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Special paper

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THE ROLE OF *LUMBRICUS RUBELLUS* HOFFM. IN DETERMINING BIOTIC AND ABIOTIC PROPERTIES OF PEAT SOILS

ABSTRACT: The field study was conducted on fifteen peat meadows located in the Biebrza river valley, north-eastern Poland, to estimate the range of changes in Lumbricidae communities with time after drainage. In a field experiment, the effects of *L. rubellus* were examined on the composition and abundance of microflora, Nematoda, Collembola, and Enchytraeidae, and on resources of exchangeable nutrients in drained peat soils.

The occurrence of 2–6 earthworm species was noted in soils of drained peats. *L. rubellus* appeared already 3–5 years after drainage and rapidly reached high densities and biomass. It showed preference for moderately or heavily moorshed soils, with high contents of total nitrogen and phosphorus, low C/N, moderate porosity, and moderate moisture. Casts of this species contained more fungi and cellulolytic microorganisms, while less bacteria and actinomycetes, as compared with their contents in the soil. Also urease activity, content of fulvic acids and concentrations of exchangeable phosphorus, magnesium, and potassium were higher in casts.

In a 4-month field experiment, different densities of *L. rubellus* were used: 2, 4, and 6 individuals in 1.5 L isolators inserted to soil. The control variant was without earthworms. It was found that high *L. rubellus* densities in peat moorsh enhanced bacteria, ammonifying microorganisms, microorganisms utilising mineral nitrogen, and seasonally also actinomycetes and cellulolytic microbes. Also total microbial biomass, dehydrogenase activity, and the rate of cellulose decomposition were higher. The abundance of soil fungi noticeably decreased.

Moreover, *L. rubellus* significantly influenced nematode composition and abundance. Within a short time, their total numbers declined, especially numbers of bacterial-feeding nematodes. Also numbers and proportions of fungivorous nematodes slightly declined. Plant-feeding nematodes were least affected by this species, and in some periods their numbers were higher in the presence of earthworms than in the control. In the field experiment, no noticeable effect of earthworms was found on total enchytraeid numbers. In the period of autumn peak of Collembola, high numbers of *L. rubellus* reduced their densities.

By modifying the composition and abundance of microflora, nematodes and mesofauna, high *L. rubellus* densities (above 200 individuals m^{-2}) can increase the rate of organic matter mineralization, intensify competition for nutrients, and indirectly they contribute to the biological decomposition of moorsh in soils of drained peat meadows.

KEY WORDS: *L. rubellus*, earthworms, peat meadow, casts, microflora, nematodes, springtails, enchytraeids, drainage

1. INTRODUCTION

Because of their profound effects on biotic and abiotic soil properties, earthworms have been in focus of soil ecology for a long time. Recently, some 150–200 papers a year have been published on various aspects of their biology and ecology. There are also monographs of this group, or separate chapters in textbooks (Satchell 1967, Lee 1985, Edwards and Bohlen 1996, Edwards 1998). In discussions concerning biological diversity they are regarded as engineering species, thus, imposing an unusually high impact on the environment (Jones *et al.* 1994, Lawton 1994, Lavelle 1997).

Despite this extensive knowledge, new questions continue to arise. In this seemingly uniform group, the role and importance of individual species in the ecosystem, their dependence on soil type, plant community, management practices, other components of edaphon, and on many other factors, have appeared to show large differences.

Among 35 earthworm species recorded from Poland (Plisko 1973, Kasprzak 1986) only 3–5 are sufficiently abundant and influential to be considered engineering species. One of them is *Lumbricus rubellus* Hoffm. occurring in top soil layers of most ecosystems sufficiently rich and moist. Nearly all the studies of this species, both field and laboratory, were conducted in mineral soils (Shipitalo *et al.* 1988, Haimi and Huhta 1990, Daniel and Anderson 1992, Krištůfek *et al.* 1992, Zhang and Hendrix 1995, Brown *et al.* 1998). Few studies of this species were conducted in drained peatlands (Kozlovskaja 1976, Makulec 1991, Chmielewski and Makulec 1993, Makulec and Chmielewski 1994). In Poland, peat soils cover an area of about 1.2 million hectares under agricultural use since a long time, mainly as hay meadows (Okruszko 1990, 1993). They typically provide suitable conditions for earthworms (Makulec 1991).

The purpose of this paper is to answer several crucial questions. The basic problem is the recognition of changes in Lumbricidae communities with time after drainage, especially in *L. rubellus* populations. The next issue is the effect of this species on the abundance of microflora and on enzymatic activity of the soils of drained peatlands, and most of all, an answer to the question whether or not the increase in microflora noted many times in guts and casts of earthworms is transferred to the soil where they occur? If so, do these changes have an indirect effect on the abundance of soil fauna typically closely associated with microorganisms, such as Nematoda, Collembola, and Enchytraeidae? Can it, thus, be expected that as a consequence of these multi-sided *L. rubellus* effects in peat soil, also processes of organic matter decomposition will be intensified and the pool of nutrients readily available to plants will increase?

Answers to these questions will allow us a deeper understanding of interactions among earthworms, microbes, microfauna and mesofauna, as well as of their role in soil processes, mainly with regard to the unfavourable process of peat loss after drainage (Roguski and Bieńkiewicz 1967, Okruszko and Kozakiewicz 1973).

For this purpose, comprehensive field observations and experiments were conducted. The field observations concerned successional changes in Lumbricidae community in a series of fifteen sites that differed in the time from drainage. A mesocosm experiment was designed to examine changes in the abundance of microflora and selected groups of soil fauna, caused by differential *L. rubellus* densities.

2. STUDY OBJECT

Lumbricus rubellus Hoffm. (Lumbricidae) is common throughout Poland (Plisko 1973, Kasprzak 1986). It shows preference for soils rich in organic matter, with C/N ranging from 8.5 to 21.2 (Bouche 1972), and pH of 3.7–7.0 (Satchell 1955). This is an epigeic species living on litter and penetrating the top soil layer. It consumes up to 52 mg g^{-1} day^{-1} of plant residues at various stages of decomposition and amorphic detritus (Pierace 1978, Shipitalo *et al.* 1988). According to Flegel *et al.* (1998), consumption of leaf litter by this species can reach even 225–473 mg g^{-1} day^{-1}, excluding the mineral fraction of soil. It has well developed calciferous glands that neutralize acid components of the diet (Piearce 1972). The time of food passage through the gut is long and it varies from 6 to 8 hours (Daniel and Anderson 1992). This species is characterized by a relatively high deposition of casts. Under laboratory conditions it deposits 80–460 mg dry mass of casts per 1 g of biomass per day (Shipitalo *et al.* 1988), and according to Martin (1982) even 1.6–3.6 g g^{-1} day^{-1}. It is relatively large – sexually mature individuals are up to 100 mm long and their weight exceeds 1 g. Among earthworms, this is the most fecund species. One individual can lay from 80 to 106 cocoons a year (Satchell 1967). Thus, the life strategy of this species is between r and K strategists among earthworms (Satchell 1980).

These traits of *L. rubellus* suggest that it can largely modify biotic and abiotic soil conditions when occurring in large numbers.

3. STUDY AREA AND METHODS

All field and experimental works were conducted in natural and drained peatlands of the middle and lower Biebrza river catchment basin and in the Narew river valley (Fig. 1). Peats of this region are of different thickness and origin and, consequently, they also differ in physico-chemical properties. Sedge-moss-peats are relatively compact, with few macropores, and they are permanently moist because of the capillary ascension of ground waters. Moorsh-forming process is relatively slow. In the text and in tables, they are de-

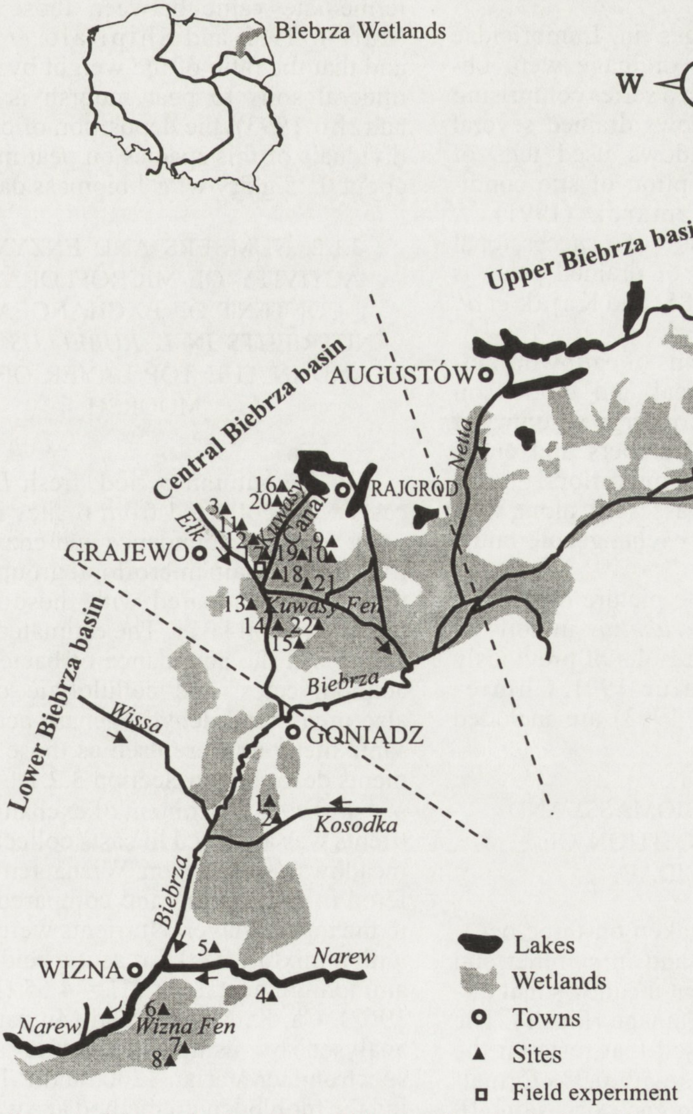


Fig. 1. Localisation of the study sites in the Biebrza valley. 1 – Dobarz (A), 2 – Dobarz (B), 3 – Toczyłowo (A), 4 – Lipniki (B), 5 – Kiślaki (C), 6 – Wizna (A), 7 – Wizna (B), 8 – Wizna (C), 9 – Kuwasy (B), 10 – Kuwasy (C), 11 –Toczyłowo (B), 12 – Toczyłowo (C), 13 – Sojczyn (A), 14 – Modzelówka (B), 15 – Modzelówka (C), 16 – Kosiły (A), 17 – Biebrza I (A), 18 – Biebrza II (A), 19 – Biebrza III (C), 20 – Kosiły (C), 21 – Łamane Grądy (C), 22 – Wykowo (C).
(A) – sedge-moss peat, (B) – tall-sedge peat, (C) – alder peat

noted by letter A. In contrast, alder-peats, denoted by letter C, are more fertile, peat decomposition and the related nutrient release is faster, porosity is higher, and moisture considerably lower. Tall-sedge peats, denoted by B, occupy an intermediate position in this sequence (Okruszko 1990, 1993).

The meadows established on drained peatlands were most often used as hay meadows, typically harvested three times a season, and only occasionally used as cattle pastures, mainly in autumn.

3.1. FIELD STUDY

Successional changes in Lumbricidae communities after peat drainage were observed during 1982–83 in a series comprising natural meadows, meadows drained several years before, and meadows used tens of years. A detailed description of site conditions is given by Kaczmarek (1991). A comprehensive analysis of successional changes in biocoenoses of drained peats is presented by Kajak (1985) and Kajak *et al.* (1985).

One of the basic forms of earthworm effects on physico-chemical and biotic soil properties is deposition of large amounts of casts. For this reason, numbers and enzymatic activity of the major microfloral groups of *L. rubellus* casts were assessed, along with the content of the main exchangeable nutrients.

For a more complete picture of the importance and role of *L. rubellus* in soils of peat meadows, also the results of previously published papers (Makulec 1991, Chmielewski and Makulec 1993) are included here.

3.1.1. NUMBERS, BIOMASS, AND SPECIES COMPOSITION OF LUMBRICIDAE

The samples were taken on three occasions: in autumn 1982, and in summer and autumn 1983 from 15 peat meadows that differed in the time after drainage (Fig. 1). The formalin method was used that rests on the extraction of earthworms with 0.3% formaldehyde (Raw 1959). On each occasion, 10 samples with a surface area of 0.09 m^2 each were taken. The abundance, biomass, and species composition of the Lumbricidae community were estimated.

A more intensive study, focused mainly on the seasonal dynamics of numbers and biomass of the dominant species, *L. rubellus*, was conducted on eight meadows established about 40 years earlier on sedge-moss and alder-peats in the Kuwasy fen (Fig. 1). Samples were taken four times a season using the method as above.

Based on the known *L. rubellus* biomass and on the literature estimates of the casts deposited by this species (Martin 1982, Shipitalo *et al.* 1988), seasonal deposition of casts was calculated. Assuming that in mineral soils *L. rubellus* deposits only 1 g dry wt. of casts per gram of biomass per day (intermediate value between those found by Martin 1982 and Shipitalo *et al.* 1988), and that the ratio of the weight by volume of mineral soils to peat moorsh is 4:1 (Okruszko 1993), the deposition of casts by individuals of this species on peat meadows is about 0.25 g dry wt g^{-1} biomass day^{-1}.

3.1.2. NUMBERS AND ENZYMATIC ACTIVITY OF MICROFLORA, AND CONTENT OF EXCHANGEABLE NUTRIENTS IN *L. RUBELLUS* CASTS AND IN THE TOP LAYER OF PEAT MOORSH

In the autumn period, fresh *L. rubellus* casts were collected from 6 sites in the Kuwasy fen. The abundance and enzymatic activity of the main microfloral groups living in them were compared with those in the top (0–10 cm) soil layer. The estimated variables comprised the abundance of bacteria, fungi, actinomycetes, and cellulolytic organisms, also urease and dehydrogenase activity. The same methods were used as those in experiments described in Section 3.2.1.

In 1995, the content of exchangeable nutrients was analysed in casts collected from 3 meadows (situated on Wizna fen) that differed in peat origin, and compared with that in the top soil layer. Nutrients were extracted with a mixture of 0.5 n acetic acid and 0.5 n ammonium acetate at pH = 4.65 (Lakanen 1962). Ca, K, Mg, Fe, and Mn cations were analysed by using the atomic absorption spectrometer Varian 1200, and P-PO_4 by using the molybdenum method at a wave length of 690 nm.

