROPERTIES OF CASTS

The chemical composition and organic matter content of casts is influenced not only by the soil in which earthworms live but above all also by they themselves – mainly through the feeding requirements typical for species, and even developmental stages, and the physiology of digestion.

Table 6. Number and biomass of species of Lumbricidae

Site	Species	Number		Biomass	
		indiv. · m^{-2}	%	g · m^{-2}	%
LB_2	*A. caliginosa*	58.3	66	15.7	44
	L. rubellus	11.1	12	8.0	23
	O. lacteum	9.7	11	4.0	11
	others	9.8	11	7.5	21
	Lumbricidae – total	88.9	100	35.2	100
LC_2	*A. caliginosa*	45.8	15	14.3	14
	L. rubellus	202.8	68	76.7	74
	O. lacteum	20.8	7	7.7	7
	others	27.8	9	4.7	5
	Lumbricidae – total	297.2	100	103.4	100
P_2	*A. caliginosa*	111.1	49	34.2	32
	L. rubellus	83.3	37	57.3	55
	O. lacteum	23.3	10	12.8	12
	others	7.8	3	0.7	1
	Lumbricidae – total	225.5	100	105.0	100
LB_3	*A. caliginosa*	195.8	85	68.4	76
	L. rubellus	20.8	9	15.7	18
	O. lacteum	5.5	2	4.3	5
	others	8.4	4	1.1	1
	Lumbricidae – total	230.5	100	89.5	100
LC_3	*A. caliginosa*	22.2	12	8.4	9
	L. rubellus	116.6	61	74.7	77
	O. lacteum	12.5	6	5.4	6
	others	40.3	21	8.0	8
	Lumbricidae – total	191.6	100	96.6	100
P_3	*A. caliginosa*	77.7	31	30.9	24
	L. rubellus	115.3	46	56.1	44
	O. lacteum	59.7	23	42.0	32
	others	0.0	0	0.0	0
	Lumbricidae – total	252.8	100	129.0	100

For sites characteristics see Table 1.

The sites on the meadows studied have 2–6 species of Lumbricidae (M a k u l e c 1997). Earlier successional stages are dominated by *Aporrectodea caliginosa* (Sav.), while advanced stages are characterized by a prevalence of *Lumbricus rubellus* Hoffm. This situation was also confirmed on the meadows studied in the period of collection of casts in September 1987 (Table 6).

On several-year-old meadows (LB), *A. caliginosa* accounts for 65–85% of the density, and 45–68% of the biomass, of the whole community of earthworms. At the same time, *L. rubellus* represents only 9–12% of the total by density and 17–22% by biomass. Older meadows (LC) have the reverse situation: with *A. caliginosa* occurring at low abundance and acounting for 12–15% of density and 8–14% of biomass, and *L. rubellus* respectively for 60–68% and 74–77%. The proportions of the two species on permanent meadows are more even, but with a prevalence of *L. rubellus* (Table 6). These sites are also abundantly inhabited by *Octolasion lacteum* (Oerley) – a species similar in its ecology to *A. caliginosa*. This species accounted for almost 24% of density and 32% of biomass in the third series of meadows and respectively for 10 and 12% in series II.

The two species differ greatly in their food requirements, places of existence, level of consumption of organic matter and rate of digestion. As a result, the casts they produce also differ, and the relative proportions resulting from their different shares in the lumbricid community will define the physico-chemical properties of the material analyzed.

4. DISCUSSION

The impact of Lumbricidae on the biotic and physico-chemical properties of the soil environment is multi-directional and relatively well-known. The material presented illustrates the role of these animals in the transformations of carbon, nitrogen, phosphorus and other micro- and macroelements important in the economy of the ecosystem.

In general, casts were always richer in carbon compounds (including the basic humus fractions) than the upper layers of the soil. This regularity has now been recorded many times in different types of natural and cultivated ecosystem. The authors give values that are similar or a little lower. G r a f f (1971) noted a 120% rise in total C in casts in relation to a meadow soil. For the soils of mountain pastures, C z e r w i ń s k i et al. (1974) gave figures for the increase at different sites of 77% and 84%. Z r a ž e v s k i j (1957) compared the total carbon contents of the casts of several species of earthworm cultured in different types of leafy litter. It emerged that the proportion of carbon in casts was dependent both on diet and the lumbricid species concerned. That said, it was the casts of *L. rubellus* that were always richer in organic matter than those of *A. caliginosa* (an increase of 44–72% as compared with 17–49%), with the same food. In the face of this, the size of differences in the content of organic matter in casts collected from the field will be determined above all by the species composition of the lumbricid community and the specific diet of the dominant species.