In 1997, the composition of soil humus fractions in *L. rubellus* casts and in the upper moorsh layers was analysed on meadows with alder and tall-sedge peats, using the Kononowa and Bielczikowa method (Kononowa 1968). Humic substances were extracted from mixed cast samples and from the soil by using a mixture of sodium pyrophosphate and sodium base at pH 13. Total nitrogen was determined by the Kjeldahl method.

3.2. EXPERIMENTAL STUDY

A field experiment was designed to assess the effect of *L. rubellus* on soil microflora and fauna and on the content of exchangeable nutrients across the area of its occurrence in the soil profile.

The experiment was conducted in the season of 1997 on the alder meadow located in the former Kuwasy fen drained 50 years earlier. This site was covered with short-grass meadows typical of fresh soils, with *Poa pratense* and *Festuca rubra* of the class Molinio-Arrhenatheretea. The mean moorsh moisture in the experimental period was 70%, pH 5.5, and C/N ratio 10.9.

Soil cores 100 cm^2 in surface area and 15 cm deep were taken from areas covered with relatively uniform meadow vegetation. They were put into bags-isolators and returned to the place from which they were taken. In total 160 isolators were prepared. The isolators were made of steelon mesh screen with a mesh size of 0.3 × 1.0 mm totally precluding movements of most groups of soil fauna, except for Protozoa, Nematoda, and small species of Enchytraeidae and Acarina. This kind of experimental procedure minimally disturbs natural conditions, and the possible distortions equally affect all the variants of the experiment.

To these isolators, earthworms were introduced in different numbers: 2, 4, and 6, corresponding to the following densities observed in the field: 200 ind. m^{-2}, this being a mean density in the season, 400 ind. m^{-2}, which is a spring or autumn maximum, and 600 ind. m^{-2}, which is a very rare density in peat meadows (Makulec 1991, 1993). The control isolators, variant 0, did not contain earthworms.

The experiment was started at the end of May. The isolators were distributed over an area of several ten square metres at distances of 20 × 20 cm. Basic microbiological and zooecological samples were taken four times a season at monthly intervals: the end of June, July, August and September. Only the isolators in which the number of *L. rubellus* found was the same as the number introduced were selected for analysis. According to Hartenstein (1984), among 9 earthworm species under study, *L. rubellus* has the lowest survival under experimental conditions. The paper presents the results of analyses after 30, 60, and 120 days of the experiment. In the third month of the experiment, high temperatures and very low soil moisture (sum of precipitation in August was 10.4 mm, soil moisture 52%) (Fig. 2) totally inhibited the activity of earthworms and other faunal groups so that no differences existed among variants of the experiment.

3.2.1. NUMBERS, BIOMASS, AND ENZYMATIC ACTIVITY OF MICROFLORA IN ISOLATORS

Samples 100 cm^3 in volume (10 cm^2 surface area and 10 cm deep) were taken directly

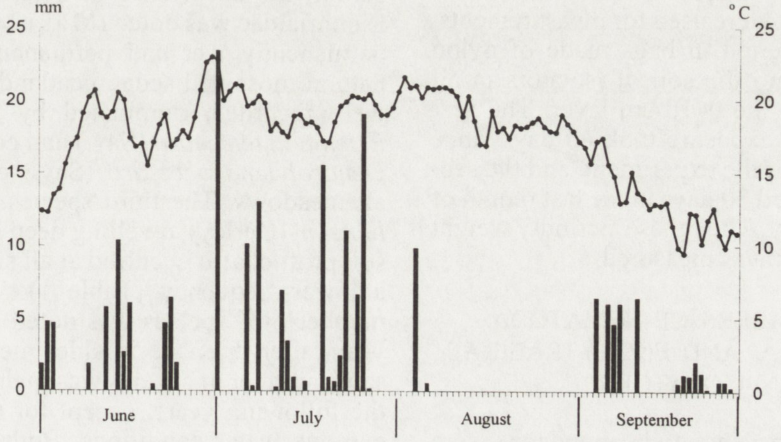


Fig. 2. Precipitation and mean daily soil temperature at 5 cm depth during the field experiment

from isolators. On each sampling date, 10 samples were taken from each variant. The plate method was used to estimate total numbers of bacteria, actinomycetes, fungi, ammonifying organisms, and cellulolytic microflora. Bacteria were cultured on agar with soil extract, actinomycetes on the substrate after Kuster and Wiliams (1964), and fungi on the Martin's (1950) synthetic medium substrate. Cellulolytic microflora was isolated on Omelianski's (Rodina 1968) substrate with cellulose discs, ammonifying organisms on nutrient agar with meat broth, and microorganisms using mineral nitrogen on nitrate-starch substrate.

The plate method produces some error because in addition to active forms, it also assesses spores of microorganisms. Because of that, the activity of two soil enzymes, dehydrogenase and urease, was measured in parallel, and at the end of the experiment also microfloral biomass C was evaluated. Dehydrogenase activity was measured by the method of TTC reduction according to Casida *et al.* (1964), urease activity by the Hoffman and Teicher (1961) method.

The biomass of active microorganisms was estimated with the substrate induced method (SIR) by the addition of a readily decomposing substrate such as glucose (Anderson and Domsch 1978, Sparling 1995). The soil from isolators was analysed at the end of the experiment, on the final sampling date.

3.2.2. CELLULOSE DECOMPOSITION RATE

The rate of cellulose disappearance is a good index of the total biological activity of the soil (Golley 1960). Filters made of ashless filter paper were used for measurements. They were inserted in bags made of nylon mesh screen into the soil of isolators in all variants within the 0–10-cm layer. The first period of their exposure took 45 days since the beginning of the experiment, and the second period lasted 30 days in the last month of the experiment. After these periods, weight loss of the bags was measured.

3.2.3. NUMBERS OF NEMATODA, COLLEMBOLA, AND ENCHYTRAEIDAE IN ISOLATORS

Samples for Nematoda abundance were taken with a soil corer 2.5 cm^2 in surface area and 15 cm deep. Ten such samples were taken, and nematodes were extracted from them by using a modified Baermann funnel method. To estimate numbers of collembolans and enchytraeids, 10–15 soil cores 100 cm^3 in volume were taken directly from the isolators and divided in the field into two layers: 0–5 cm and 5–10 cm. Collembolans were extracted with a modified Tullgren apparatus (Kempson *et al.* 1963), and enchytraeids by using the wet funnel method after O'Connor (1962).

The following tests were used for statistical analyses: t-Student, Mann-Whitney, Wilcoxon, and two-way analysis of variance (Statgraphics SG Plus). To estimate environmental determinants of Lumbricidae, canonical analysis – RDA (Redundancy Analysis) was used in the programmes CANOCO 3.1 and CanoDraw 3.0 (ter Braak 1996).

A statistical significance at the level of $P<0.05$ was used. The names of the tests used are given in tables and figures. Because of a large variation in the results of field experiments, also significance levels of $0.05<P \leq 0.1$ are given to indicate tendencies or trends.

4. RESULTS

4.1. COMMUNITIES OF LUMBRICIDAE IN NATURAL AND DRAINED PEAT MEADOWS

In a series of 15 sites ranging from natural peatland, through newly-drained meadows, to meadows drained nearly 100 years earlier, the occurrence of 2 to 6 species of Lumbricidae was noted (Makulec 1991). In permanently wet and permanently flooded natural moss and sedge peatlands, 3 species were recorded, dominated by amphibiotic *Eiseniella tetraedra* (Sav.) and cosmopolitan *Dendrobaena octaedra* (Sav.) occurring in all meadows. The third species, *Octolasion lacteum* (Oerley), dwelling deep layers of the soil profile, also occurred at all sites but with a lower frequency (Table 1). The highest number of 6 species was noted already 3–5 years after drainage in alder meadows. The same number of species was maintained over the following years, except for the years of extreme water conditions. Both desiccation (site 8) and prolonged immersion leading to

Table 1. Constancy of the occurrence (%) of Lumbricidae species in natural and drained peat meadows (after Makulec 1991)

Species	Sites (peat origin)														
	1(A)	2(B)	3(A)	4(B)	5(C)	6(A)	7(B)	8(C)	9(B)	10(C)	11(B)	12(C)	13(A)	14(B)	15(C)
	Years since drainage														
	0	0	1–3	1–5	1–5	15–20	15–20	15–20	25	25	50	50	100	100	100
Lumbricus rubellus Hoffm.	–	–	3.4	70.0	100	100	–	–	100	46.6	100	96.6	–	100	96.6
Dendrobaena octaedra (Sav.)	31.6	35.0	89.6	100	93.7	46.6	82.1	60.0	73.3	33.3	80.0	46.6	36.6	10.0	50.0
Dendrodrilus rubidus (Sav.)	–	–	41.4	70.0	25.0	80.0	46.4	–	60.0	3.3	6.6	3.3	–	–	–
Octolasion lacteum (Oerley)	5.2	15.0	17.2	15.0	50.0	40.0	39.3	3.3	10.0	3.3	23.3	16.6	60.0	56.6	66.6
Eiseniella tetraedra (Sav.)	68.4	15.0	–	–	25.0	3.3	–	–	–	–	3.3	–	16.6	3.3	–
Aporrectodea caliginosa (Sav.)	–	–	–	–	6.2	–	–	–	–	–	3.3	–	–	16.6	23.3

A – sedge-moss peat, B – tall-sedge peat, C – alder peat. For explanations of sites symbols see Fig. 1

secondary paludification (site 13) reduced the number of species to 2–3.

L. rubellus appeared already in the first 3–5 years after drainage, in largest numbers in alder-moorsh soils, and then occurring with a high frequency in all samples taken from the majority of sites (Table 1). At the beginning, it accounted for only 1–27% of the total number of earthworms but for as much as 8–70% of the biomass (Figs 3 and 4). In successive years, it became the dominant species accounting for 60–80% of the density and 80–94% of the biomass of the total earthworm community.

The results of the canonical analysis show that 27% of the variation in the abundance of species and 97% of the variation species-habitat relations can be explained by the first two axes (Fig. 5). The first one is positively correlated with the time after drainage, pH, and mucking degree, whereas negatively correlated with moorsh moisture.

Amphibiotic *E. tetraedra* was closely associated with natural meadows or with newly drained meadows characterised by high wetness, relatively low pH, and low degree of mucking. *D. octaedra* and *D. rubidus* were most abundant in meadows several to more than 10 years after drainage, with low pH, low degree of mucking, and with a low content of minerals. *O. lacteum* occurred at sites with high pH, many years after drainage, and moderately moorshed. *L. rubellus* and *A. caliginosa* showed preference for meadows with relatively low moisture, 20–25 years after drainage.

4.2. NUMBER AND BIOMASS DYNAMICS AND ESTIMATED CAST DEPOSITION IN *L. RUBELLUS*

Meadows of the Kuwasy peatland are characterized by suitable water regime due to the Kuwasy Canal, enhancing abundant occurrence of earthworms. *L. rubellus* contributed to 80–90% of the density and almost in all cases to over 90% of the biomass of earthworms in that area. In general, this species was most abundant in June, and occasionally peak numbers were shifted to summer months (Fig. 6). In these periods, the upper layer of peat moorsh was inhabited by 50 to almost 300 individuals m^{-2}.

Changes in biomass showed a more regular pattern. Typically, it steadily increased already from May through August–September. A comparison of *L. ru-*

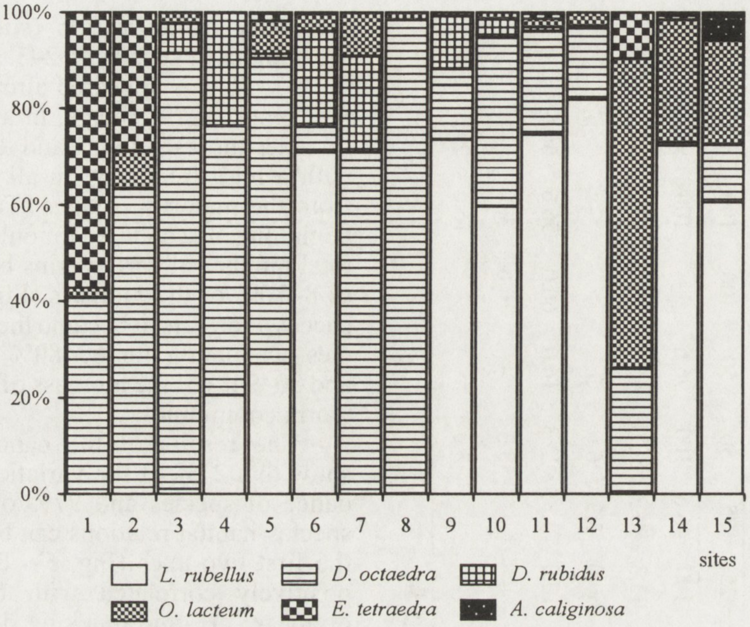


Fig. 3. Contribution of particular species to total Lumbricidae density (after Makulec 1991) (For explanations of sites symbols see Fig. 1)

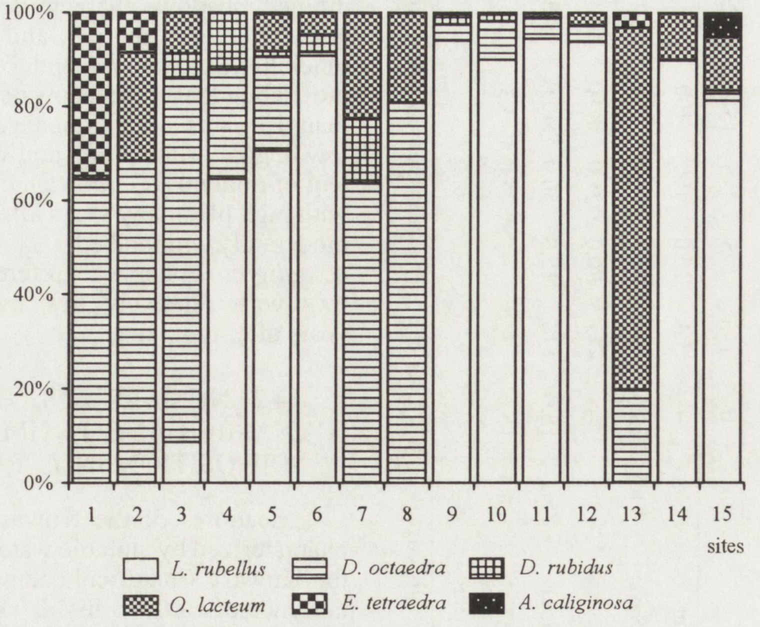


Fig. 4. Contribution of particular species to total biomass of Lumbricidae community (after Makulec 1991) (For explanations of sites symbols see Fig. 1)

bellus biomass on the first and last sampling dates showed that from a few to 138 g m^{-2} of dead tissues of this species were transferred to other trophic levels as a result of elimination.

The mean body weight of individual earthworms steadily increased, reaching a maximum in early autumn (Fig. 6). As densities were low at that time, the high total biomass of earthworms was mainly an effect of individual growth, rather than of emergence of young individuals from cocoons.

The selected study sites were characterized by a relatively narrow range of variation in habitat factors (Churski, unpublished, Pętal and Churski 1991, Konecka-Betley

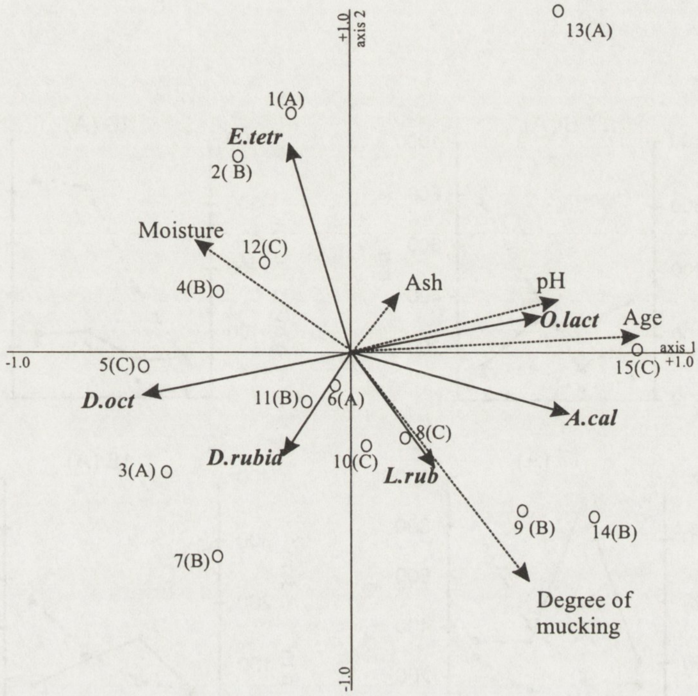


Fig. 5. Ordination diagram of six earthworm species and soil physico-chemical data from peat soils. Earthworm species are indicated by solid arrows, environmental variables by dashed arrows and sites by circles. Eigenvalues of first and second axes are 0.208 and 0.065, respectively. The first axis correlates with the time after drainage (r = 0.52), pH (r = 0.38), mucking degree (r = 0.32), and moisture (r = –0.28).
Abbreviations: *L.rub – Lumbricus rubellus*, *D.rubid – Dendrodrilus rubidus*, *D.oct – Dendrobaena octaedra*, *A.cal – Aporrectodea caliginosa*, *E.tetr – Eiseniella tetraedra*, *O.lact – Octolasion lacteum*
For explanations of sites symbols see Fig. 1.

and Czępińska-Kamińska 1993). The results of canonical analysis show that 87% of the variation in the mean abundance and biomass of *L. rubellus* can be explained by the first two axes (Fig. 7). The first one is positively correlated with the content of total nitrogen and phosphorus and with peat density by volume. Mineral components of moorsh, pH, total carbon, calcium and silica are correlated with the second axis. *L. rubellus* shows preference for moorsh with low C/N, low porosity, but rich in nitrogen and total phosphorus, and with a high density by volume.

In terms of mean numbers and biomass (Table 2), drained peat meadows are among the sites abundantly inhabited by earthworms, such as fertile oak-hornbeam forests, pastures, and gardens (Lee 1985). Clearly, their activity should substantially influence the functioning of the whole soil subsystem. One of the forms of this influence is deposition of large masses of casts. Using the procedure described above, it has been calculated that the dominant species in peat soils, *L. rubellus,* deposits about 12–35 t ha^{-1} of casts in the period from May through October. If the mean weight by volume of peat moorsh at the study sites was, on average, 0.26 g cm^{-3} (Churski, unpublished), then a food mass equivalent to 0.5–1.3-cm moorsh layer passed through the gut of this species over the season.

4.3. MICROFLORA AND ENZYMATIC ACTIVITY OF *L. RUBELLUS* CASTS AND PEAT SOILS

Large differences were found in numbers of the main groups of microorganisms between *L. rubellus* casts and the top soil layer of peat meadows (Fig. 8). On most sites, especially with high numbers of bacteria in the soil, bacterial densities in casts of this species were 2–4 times reduced as compared with those in the soil. In soils with low densities of bacteria, their densities in casts tended to increase.

Numbers of fungi in casts were 2–6 times higher than in the soil inhabited by earthworms. The relative increase was higher at sites poor in fungi.

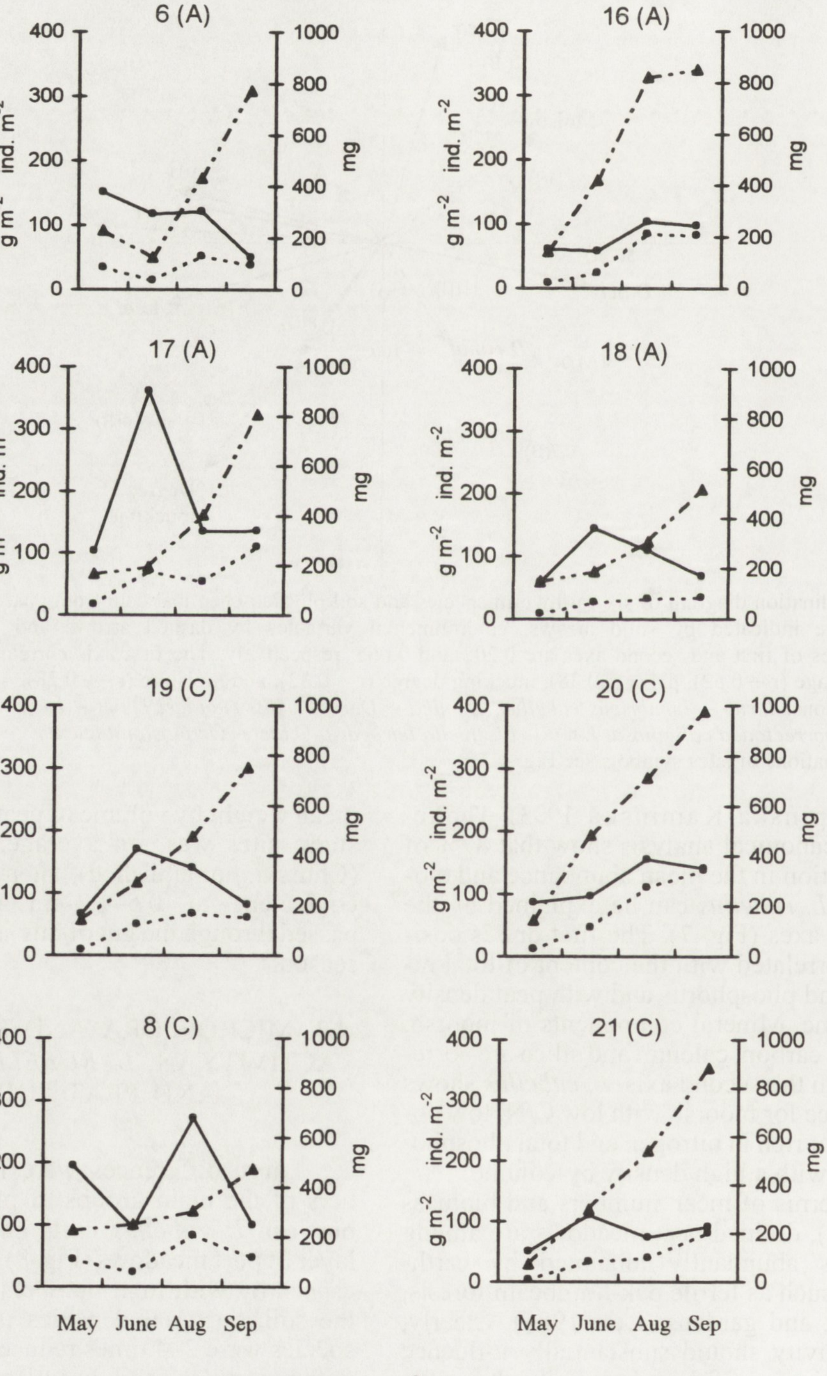


Fig. 6. The abundance, total biomass and mean weight of *L. rubellus*. (For explanations of sites symbols see Fig. 1)

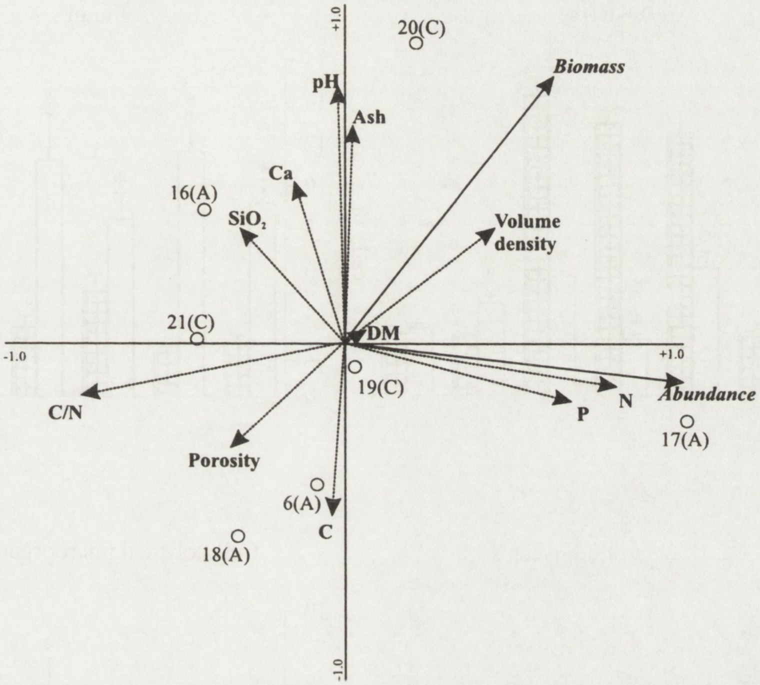


Fig. 7. Ordination diagram of *L. rubellus* abundance and biomass and soil physico-chemical data from peat soils. The abundance and biomass are indicated by solid arrows, environmental variables by dashed arrows and sites by circles. Eigenvalues of first and second axes are 0.869 and 0.131, respectively. The first axis correlates with the total content of N (r = 0.80), P (r = 0.67), C/N (r = –0.78), volume density of peat (r = 0.44) and porosity (r = –0.34). The second axis correlates with the pH (r = 0.77), ash content (r = 0.65) and total content of C (r = –0.52), Ca (r = 0.49) and SiO_2 (r = 0.34). Abbreviations: DM – degree of mucking
(For explanations of sites symbols see Fig. 1)

Table 2. Mean abundance, biomass and estimated cast deposition of *L. rubellus*

	Sites							
	6(A)	16(A)	17(A)	18(A)	19(C)	20(C)	8(C)	21(C)
abundance (indiv. m^{-2} $season^{-1}$)	110.4	80.3	184.0	94.9	114.9	119.8	165.3	81.8
biomass (g m^{-2} $season^{-1}$)	35.3	50.4	63.2	26.2	47.1	77.0	49.7	39.5
casts (t d.w.ha^{-1} $season^{-1}$)	15.9	22.7	28.4	11.8	21.2	34.6	22.4	17.8

Also proportions of the two groups of microorganisms in earthworm casts differed from those in the soil. An increase in numbers of fungi combined with a decrease or with only a small increase in the number of bacteria in casts lowered the ratio of bacteria to fungi in casts relative to that in the soil. This means that the contribution of bacteria to transformation of soil organic matter was reduced in favour of fungi, this enhancing the accumulation of carbon and organic nitrogen in casts.