The most abundant species of earthworm in the soils of the studied meadows – *A. caliginosa* and *L. rubellus* – are members of different ecological groups. On the basis of analysis of the contents of guts and casts, P i e a r c e (1978) classed the former as a geophage and the latter as a detritophage. *A. caliginosa* occurs only in mineral soils, in the arable layer of the profile. Guts were found to contain small amounts of amorphous organic substances, mainly of root origin, as well as a prevailing mass of mineral constituents. *L. rubellus* is a surface species which occurs to depths of 10–20 cm and consumes slightly-decayed litter and soil detritus. The share of the mineral fraction in gut contents is not great (P i e a r c e 1978).

The highly different trophic statuses and different degrees of dominance of the two species will have an important influence on the quality of casts collected in the field. Thus the aforementioned increase in the carbon content of earthworm casts (particularly compared with the 5–10 cm soil layer) on progressively older meadows is probably linked with the increase in the poportional representation of the epigeic species *L. rubellus*. Its casts are rich in organic matter at varying stages of decomposition and colonized by a rich bacterial flora reproducing in the posterior section of the gut and shortly after excretion (P a r l e 1963, C h m i e l e w s k i and M a k u l e c 1993). The action of this may lead to the emergence of complex humus substances of the fulvic acid type (E d w a r d s and L o f t y 1977). Large amounts of these compounds are also found in macerated plant material consumed by earthworms. The steady increase in concentrations of fulvic acids – and the decrease in the C_{HA} : C_{FA} ratio – along the successional sequence of meadows, is a result of the greater proportion of the casts of this species in the material collected for analysis. Clear directional changes along the successional sequence of meadows are not only shown by total carbon and humus compounds but also by total nitrogen and some exchangeable cations, The increase in the carbon content, and the simultaneous fall in the concentration of nitrogen, result in the increase of the C : N ratio for casts as one moves along the sequence of successively older meadows. This favours the microbiological processes of the humification of organic matter, as attested to by the increase in humic and fulvic acids already discussed.

Exceptionally high concentrations are recorded in the case of exchangeable phosphorus (Table 4). In relation to the upper (0–5 cm) layer of the soil, the values in casts range from 65% to 670%, while in relation to the deeper (5–10 cm) layer there is between 240 and 1530% more of this element, and at that in a form more easily available to plants. L u n t and J a c o b s o n (1944) recorded concentrations of phosphorus in casts that were 7 times higher than in soils, while G r a f f (1971) obtained a figure of 6 and C z e r w i ń s k i et al. (1974) values of between 4 and 11 times. This phenomenon may be of exceptionally great significance, not only for plants but also for the development of the microflora – particularly in the light of the thesis on the limiting role of shortages of phosphorus in advanced stages of succession (S c h e u 1990).

Exchangeable cations show basically similar trends to the aforementioned elements (Table 5). Some of them are also removed with metanephridial fluids through the integument and do not enter casts (K a l i n o w s k a and M a k u l e c 1978). Calcium is particularly worthy of note. On many-year-old meadows, its concentration in casts was 2–3 times greater than in the upper layer of the soil. Similar results were obtained by the already cited L u n t and J a c o b s o n (1944) and by C z e r w i ń s k i et al. (1974). The increase in the concentration of calcium, and also of other cations, along the successional sequence of meadows is alo a result of the increase in the level of representation of *L. rubellus* in the lumbricid community. This species consumes substrates rich in calcium and at the same time excretes excess amounts via well-developed calciferous glands. In contrast, *A. caliginosa* has poorly-developed and inactive glands, and its diet contains only small amounts of calcium (Pïearce 1972).

Magnanese provides further confirmation of the thesis concerning the joint role of the two species in the shaping of contents of humus and exchangeable cations in the upper layer of the soil (Table 5). This microelement is associated mainly with the mineral fraction of the soil, occurring in trace amounts in organic matter. The highest concentrations were recorded in casts from the youngest meadows, on which the geophagous *A. caliginosa* is dominant. Many-year-old and permanent meadows have limited increases not exceeding 10%.

The described changes in the contents of carbon, nitrogen and cations are most visible proceeding along the successional sequence from several-year-old meadows (LB) to many-year-old meadows (LC). The further progression to permanent meadows (P) is not always accompanied by continuations of these trends – in the case of either total carbon or contents of the other elements. This situation is probably determined by the appearance of one more geophagic species – *O. lacteum* (Table 6). Together with *A. caliginosa*, the two species often account for more than 50% of the density and biomass of earthworms in the soils of permanent meadows. At the same time, these sites occupy a position intermediate between meadows with a high degree of dominance of *A. caliginosa* and those on which *L. rubellus* is more abundant.