Actinomycetes were considerably less abundant in casts than in the soil inhabited by *L. rubellus*. In contrast, the abundance of cellulolytic microflora was higher in casts compared with the top layer of the moorsh peat. This was likely to be an effect of a higher proportion of easily decomposable plant residues in the food of earthworms and in their casts, as compared with their content in the soil (Piearce 1978), which is a substrate promoting the development of this physiological group of microorganisms. Actinomycetes participate mainly in decomposition of more complex organic substances such as lignins, bitumins, hemicelluloses, chitin, or humic acids that are more abundant in peat

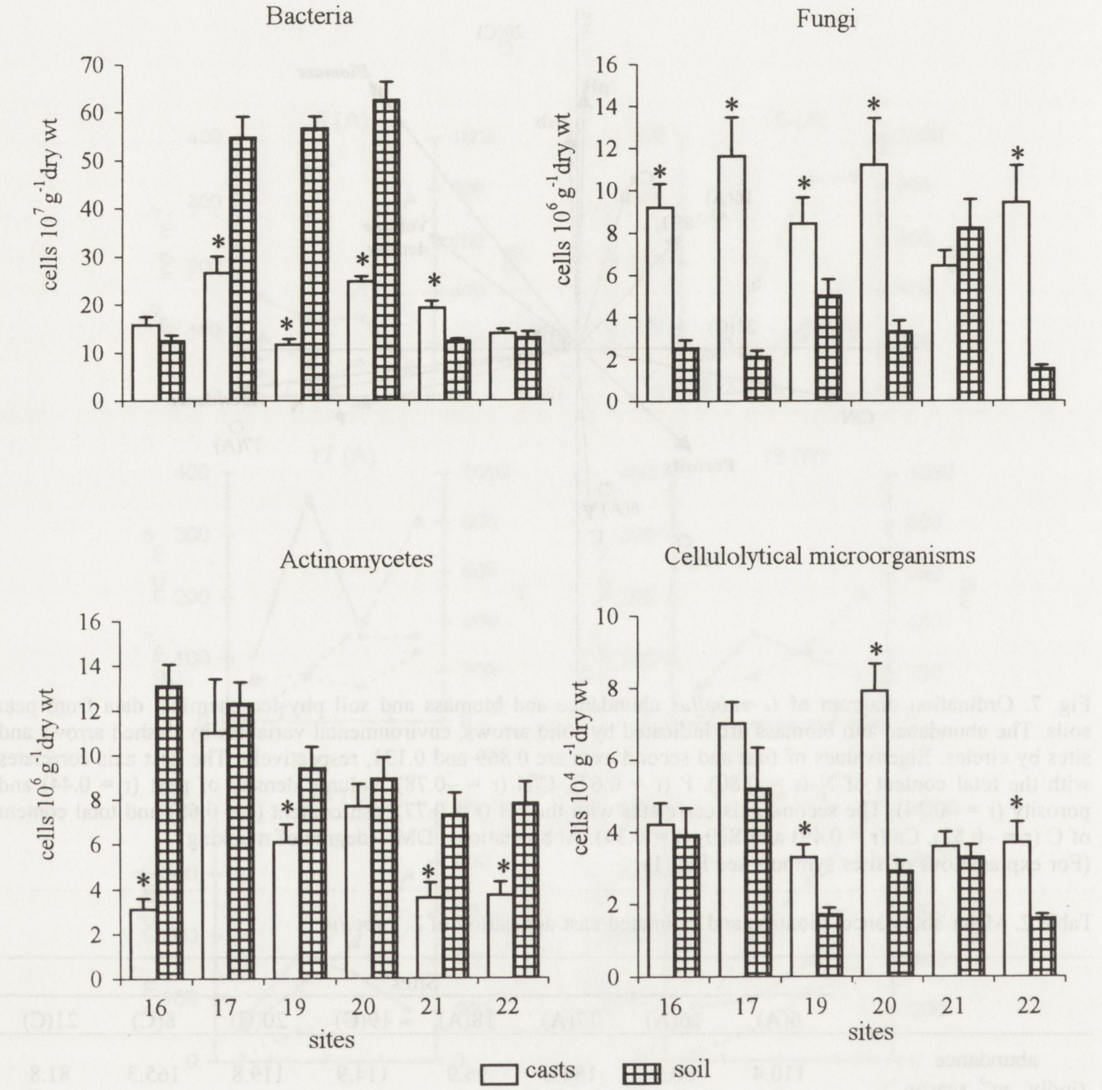


Fig. 8. The abundance of microorganisms (mean + SE) in *L. rubellus* casts and in soil (0–10cm) (after Chmielewski and Makulec 1993, modified).
* – $P < 0.05$, t-test; n = 10. For explanations of sites symbols see Fig. 1.

moorsh accounting for only small part of the food mass (Paul and Clark 1996).

The activity of selected soil enzymes is a better method than the plate method for estimating the effects of microorganisms on soil processes. However, it also has some drawbacks. Most enzymes are of microbiological origin but a part of them, which is difficult to assess, consists of endoenzymes of live and dead animals, roots, and plant residues (Skujins 1967).

Urease activity in *L. rubellus* casts showed more uniform tendencies than microflora, and it was almost always higher than in the top soil layer (Fig. 9). This was not the case of dehydrogenase, and differences between casts and peat moorsh were not significant.

4.4. EXCHANGEABLE CATIONS AND HUMUS CONTENT IN *L. RUBELLUS* CASTS AND PEAT SOIL

Digestive processes in earthworm gut and intense development of microflora in casts accounted for an increase in the concentration of nutrients in the forms readily available for plants (Fig. 10). The concentration of calcium in *L. rubellus* casts on the tall-sedge and sedge-moss meadows was lower by 10–50%, especially when compared with a deeper soil layer. No clear differences were

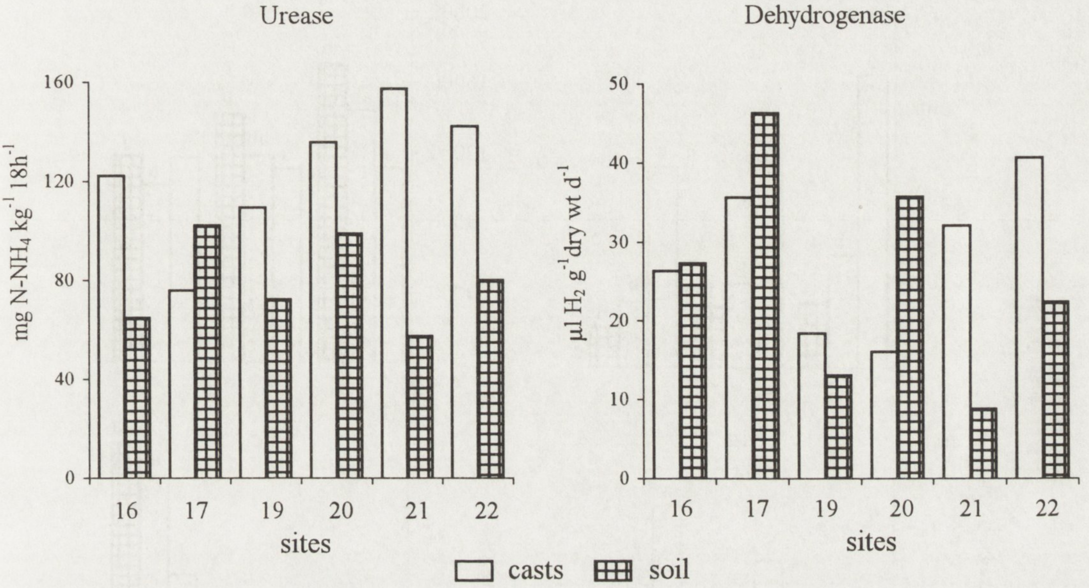


Fig. 9. Enzymatic activity in earthworm casts and in peat soil
(Urease – $P < 0.03$, dehydrogenase – not significant: Wilcoxon test. For explanations of sites symbols see Fig. 1.)

noted only in alder peats. A similar situation was found for exchangeable iron. The concentration of Fe in casts was lower than in the top layer of peat soil by about 50% (Fig. 10).

Concentrations of the readily available forms of all the other nutrients analysed in casts markedly increased – by factors of 2–4 for magnesium, 2–3 for potassium, and 2, on the average, for manganese. It is worth noting a very high increase in the concentration of phosphate anion by a factor of 8 in the alder meadow. The analysis of variance revealed statistically significant differences in concentrations of all the exchangeable nutrients between casts and peat moorsh (Table 3). In the case of manganese and phosphorus, also peat type was important.

Peat moorshes are characterized by very high contents of total carbon, including carbon in soil humus (Konecka-Betley and Czępińska-Kamińska 1993, Okruszko 1993). For this reason it is difficult to discern changes in humus composition caused by microorganisms and soil animals. *L. rubellus* casts contained a little less carbon and total nitrogen compared with the soil but this did not change the C/N ratio (Table 4). Earthworm casts at both sites contained a little more fulvic acids, that is, precursors of stable forms of the soil humus. Concurrently, the proportion of humic acids characteristic of peat moorsh declined. As a result, both the ratio of the two humus acids and the degree of cast humification were lower compared with those in the two layers of the peat soil.

4.5. THE EFFECT OF DIFFERENTIAL *L. RUBELLUS* DENSITIES ON MICROFLORA AND ENZYMATIC ACTIVITY OF PEAT SOIL IN A FIELD EXPERIMENT

After 30 days of the experiment, at a relatively low abundance of bacteria in the control variant, their total numbers almost doubled in the variants with moderate and highest earthworm densities (Fig. 11). After 60 days of the experiment, the total density of bacteria increased in all the variants, and in the variant without earthworms more than 5 times, but differences among variants were not as clear as in the preceding period. Only in the variant with the lowest number of *L. rubellus* the increase in numbers of bacteria approached significance, which may be a delayed effect observed in preceding month in the variant with high earthworm numbers. At the end of the experiment, significantly more bacteria occurred in the variant with 4 earthworms, and in the variant with the highest number of earthworms, the number of bacteria tended to decline. The analysis of variance showed a significant effect of earthworms on the total density of bacteria in the experiment (Table 5).

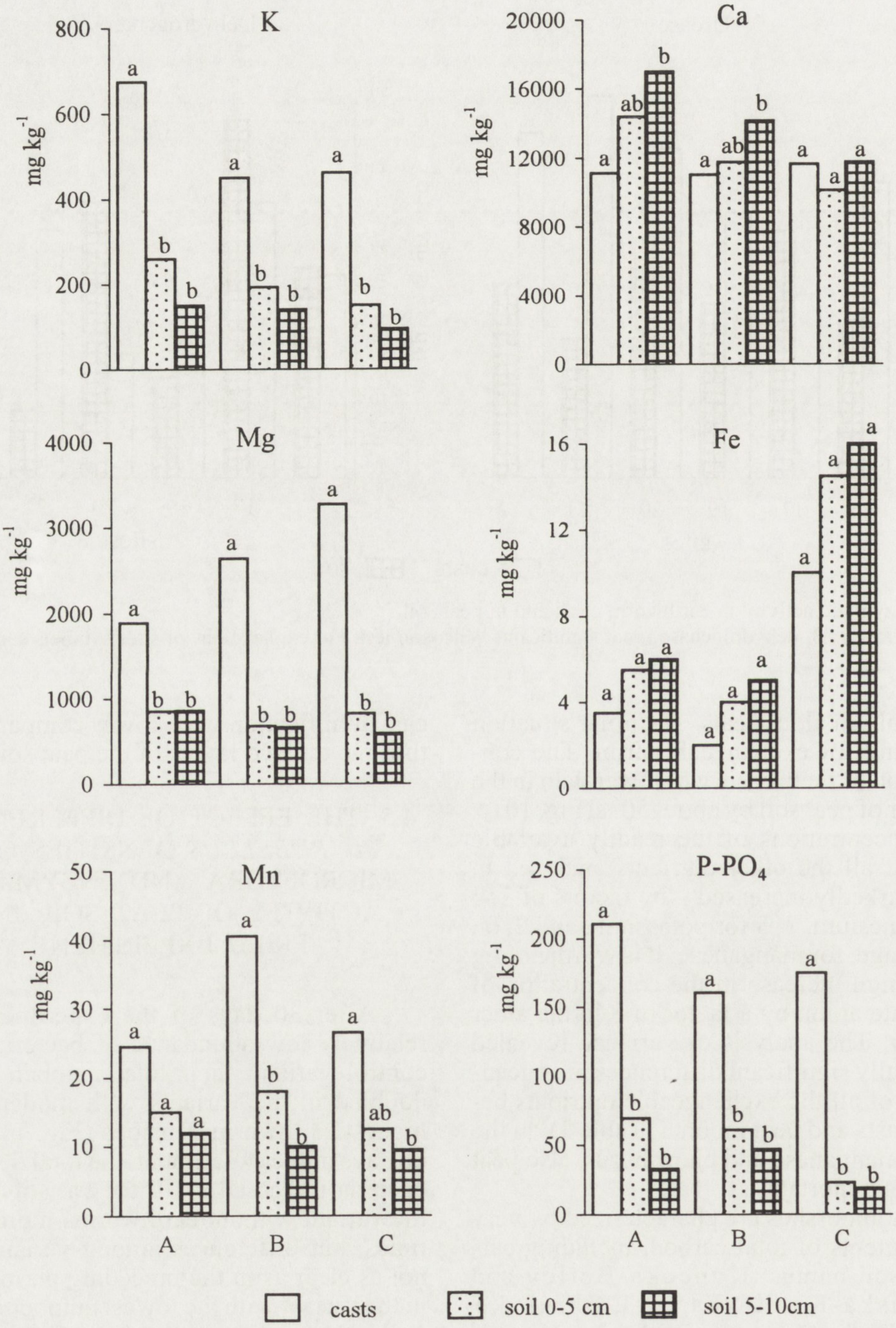


Fig. 10. Concentrations of exchangeable elements in *L. rubellus* casts and in soil. (Bars sharing the same letter are not significantly different).
A – sedge-moss, B – tall-sedge, C – alder peat

After 30 days, the abundance of fungi decreased to almost three times in the variants with *L. rubellus* as compared with the control. This is an opposite situation to that earlier observed when casts were compared with upper soil layers (Fig. 8). After 60 days of the experiment, the number of fungi increased only at the lowest earthworm density, and in the other variants it was similar to that in the control. In autumn, on the fourth sampling date, fungi were again less abundant in all variants with earthworms, as compared with the control. The analysis of variance

Table 3. Results of two-factor ANOVA analysis of exchangeable nutrient contents in casts and in soils differing by peat origin. F values and levels of significance are shown (n = 6)

Nutrient	Place (casts, soil layers) (d.f. = 2)		Peat origin (sites) (d.f. = 2)		Interaction (place and site) (d.f = 4)	
	F	*P*	F	*P*	F	*P*
K	65.04	0.000	6.33	0.02	1.57	0.26
Ca	5.58	0.02	5.19	0.03	1.78	0.21
Mg	196.19	0.000	5.78	0.02	11.65	0.001
Fe	12.20	0.003	87.80	0.000	1.01	0.45
Mn	15.29	0.001	1.81	0.21	1.08	0.42
P/PO_4	66.68	0.000	2.59	0.12	1.18	0.38

d.f. – degree of freedom

Table 4. Humus fractions in *L.rubellus* casts and in the peat soil

	N%	C%	C/N	C_{KH}%	C_{KF}%	C_P%	C_{KH}/C_{KF}	Degree of humific.
tall-sedge peat								
casts	2.92	35.94	12.3	8.31	6.35	21.28	1.3	40.8
soil:								
0–5 cm	3.05	37.20	12.2	11.80	5.09	20.31	2.3	45.4
5–10 cm	2.95	36.84	12.5	10.24	6.09	20.51	1.7	44.3
alder peat								
casts	3.25	35.50	10.9	7.42	6.68	21.40	1.1	39.7
soil:								
0–5 cm	3.35	36.44	10.9	9.28	5.94	21.22	1.6	41.8
5–10cm	3.40	35.14	10.3	9.95	6.01	19.18	1.7	45.6

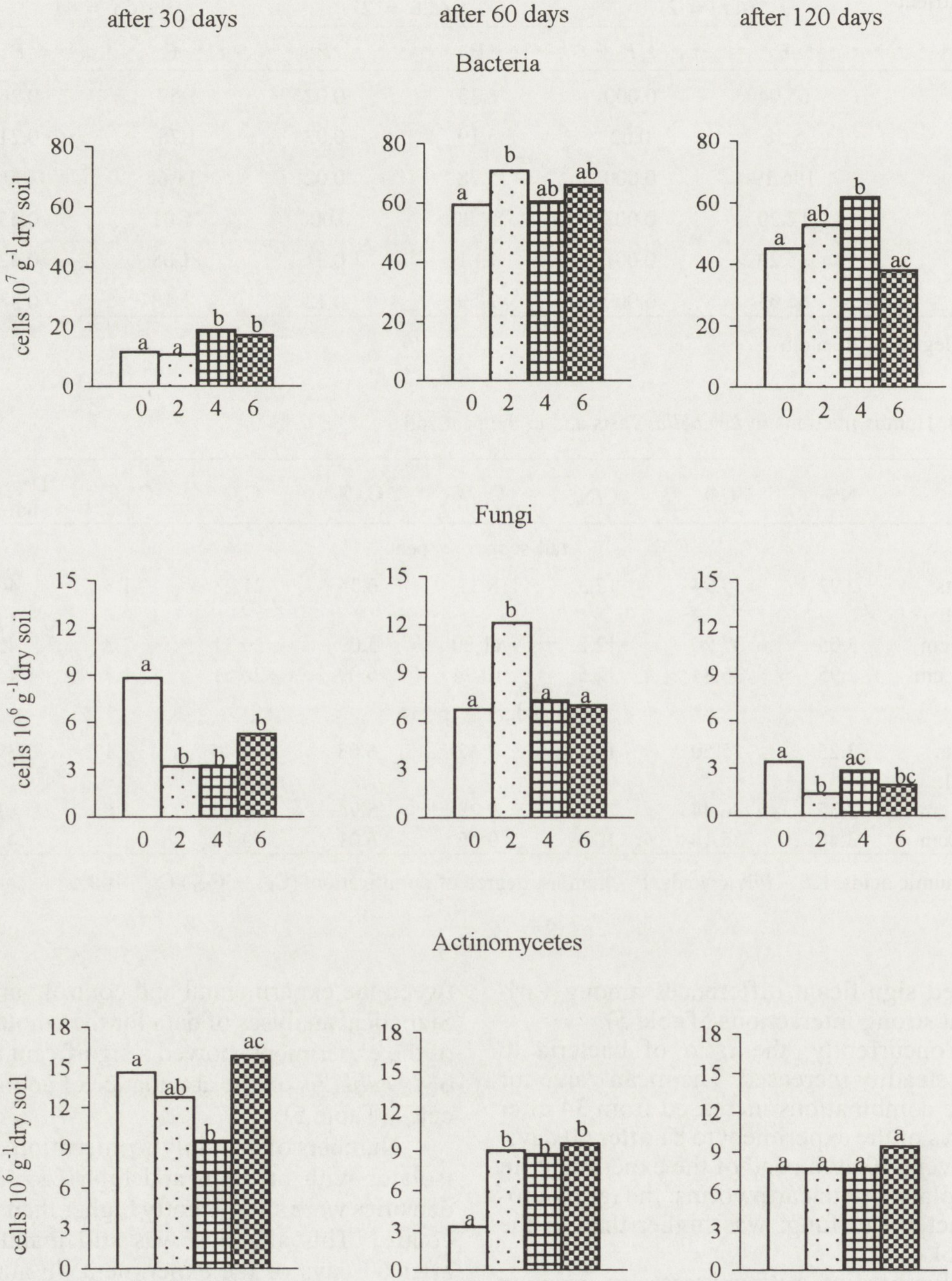
KH – humic acids, KF – fulvic acids, P – humins, degree of humification: $(C_{KH} + C_{KF})/C_{total}$ 100%

showed significant differences among variants at strong interactions (Table 5).

Concurrently, the ratio of bacteria to fungi steadily increased. The mean value for all the combinations increased from 34 after 30 days of the experiment to 81 after 60 days, and over 230 at the end of the experiment. In the isolators with earthworms, the ratio of total bacteria to fungi was higher than in the control.

Numbers of Actinomycetes in isolators that differed in the number of earthworms slightly decreased after 30 days of the experiment only in the variant with the medium *L. rubellus* density (Fig. 11). After 60 days, their numbers were three times those in the control isolators. At the end of the experiment, no significant differences were observed between the experimental and control variants. Statistical analyses of data for the whole time of the experiment showed a significant effect of *L. rubellus* on the abundance of actinomycetes (Table 5).

Numbers of cellulolytic microflora in the isolator with medium and high *L. rubellus* densities were significantly higher than in the control. This situation was still maintained after 60 days of the experiment. In autumn, the density of this group markedly decreased in the presence of earthworms, even by half, as compared with the control. As a result of opposite tendencies, no significant effect of earthworms on the abundance of this group of microorganisms was found for the whole experimental period (Table 5).


after 30 days
after 60 days
after 120 days
Bacteria
cells 10^7 g^{-1} dry soil
80
60
40
20
0
a
a
b
b
0 2 4 6
a
b
ab
ab
0 2 4 6
a
ab
b
ac
0 2 4 6
Fungi
cells 10^6 g^{-1} dry soil
15
12
9
6
3
0
a
b
b
b
0 2 4 6
a
b
a
a
0 2 4 6
a
b
ac
bc
0 2 4 6
Actinomycetes
cells 10^6 g^{-1} dry soil
18
15
12
9
6
3
0
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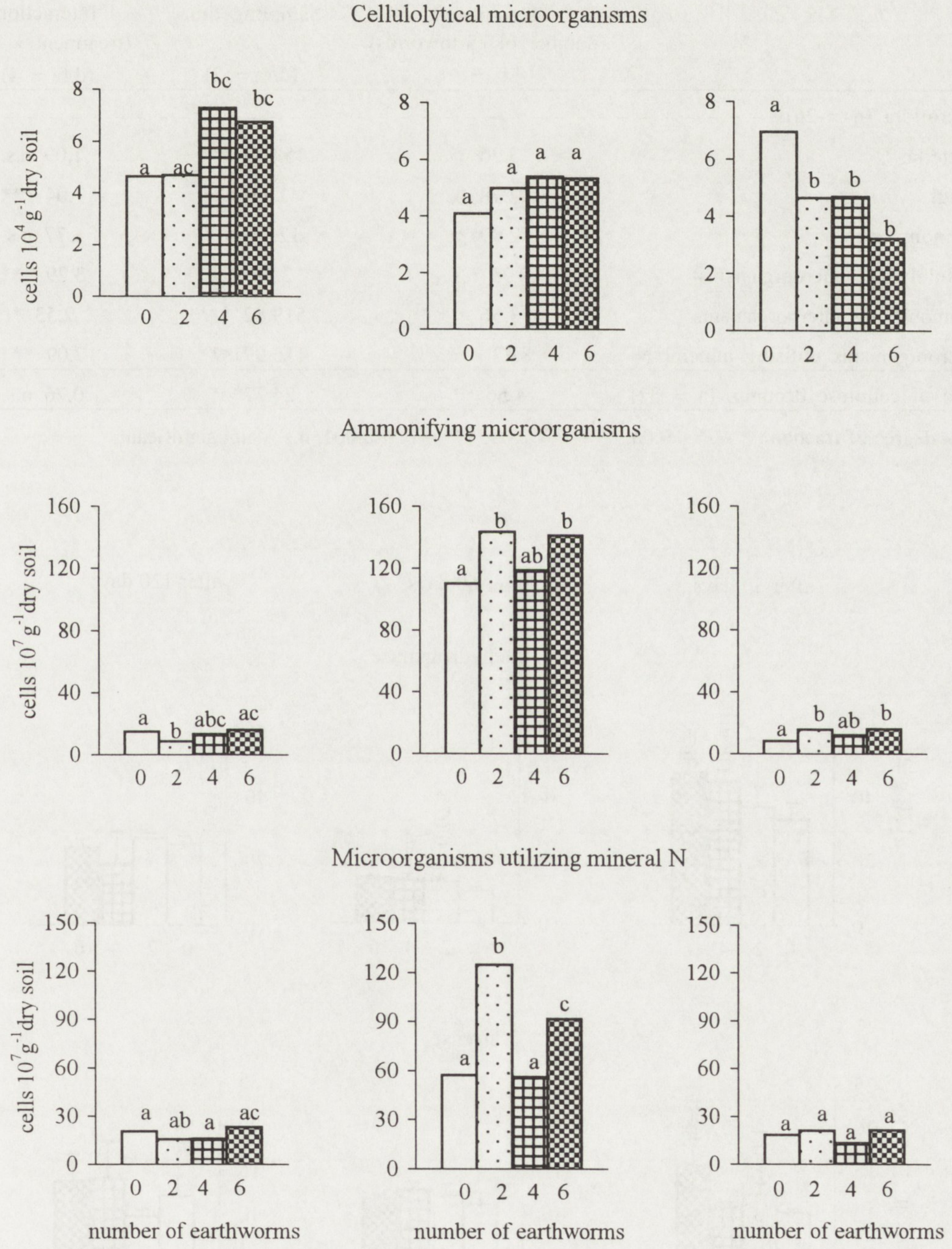


Fig. 11. Microfloral abundance in isolators with different *L. rubellus* density on three sampling dates (Bars sharing the same letter are not significantly different)

Table 5. Results of two-factor ANOVA analysis of *L. rubellus* effect on numbers of microorganisms and rate of cellulose decomposition. F values and levels of significance are presented

	Treatment (number of earthworms) (d.f. = 3)	Sampling time (d.f. = 2)	Interaction (treatment × time) (d.f. = 4)
Microflora (n = 26):			
Bacteria	3.26 *	159.33 ***	1.09 n.s.
Fungi	2.78 *	41.11 ***	7.04 ***
Actinomycetes	2.99 *	12.77 ***	1.77 n.s.
Cellulolytical microorganisms	0.73 n.s.	2.21 n.s.	3.29 ***
Ammonifying microorganisms	3.56 *	519.82 ***	2.53 *
Microorganisms utilising mineral N	8.73 ***	116.99 ***	7.09 ***
Rate of cellulose decomp. (n = 32)	4.56 **	24.77***	0.76 n.s.

d.f. – degree of freedom, * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$, n.s. – not significant.

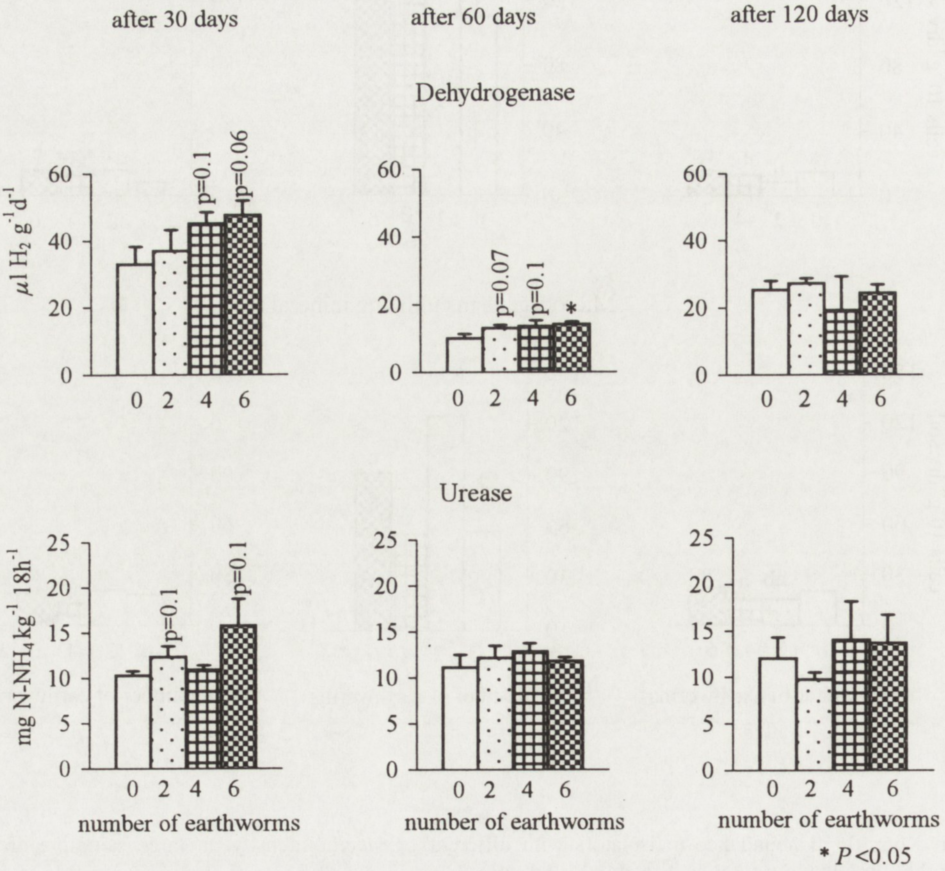


Fig. 12. Soil enzymatic activity in isolators with different *L. rubellus* number on three sampling dates (mean + SE)

Changes in numbers of ammonifying microorganisms and microorganisms using mineral nitrogen followed similar patterns but directions of changes were more variable. However, numbers of these groups tended to increase at the lowest and the highest earthworm densities in isolators, mainly after 60 and 120 days of the experiment. Analysis of the data set for the whole experimental period showed, however, a significant effect of differential *L. rubellus* densities on numbers of these two groups of microorganisms (Table 5).

After 30 days of the experiment, both dehydrogenase activity and urease activity increased with the number of earthworms, and differences approached significance (Fig. 12). These relations were maintained over the following month, and disappeared in autumn on the last sampling date.

4.6. BIOMASS OF MICROORGANISMS IN ISOLATORS WITH DIFFERENT *L. RUBELLUS* DENSITIES

Microbial biomass expressed as carbon content was higher in the isolators with earthworms compared with the control in both the soil layers after 120 days of the experiment (Fig. 13). The highest level was found in the variant with medium *L. rubellus* numbers. The analysis of variance confirmed a significant effect of earthworms on soil microbial biomass in the experiment (F = 6.39, P = 0.002, n = 8).