The material presented combines with the results of an earlier work (Makulec 1997) to show the very important role played by earthworms in the renewal of the humus resources of soils and the shaping of feeding conditions for plants and microflora in the surface layers of meadow soils, In the course of a season, several to tens kg dry wt m^{-2} of humus-, nitrogen-, phosphorus- and exchangeable cation-rich casts are excreted into the surface or upper parts of the soil profile (Makulec 1997). The renewal of soil humus resources occurring with succession from cultivated to many-year-old meadows is to a great extent the result of the activities of earthworms, especially epigeic and detritivorous species.

5. CONCLUSIONS:

1. Total contents of carbon, fulvic and humic acids and humins in earthworm casts are 2–3 times greater than those in the upper layer of the soil.

2. The ratio of humic to fulvic acids in casts is lower on older meadows, while the relative proportion of fulvic acids (the youngest humus fraction) is greater.

3. The nitrogen contents of earthworm casts are twice as high as those in the upper layer of the soil, but are lower on older meadows. Values for the C : N ratios of casts are greater on older meadows.

4. The contents of main exchangeable cations in casts are 2–3 times greater than those in the surface layer of the soil.

Phosphorus undergoes a particularly high degree of concentration.

5. The regularities noted may result from changes in the proportions of two lumbricid species along the successional sequence of meadows studied. Young meadows are dominated by the geophagic *A. caliginosa*, while many-year-old and permanent meadows are dominated by the detritophagous *L. rubellus*.

6. SUMMARY

Research involved two successional sequences of meadows (series II and III) within Suwałki Landscape Park (north-eastern Poland). Each series included several-year-old meadows (LB_2 or LB_3), many-year-old meadows (LC_2 or LC_3) and permanent meadows (P_2 or P_3). Selected features of the sites are set out in Table 1.

The abundance, biomass and species composition of Lumbricidae at the sites were assessed in September 1987. Worm casts were collected at the same time, from the same places, along with soil samples from the 0–5 and 5–10 cm layers. Analysis concerned the total contents of carbon and nitrogen, the fractional composition of humus and the exchangeable elements $P\text{-}PO_4$, K, Mg, Ca and Mn) in earthworm casts and in the soil.

Compared to surface soil layers, lumbricid casts are 2–3 times richer in total carbon, fulvic and humic acids (C_{FA} and C_{HA}) and humins (Tables 2 and 3). Values of the $C_{HA} : C_{FA}$ ratio for casts were lower on older meadows, while the relative proportion of fulvic acids – the youngest humus fraction – was greater. This points to the significant role of these animals in the renewal of soil humus resources as succession proceeds on ley meadows.

The analyzed exchangeable elements also showed higher contents in casts than in the soil. Particularly significant here was phosphorus, whose share was 4–8 times greater (Table 4). Amounts of exchangeable K, Mg and Ca in casts are also higher than in soils, and are greater on older meadows (Table 5).

The regularities noted may be the result of changes in the proportions of two lumbricid species as succession proceeds from several-year-old to permanent meadows (Table 6). Earlier stages (LB_2 and LB_3) are dominated by *Aporrectodea caliginosa*, a geophagic species typical of cultivated fields, which consumes small amounts of amorphous organic matter mixed in with the mineral fraction of soils. In contrast, the species prevalent on many-year-old and permanent meadows (LC_2, LC_3 and P_2, P_3) is *Lumbricus rubellus*, an epigeic species living on somewhat-decomposed litter and soil detritus with a limited admixture from the mineral fraction. The very different trophic statuses and different degrees of dominance of these species will define the quality of casts collected in the field.

7. POLISH SUMMARY

Badania prowadzono w dwóch ciągach sukcesyjnych łąk (seria II i seria III) na terenie Suwalskiego Parku Krajobrazowego (północno-wschodnia Polska). W skład każdego szeregu wchodziła łąka kilkuletnia (LB_2 lub LB_3), łąka wieloletnia (LC_2 lub LC_3) oraz łąka trwała (P_2 lub P_3). Wybrane cechy stanowisk zawiera tab1.

We wrześniu 1987 oceniano liczebność, biomasę oraz skład gatunkowy Lumbricidae. Rownocześnie zebrano z tych samych miejsc koprolity oraz pobrano kontrolne próbki gleby z dwóch poziomów: 0–5cm i 5–10 cm. Analizowano ogólną zawartość węgla i azotu, skład frakcyjny próchnicy oraz pierwiastki wymienne ($P\text{-}PO_4$, K, Mg, Ca, Mn) w odchodach dżdżownic i w glebie.