4.7. THE RATE OF CELLULOSE DECOMPOSITION

The rate of decomposition of cellulose filter papers was significantly higher in variants with earthworms as compared with the control during the first 45 days of the experiment (Fig. 14). In the last month of the experiment, cellulose decomposition was less intense, but still higher in the isolators with earthworms. The two-factor analysis of variance confirmed the significant effect of earthworms on the rate of cellulose decomposition (Table 5).

4.8. THE EFFECT OF *L. RUBELLUS* ON SELECTED GROUPS OF SOIL FAUNA

4.8.1. NEMATODA

Clear changes in the composition and abundance of soil microflora caused by *L. rubellus* had a direct and indirect influence on micro- and mesofauna of peat soils.

Nematodes were closely associated with soil microflora. After 30 days of the experiment, their numbers significantly decreased with increasing earthworm numbers in the isolators (Fig. 15). The proportions of bacterial feeders and fungal feeders markedly declined , while the proportion of plant feeders increased (Fig. 16). The proportions of predators and omnivores slightly increased, implying an increased community stability. After

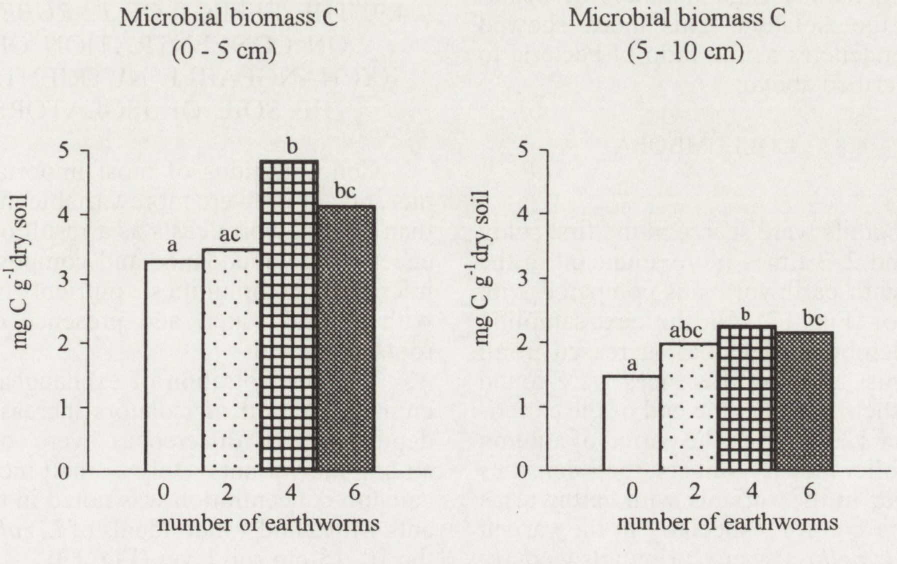


Fig. 13. Microbial biomass C in two soil layers in isolators with different *L. rubellus* numbers (Bars sharing the same letter are not significantly different)

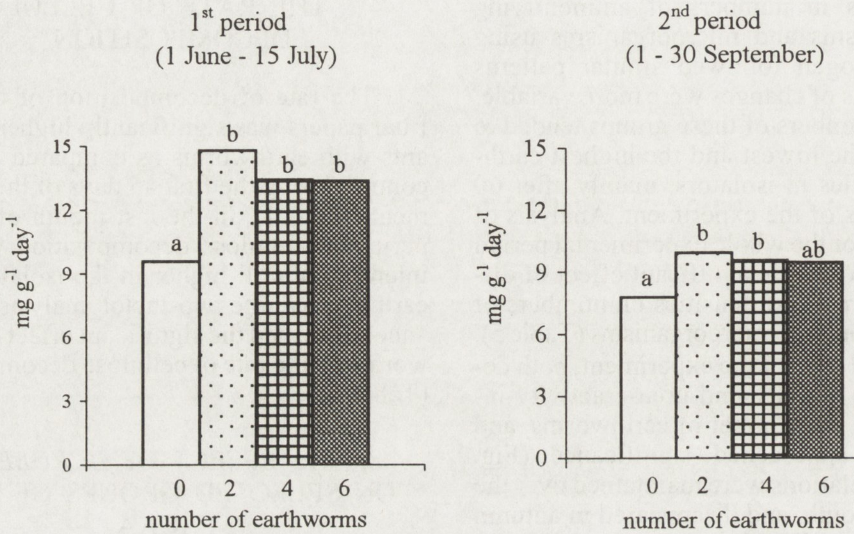


Fig. 14. Rate of cellulose decomposition in isolators with different numbers of *L. rubellus*

60 days of the experiment, in variants with 4 and 6 earthworms, an increase was observed in plant feeders. The proportions of fungal feeders decreased in the isolators with *L. rubellus*. At the end of the experiment, no significant differences in the number of nematodes were observed, except for the fungal feeders that were less abundant in the variant with medium numbers of earthworms.

The ratio of bacterial feeders to fungal feeders was the lowest in the variant without earthworms as compared with all the other variants (Table 6). The highest values were recorded after the first 30 days of the experiment, at generally high numbers of nematodes in the isolators. This index showed similar tendencies as the ratio of bacteria to fungi described above.

4.8.2. COLLEMBOLA

Springtails were scarce in the first study period, and 2–3 times more abundant in the variants with earthworms as compared with the control (Fig. 17). On the next sampling date, collembolan densities increased in all the variants, and no differences were found between them. Only at the end of the experiment, after 120 days, in the period of autumn peak in collembolan numbers, their densities were lower in the variants with earthworms than in the control, especially in the variant with 4 *L. rubellus,* where springtails were reduced to 13-times as compared with their density in the control.

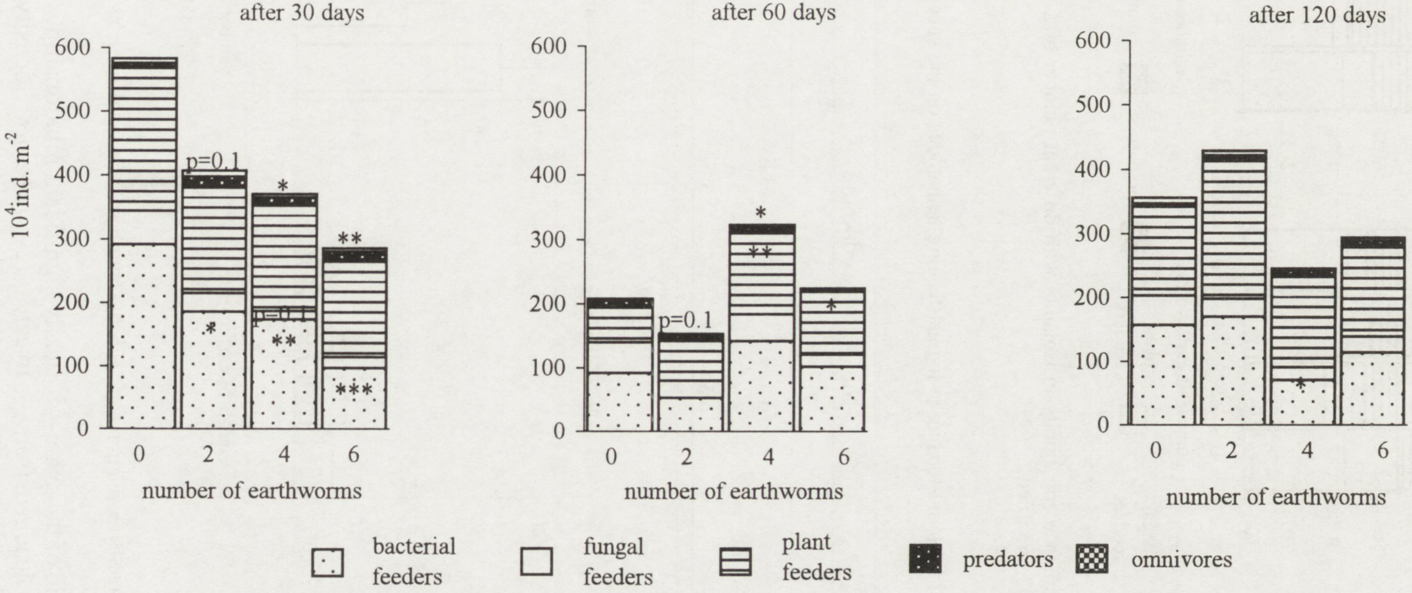
4.8.3. ENCHYTRAEIDS

After 30 and 60 days of the experiment, enchytraeid densities were high and similar in all the variants (Fig. 18). Differences in variants with 4 and 6 earthworms compared with the control were not statistically significant. After 120 days of the experiment, their densities were very low, 4–7 × 10^3 individuals m^{-2}, and they did not depend on *L. rubellus* density.

4.9. THE EFFECT OF *L. RUBELLUS* ON CONCENTRATION OF EXCHANGEABLE NUTRIENTS IN THE SOIL OF ISOLATORS

Concentrations of most important cations and anions were more variable in the soil than in earthworm casts as a result of differences in the abundance and composition of microbial communities, nutrient transport with ground water, and presence of plant roots in the soil.

The concentration of exchangeable calcium in the soil of isolators increased with depth but no differences were observed among the variants. Only a small increase in calcium concentration was noted in the variants with 2 and 4 individuals of *L. rubellus* in the 10–15-cm soil layer (Fig. 19).



* p<0.05, ** p<0.01, *** p<0.0001 - above the bars concern the total number of nematods, inside the bars concern the number of the trophic groups. All differences are related to the control.

Fig. 15. The abundance of nematodes in relation to the earthworm density (after Ilieva-Makulec and Makulec 2002, modified)

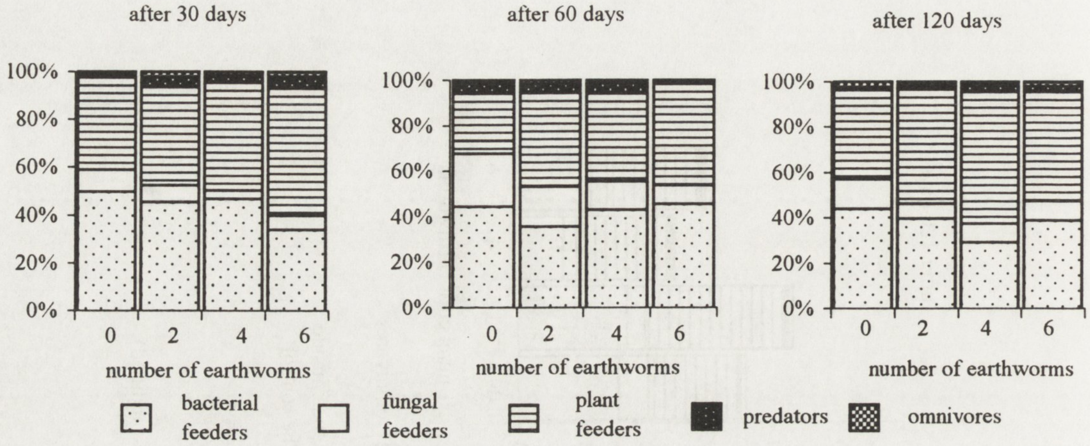
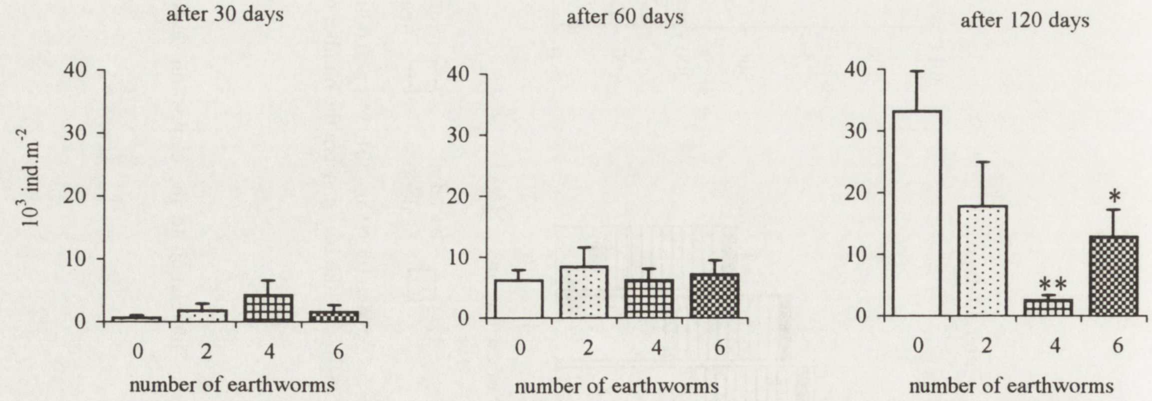


Fig. 16. Trophic structure of the nematode community in isolators with different number of *L. rubellus* (after Ilieva-Makulec and Makulec 2002, modified)

Table 6. The ratio of the numbers of bacterial-feeding to hyphal-feeding nematodes on the successive sampling dates

Sampling date	Number of earthworms			
	0	2	4	6
after 30 days	5.5	6.5	13.6	5.6
after 60 days	1.9	2.0	3.4	5.5
after 120 days	3.4	6.3	3.6	4.6



* $P < 0.05$, ** $P < 0.01$

Fig. 17. Total Collembola densities (+SE) in relation to *L. rubellus* numbers (after Makulec *et al.* 2001)

Potassium, the most mobile of the examined nutrients, can be readily leached from casts, litter, and even from green plant parts. Its concentration was not closely related with earthworm numbers. The concentration of potassium in the upper soil layer was 4–5-times that in the two deeper layers. No statistically significant relationship was found between *L. rubellus* density and the concentration of calcium or potassium in the isolated soil (Table 7).

The concentrations of exchangeable magnesium and also the content of phosphate anion were significantly higher in the isola-

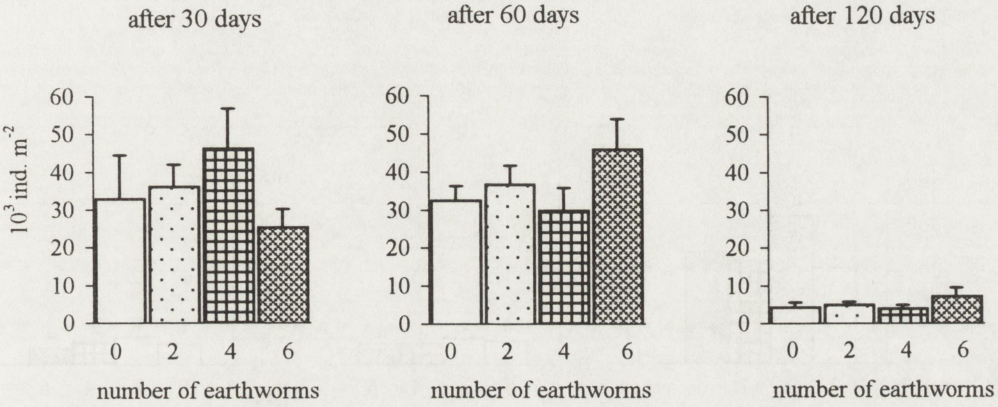


Fig. 18. Influence of *L. rubellus* on the total Enchytraeidae numbers (mean + SE)

tors with earthworms, especially in 0–5 cm and 5–10 cm soil layers (Fig. 19). They were significantly dependent on *L. rubellus* density (Table 7).

In the soil, like in casts, *L. rubellus* activity reduced the concentration of exchangeable iron almost by half, especially in variants with medium and high earthworm densities in the isolators (Fig. 19). This was the case of all the three soil layers.

Manganese concentration showed some differences only in the top moorsh layer, where in the variants with 2 and 6 *L. rubellus* individuals it was higher than in the control. The analysis of variance did not show a significant effect of *L. rubellus* density on the concentration of exchangeable manganese (Table 7).

5. DISCUSSION

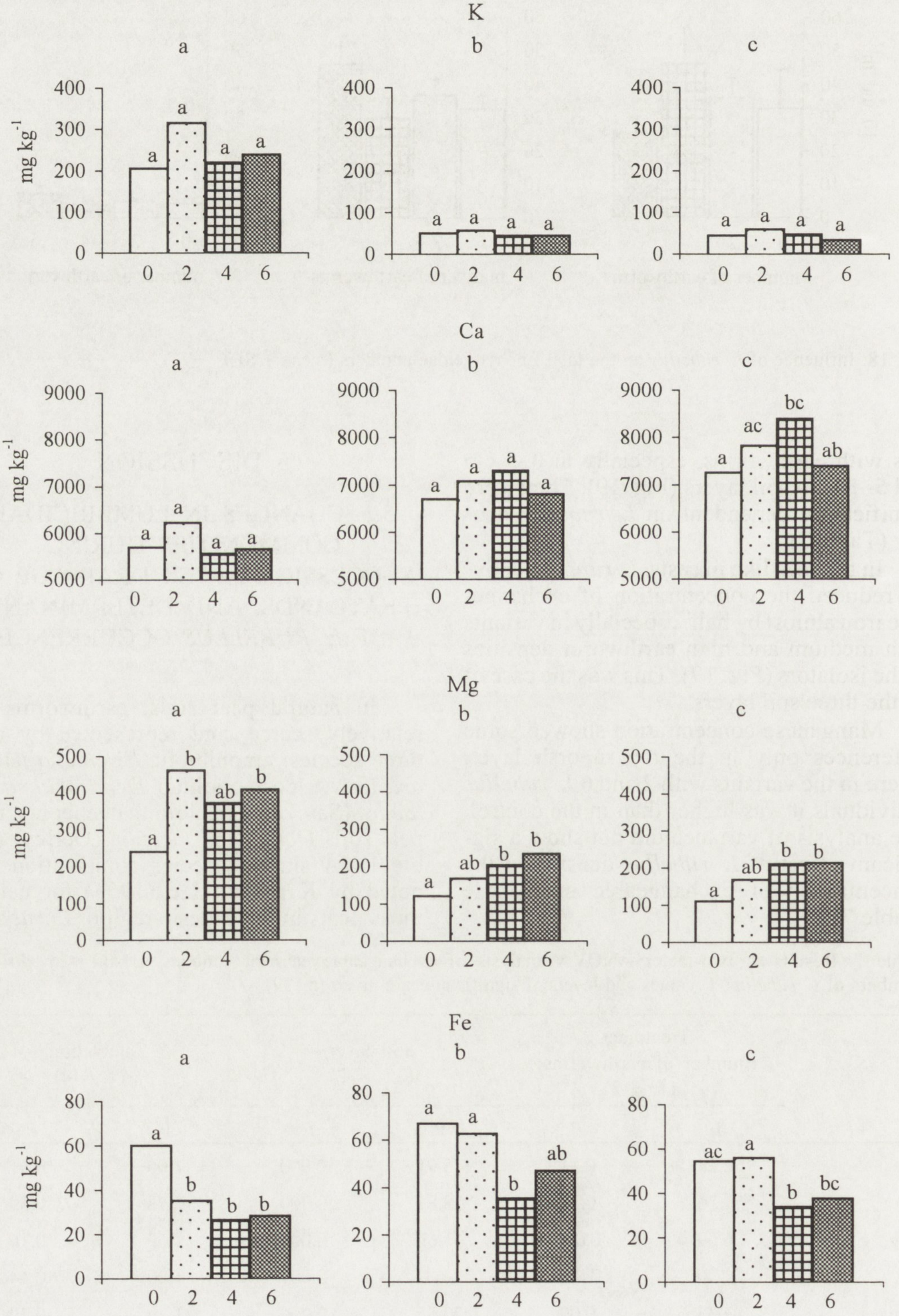
5.1. CHANGES IN LUMBRICIDAE COMMUNITIES DURING SUCCESSION AFTER DRAINAGE OF PEATLANDS, AND DETERMINANTS OF *L. RUBELLUS* OCCURRENCE

In natural peat soils, earthworms are relatively scarce, and represented by only three species: amphibiotic *Eiseniella tetraedra* (Sav.), cosmopolitan *Dendrobaena octaedra* (Sav.), and inhabiting deeper layers of peat soils *Octolasion lacteum* (Oerley) (Table 1). A similar species composition was noted by Kipenvarlic (1953) for natural moss peats in the Polesie region. *L. rubellus*

Table 7. Results of two-factor ANOVA analysis of exchangeable element contents in soil with different numbers of *L. rubellus*. F values and levels of significan ceare given (n = 9).

	Treatment (number of earthworms) (d.f. = 3)		Soil layer (d.f. = 2)		Interaction (d.f. = 4)	
	F	*P*	F	*P*	F	*P*
K	2.24	0.11	75.91	0.000	1.06	0.41
Ca	1.76	0.18	28.87	0.000	0.78	0.59
Mg	6.69	0.002	41.67	0.000	1.69	0.16
Fe	11.84	0.000	6.11	0.007	1.00	0.44
Mn	2.33	0.09	22.55	0.000	1.29	0.29
P/PO_4	10.18	0.000	35.91	0.000	3.14	0.02

d.f. – degree of freedom


K
a
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mg kg^{-1}
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a a a a
Ca
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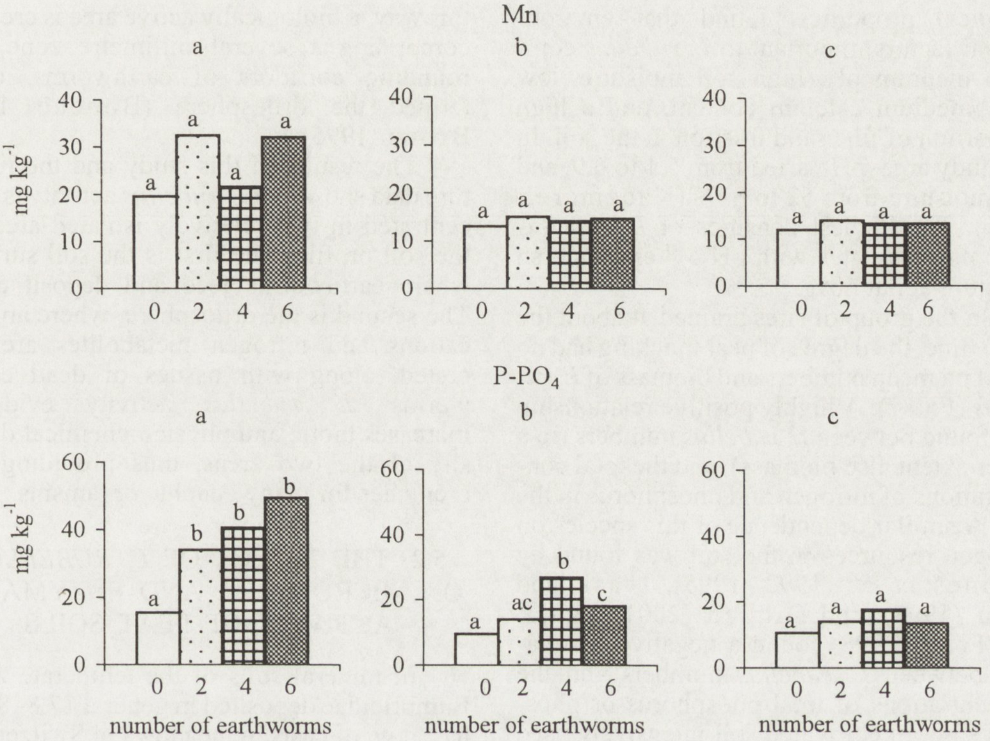

a - soil 0-5cm, b - soil 5-10cm, c - soil 10-15cm
(bars sharing the same letter are not significantly different)

Fig. 19. Concentrations of exchangeable elements in isolators with different *L. rubellus* density

was not found in natural peatlands. This was confirmed by Furmańczuk (1979), who conducted intensive studies in the same meadows.

Already in the first years after peat drainage, the number of earthworm species markedly increases (Makulec 1991). In the study area, it reached the highest value of 6 species within a short time (Table 1). A similar process was observed by Arzamasov *et al.* (1980) in drained Polesian peats and by Kozlovskaja (1980) in Karelia region.

L. rubellus appears already in the first three years after drainage, and colonizes the drained peat meadows in very high densities. Colonization of new areas by this species is likely to follow various pathways. *L. rubellus* is a mobile species, and, as found on polders and post-exploitation bogs where it was introduced, this species can extend its range by 10–14 m a year (Curry and Boyle 1987, Marinissen and van den Bosch 1992). In the Biebrza meadows under study, it can migrate from oak-hornbeam islands and from farmland. It seems, however, that the colonization of drained areas is an effect of the transport of cocoons and young individuals by water flowing through drainage canals after spring thaw or intense rainfall. This species can survive 31–50 weeks in the soil permanently submerged, provided that it contains sufficient amount of oxygen (Roots 1956). Also the transport of cocoons on wheels of agricultural machines and cattle hoofs can be of some importance to *L. rubellus* spreading.

The abundance of *L. rubellus* in a series of habitats from natural to drained meadows was closely and positively associated with the degree of peat moorshing, time after drainage, and pH (Fig. 5). Among the study sites, this species showed preference for meadows with rather low moisture content in the peat moorsh. Briones *et al.* (1995), who analysed the occurrence of earthworms on over 60 sites with largely varying physico-chemical properties, found that environmental factors important to *L. rubellus* comprise medium pH, high soil moisture, low C/N, medium calcium content, and a high proportion of fine sand fraction in the soil. In the study area, pH varied from 5.1 to 6.9, and soil moisture from 52 to 81% (Kaczmarek 1991). The highest densities of *L. rubellus* were noted at sites with pH 5.8 and moorsh moisture about 60%.

In the group of sites drained at about the same time, the degree of peat mucking had no effect on mean numbers and biomass of *L. rubellus* (Fig. 7). A highly positive relationship was found between *L. rubellus* numbers (to a lesser extent also biomass), and the total concentrations of nitrogen and phosphorus in the soil. A similar dependence of this species on nitrogen resources in the soil was found by Briones *et al.* (1992, 1995), Ivask and Truu (1998), and Didden (2001). Ivask and Truu (1998) found a negative correlation between *L. rubellus* numbers and the concentrations of total phosphorus or phosphates but in cultivated soil intensively used and treated with mineral fertilizers. In peat meadows, the content of both nitrogen and phosphorus is crucial to *L. rubellus* occurrence.

The occurrence of *L. rubellus* in drained peat bogs was determined by food resources, pH, moisture, and also by the amount of soil macropores. The biomass of this species, and to a lesser extent also its numbers, were negatively correlated with porosity, and positively with density by volume of the peat (Fig. 7). Meadows of the Kuwasy fen are characterized by a high porosity of 82–88% and a low density of 0.20–0.30 g cm^{-3} (Churski, unpublished), often due to the drying of the top moorsh layer, especially in alder peats. Hence high numbers and biomass of *L. rubellus* are observed in moss and sedge moorsh with a lower porosity and higher density of peat.

In peat moorsh, *L. rubellus* penetrates a 8–10 cm-layer, thus not so deep as in mineral soils (Satchell 1955, Francis and Fraser 1998). Most readily it occupies natural macropores between little decomposed peat fragments, and corridors made by entomofauna or by roots of dicotyledonous plants. These spaces are permanently coated with a thin layer of mucus rich in nitrogen compounds and exchangeable nutrients secreted by the metanephridial system. They are places of microbial and microfaunal proliferation. In this way, a biologically active area is created, comprising a several-millimetre zone surrounding corridors of earthworms, often termed the drilosphere (Bouche 1975, Brown 1995).

The results of this study and the literature data show that *L. rubellus* activity is concentrated in two relatively isolated areas of the soil profile. The first is the soil surface, where earthworms feed and deposit casts. The second is the drilosphere, where anions, cations and nitrogen metabolites are excreted, along with tissues of dead earthworms. *L. rubellus* activity evidently increases biotic and physico-chemical diversity of the two areas, thus providing microniches for many edaphic organisms.

5.2. THE EFFECT OF *L. RUBELLUS* ON MICROFLORA AND ENZYMATIC ACTIVITY OF PEAT SOILS

In mineral soils of the temperate zone, Lumbricidae deposited in general 17.8–81.0 t ha^{-1} d.w. of casts in meadows in Switzerland (Stöckli 1928), 91.4 t ha^{-1} in meadows in Germany (Dreidax 1931), and 18.8–40.4 t ha^{-1} in a perennial pasture in England (Darwin 1881). In soils of drained peat meadows, *L. rubellus* alone deposited 12–35 t ha^{-1} d.w. of casts a season (Table 2), that is, almost half of the amount quoted above for *Lumbricidae* communities in fertile mineral soils. Earthworm casts retain their form even for several weeks , depending on the species and its diet, soil type, moisture, or intensity of precipitation. Then, they split into small, very stable aggregates that determine the fertility, porosity, water-holding capacity, and aeration of the top soil layer (Edwards and Bohlen 1996). Their stability is due to fungal hyphae (Parle 1963b), presence of bacterial mucus, and mineral-organic substances, mainly calcium humates (Shaw and Pawluk 1986).