Koprolity Lumbricidae sa 2–3 razy zasobniejsze w węgiel ogólny, kwasy fulwowe (C_{FA}) i huminowe (C_{HA}) oraz w huminy w porównaniu do wierzchnich warstw gleby (tab.2, tab.3). Stosunek $C_{HA} : C_{FA}$ w odchodach dżdżownic maleje, a względny udział kwasów fulwowych – najmłodszej frakcji humusu rośnie wraz z wiekiem łąk. Wskazuje to na znaczącą rolę tych zwierząt w odnawianiu zasobów hu-

musu glebowego w toku sukcesji łąk przemiennych.

Rownież analizowane pierwiastki wymienne wykazują wyższą zawartość w koprolitach w porównaniu do gleby. Szczególne miejsce zajmuje fosfór, którego udział wzrasta 4–8-krotnie (tab.4). Także ilość wymiennego K, Mg i Ca w odchodach jest wyższa w porównaniu do gleby i wzrasta w miarę starzenia się łąk (tab.5).

Stwierdzone prawidłowości mogą być wynikiem zmian udziałów dwóch gatunków Lumbricidae w toku sukcesji od łąk kilkuletnich do trwałych (tab.6). Na wczesnych stadiach (LB_2, LB_3) dominuje *Aporrectodea caliginosa*, gatunek geofagiczny, typowy dla pól uprawnych, konsumujący niewielkie ilości amorficznej materii organicznej wymieszanej z frakcją mineralną gleby. Na łąkach wieloletnich (LC_2, LC_3) i trwałych (P_2, P_3) przeważa *Lumbricus rubellus*, gatunek epigeiczny, odżywiający się słabo rozłożoną ściółką i detrytusem glebowym z niewielką domieszką części mineralnych. Krańcowo odmienna trofia oraz różny stopień dominacji tych gatunków będą określać jakość zbieranych w terenie koprolitów.

8. REFERENCES

1. Chmielewski K., Makulec G. 1993 – Microflora and enzymatic activity of earthworm (Lumbricidae) casts in hydrogenous soil – Z. Probl. Nauk Rol., 406: 135–138.
2. Czerwiński Z., Jakubczyk H., Nowak E. 1974: The effect of earthworms on the pasture soil – Ekol. pol. 22: 635–650.
3. Edwards C. A., Lofty J. R. 1977 – Biology of Earthworms. Chapman and Hall, London, 333 pp.
4. Graff O. 1971 – Stickstoff, Phosphor und Kalium in der Regenwurmlosung auf der Wiesenversuchsflche des Solling–projektes. (In: IV Colloquium Pedobiologiae), 503–515.
5. Jankowski W. 1997 – The plant communities of meadows and pastures of Suwałki Landscape Park (north-eastern Poland) – Ekol. pol. 45: 587–607.
6. Kajak A. 1997 – Preface, Scope of studies, experimental desing, study area – Ekol. pol. 45: 581–585.
7. Kalinowska A., Makulec G. 1978 – The effect of mineral fertilization (NPK) on nutrient metabolism in earthworms (Lumbricidae) – Pol. ecol. Stud. 4, 1:157–166.
8. Kononowa M. 1968 – Materia organiczna gleby. [Soil organic matter.] – PWRiL, Warszawa, 391pp.
9. Kusińska A., Łakomiec I. 1997 – Contents of humus fractions in the soil of age-differentiated meadows in the Suwałki Landscape Park (north-eastern Poland) – Ekol. pol. 45: 609–618.
10. Lakanen E. 1962 – On the analysis of soluble trace elements – Ann. Agric. fenn 2: 109–117.
11. Lunt H. A., Jacobson G. M. 1944 – The chemical composition of earthworm casts – Soil Sc. 58: 367–375.
12. Makulec G. 1997 – Density and biomass of earthworms (Lumbricidae) on leys and permanent meadows – Eko. pol. 45: 815–823.
13. Parle J. N. 1963b – Micro-organisms in the intestines of earthworms – J. gen. Microbiol., 31: 1–11.
14. Piearce T.G. 1972 – The calcium relations of selected Lumbricidae – J. Anim. Ecol., 41: 167–188.
15. Piearce T. G. 1978 – Gut contents of some lumbricid earthworms – Pedobiologia, 18: 156–157.
16. Raw F. 1959 – Estimating earthworm populations by using formalin – Nature (London), 184: 1661–1662.
17. Scheu S. 1990 – Changes in microbial nutrient status during secondary succession and its modification by earthworms – Oecologia 84: 351–358.
18. Stefaniak O., Ślizak W., Gorlach K. 1997 – Microflora colonizing grass litter exposed in bags on differently-aged meadows – Ecol. pol. 45: 695–708.
19. Zraževskij A. I. 1957 – Doždevye czervi kak faktor plodorodija lesnych pozv. – Izd. AN USSR, Kiev, 298pp.