Microfloral composition and abundance of earthworm casts depend on many factors. Food preference of a species is important. According to Lee (1985), this is the only factor determining the commonly observed increase in the total abundance of microorganisms in casts. It has been found that all epigeic earthworm species show a higher preference for organic matter mixed with soil as their food than for organic residues alone, without admixture of mineral components (Doube *et al.* 1995). Enormous amounts of microbes pass through the gut of earthworms with food, and a large part of them is digested. Protozooans, algae, broken up fungal hyphae, and dead plant residues are readily decomposed in the guts of many species (Edwards and Fletcher 1988, Brown 1995). In the fore section of *L. rubellus* gut, Krištůfek *et al.* (1994) observed under microscope dead and digested bacterial cells, empty fungal hyphae, and scarce live bacteria, the number of which increased in the hind part of the gut.

Epigeic earthworm species have a rich and diverse system of digestive enzymes, including cellulase (Tracey 1951, Hartenstein 1982, Urbasek and Pižl 1991, Brown 1995, Kavian *et al.* 1999). These enzymes in association with microfloral exoenzymes allow digestion of different organic materials contained in the food.

Most studies on the composition and numbers of microflora in the guts and casts of earthworms were conducted using *L. terrestris* (Kulińska 1961, Parle 1963a, Satchell 1983, Subler and Kirsch 1998, Wolter and Scheu 1999). Studies on *L. rubellus* were rare, and show rather large differences in the development of microflora in the guts of these two species (Daniel and Anderson 1992, Krištůfek *et al.* 1992, Pedersen and Hendriksen 1993, Krištůfek *et al.* 1994).

The time of the passage of food through the gut of *L. rubellus* is relatively long and enhances the proliferation of microflora (Daniel and Anderson 1992). Krištůfek *et al.* (1992) have found an almost four-time increase in numbers of bacteria, actinomycetes, fungi, and fluorescent bacteria in the hind part of *L. rubellus* gut as compared with the fore part. It may, thus, be expected that the total amount of microflora in casts will be multiplied. But the results of this study (Fig. 8) showed a more complex pattern. The number of fungi and cellulolytic microflora increased, whereas the number of bacteria and actinomycetes decreased. In similar studies conducted in other peat meadows also a decrease, or only a small increase, was observed in numbers of bacteria, and a clear increase in numbers of fungi, ammonifying microflora, utilising mineral nitrogen, in cellulolytic microflora, and actinomycetes in casts compared with the top moorsh layer (Makulec and Chmielewski 2002). It is possible that when bacteria are numerous in the soil, they may be digested, or some groups may be inhibited, in the gut of *L. rubellus.* Pedersen and Hendriksen (1993) using both the plate method and the direct count noted that the abundance of bacteria in mixed casts of *L. rubellus, L. castaneus,* and *L. festivus* was reduced to one-tenth as compared with their abundance in cattle dung supplied as food. The authors added selected strains of four common Gram-negative bacteria to the substrate, and they found large differences in their survival in the gut of earthworms. The densities of two species in casts were lower than in the potential food, whereas the concentrations of the two remaining species did not noticeably changed in the gut and casts.

Daniel and Anderson (1992) found a decrease or statistically not significant increase in microfloral biomass, and a concurrent significant increase in CO_2 evolution from *L. rubellus* casts compared with the control soil in a laboratory experiment. This paradox they explain as a result of the stimulation of microbial metabolic activity in the gut of *L. rubellus*. Scheu (1987) observed a nearly 30% increase in microfloral biomass in fresh *A. caliginosa* casts compared with the soil.

It can be suggested that the abundance of microbes in casts is determined not only by the diet and specific character of transformations in the gut of earthworms, but also by the properties of the soil they dwell. In general, in peats with low microfloral abundance, the relative increase in casts is higher. An important factor is also the season of the year and the related resources of dead organic matter. Numbers of microflora in *L. rubellus* casts in drained soils of peats in Siberia are increased in spring and autumn when fresh plant residues easily decomposable are abundant (Kozlovskaja 1976). In summer, when earthworms forage on older and more resistant to decomposition materials, the total abundance of microflora in casts is reduced.

The obvious increase in the abundance of fungi may be an effect of the fragmentation of hyphae during ingestion and comminution of plant residues, enhancing spore development, and fast spreading of microbes during the first hours after cast deposition (Brown 1995). Laboratory experiments showed an unusual preference of *L. rubellus* for fungi, including the genera *Fusarium* and *Cladosporium* (Bonkowski *et al.* 2000). Earthworms of this species ingested up to 75% of the hyphae already after six days of the experiment. But the authors stated that the abundant development of the hyphae of some species was a signal providing information on the degree of plant material decomposition, rather than a direct source of food for *L. rubellus*. Individual *L. terrestris* captured in the field contained in the gut hyphae of the total length exceeding 5 times the length of hyphae in the surrounding soil (Wolter and Scheu 1999). No significant differences were found in the concentration of fungi between the fore and hind portions of the gut, implying that they were not digested in the gut. But direct observations by Krištůfek *et al*. (1994) show that the content of fragmented fungal hyphae is digested.

The ratio of bacteria to fungi in the casts was lower than in the top soil layer. This indicates an increased and more efficient accumulation of organic matter in casts, and capture of the released nutrients. The C/N ratio in bacterial cells is relatively stable and equals to 4:1, whereas in fungal biomass it is generally higher and equals to 10:1 on the average (Paul and Clark 1996). This implies that fungi immobilize soil nitrogen to a lower extent than do bacteria of similar biomass.

In drained peat meadows, actinomycetes play an important role. Generally it is argued that their main function is decomposition of complex organic substances constituting the bulk of the drained peat. In this way they may be responsible for the biological decomposition of drained moorsh (Roguski and Bienkiewicz 1967, Okruszko 1993). Thus, decline in their abundance can reduce the rate of biological peat oxidation in the casts.

Organic matter, mainly particulate plant debris, forms over 40% of the food mass in the hind portion of *L. rubellus* gut (Rożen *et al*. 1995). This provides an excellent substrate for the development of cellulolytic microflora in earthworm casts (Fig. 8). As numbers of bacteria and actinomycetes decline in the casts, it may be suggested that this physiological group consists mainly of fungi. Increased activity of cellulolytic organisms, and also hemicellulolytic, amylolytic, and proteolytic organisms, was also observed by Loquet *et al*. (1977).

A large part of soil urease derives from plants (Skujins 1967). Thus, its clearly increased activity in casts may to some extent be an effect of the accumulation of dead organic matter contained in the food of *L. rubellus* (Fig. 9). The excretion of large amounts of urea through the metanephridial system of earthworms (Needam 1957) also enhances its activity . It has been found that an adult *L. rubellus* excretes about 580 μg of mineral nitrogen per gram biomass per day (Whalen *et al*. 2000).

A statistically significant manifold increase in urease and dehydrogenase activity in casts of this species was noted in the soils of three meadows that differed in the origin of peat moorsh (Makulec and Chmielewski 2002). This provides evidence for a high metabolic activity of casts, and corroborates the results of respiration measurements described above.

Thus, the microfloral abundance in casts primarily depends on the species of earthworm and its food selectivity, but also on the composition and actual abundance of microbes in the soil, on their activity and resistance to conditions in the gut, and on competitive and antibiotic interactions among microorganisms themselves. Krištůfek *et al*. (1993) isolated 8 strains of actinomycetes of the genus *Streptomyces* from *L. rubellus* guts, as compared with 15 recorded from 0–10 cm soil layer. Most of them had antibiotic properties for Gram-positive bacteria and fungi.

In the second area of *L. rubellus* activity, that is, in the drilosphere, the interactions of this species with microbes are more complex. This is mostly a result of more complex interactions, usually bilateral, in which also other important edaphon components are involved, such as micro- and mesofauna. Seasonal variation is also important.

In the experimental soil, unlike in the casts, the abundance of bacteria increased in the presence of *L. rubellus*, especially in the initial period. Already after one month, bacterial density can be twice as high at a high earthworm density (Fig. 11). This, however, could have been due to a marked decline in densities of nematodes feeding on bacteria to a larger extent than the stimulating effect of earthworms (Fig. 15). But in a period longer than 30 days, the effect of the number of individuals (4/isolator) prevailed. It is, thus, possible that at the highest *L. rubellus* densities, the turnover of bacterial biomass was faster at its relatively lower standing crop.

Also Zraževskij (1957) found a threefold increase in bacterial abundance in peat soil after the introduction of earthworms or their casts. Atlavinyte (1975) noted in pot experiments a five-fold increase in the abundance of microbes when earthworms were present in mineral soil.

Unlike in the casts, the abundance of fungi in the soil dwelled by earthworms was significantly lower, especially at the beginning and at the end of the experiment. As the total abundance of bacteria increased in the peat, this means that the ratio of bacteria to fungi increased, and as a consequence the accumulation of organic carbon could be reduced, the rate of soil mineralization could increase, and the competition for soil nitrogen could be intensified. An increase in bacterial to fungal biomass in the forest soil colonized by earthworms was also observed by Scheu and Parkinson (1994) in a microcosm experiment with epigeic *D. octaedra.*

An increase in fungi in the gut of *L. rubellus* (Krištůfek *et al.* 1992) and, consequently, in casts is indicative of a stimulating effect of this species, probably through enhancing the development of some spores (Brown 1995). This effect, however, is limited to the soil top layer, where casts are deposited. In the 0–10-cm soil layer, the abundance of fungi was reduced, probably as a result of grazing on fungi and competitive interactions between microbes, difficult to identify, also because of micro- and mesofauna activity. After 30 and 120 days of the experiment, also densities and proportions of nematodes feeding on fungi were reduced in the isolators with *L. rubellus*, probably as a result of reduced food resources, or direct consumption by earthworms. Zhang and Hendrix (1995) conclude that the grazing by *L. rubellus* can interrupt a specific “fungal bridge” created by hyphae between the litter and deeper soil horizons, impairing its growth and development, and it can limit the movement of organic carbon down the soil profile.

Actinomycetes, because of their participation in the decomposition of aromatic compounds, including soil humus, can be responsible for the decomposition and disappearance of “old” peat (Myśkow 1968, Okruszko 1993, Paul and Clark 1996). In casts, this process is limited by the presence of “fresh” plant debris and reduction of actinomycete density (Fig. 8). In peat moorsh, in summer months, when the input of easily decomposable litter to the soil is small, earthworms enhance the development of these microorganisms, and by doing this they may contribute to the disappearance of peat.

The densities of two interconnected groups of microorganisms participating in the transformation of soil nitrogen, that is, ammonifying bacteria and microorganisms using mineral nitrogen, followed a similar patterns of changes on successive sampling dates. Their densities were similar and highest after 60 days of the experiment (Fig. 11). This similarity is indicative of an intensive decomposition of organic nitrogen compounds, combined with an equally intensive assimilation of mineral forms of nutrients by microorganisms. It suggests a rather economical allocation of soil nitrogen, and its high immobilization in the biomass of microorganisms, roots, and fauna in the soil with earthworms. Haimi and Huhta (1990) and Haimi and Boucelham (1991) noted a high increase in the concentration of mineral nitrogen in leachates from mesocosms with *L. rubellus* from poor forest soil. In similar experiments, Brown *et al.* (1995) observed an almost 10-fold increase in the rate of nitrogen release from the litter in presence of *L. rubellus*, as compared with the control soil. They did not find, however, changes in the concentration of mineral nitrogen in the soil.

L. rubellus showed preference for soils rich in nitrogen (Fig. 7), and has a high demand for its organic form (Satchell 1967). Tissues of this species contain 8.45% nitrogen in ash-free mass (Parmelee and Crossley 1988), and a daily turnover of this nutrient is about 3% (calculated from Whalen *et al.* 2000). At high earthworm densities in isolators, a large part of nitrogen is bound in their tissues. This is indicative of a rather strong competition for this nutrient among live components of the soil, and of a rather low level of mineral forms of nitrogen in peat moorsh.

This suggestion is further supported by high levels of microbial biomass C in the field experiment (Fig. 13). In peat soils, after 120 days of the experiment, microbial biomass C in the 0–5-cm moorsh layer was higher by 48% and 25% in the variants with 4 and 6 earthworms of *L. rubellus*, respectively, as compared with the control (Fig. 13).

Brown *et al.* (1995) did not find significant changes in the biomass of microorganisms in a 60-day laboratory experiment with *L. rubellus*. In contrast, Hendrix *et al.* (1998) observed a significant decrease in microbial biomass at sites occupied by *L. rubellus* and *A. caliginosa* on uncultivated sandy and loamy soils. A decrease in microbial biomass was also noted by Ruz-Jerez *et al.* (1992), and Zhang and Hendrix (1995) in pot experiments with *L. rubellus*. Blair *et al.* (1997) found an increase in microbial biomass-N after the reduction of earthworm density by 70%. Microbial respiration significantly increased in the soil with *L. rubellus* (Ruz-Jerez *et al.* 1992, Brown *et al.* 1995). In mesocosm experiments with *L. rubellus*, the respiration of soil microflora increased by 15–18% (Haimi and Huhta 1990).

Absence of agreement between the results of the present study and the results of the studies reported above may be ascribed to specific properties of peat soils typically characterized by higher densities of microflora, as compared with those in mineral soils. Moreover, the majority of the cited authors used the fumigation-incubation method for estimating biomass, and experiments were conducted in small and closed vessels filled with a specifically prepared soil. Except for the field studies conducted by Brown *et al.* (1995), the experimental *L. rubellus* densities did not exceed 200 ind. m^{-2}, which corresponds to the lowest variant in the experiment in peat soils. Tiunov and Scheu (2000) found that the microbial biomass-C increased 2.3–4.7 times around corridors and burrows of *L. terrestris*, the species with a diet similar to that of *L. rubellus*. Subler *et al.* (1997) also found a significant increase in microbial biomass-N on the plots with *L. terrestris* addition. As noted earlier, *L. rubellus* most readily uses the already existing soil macropores, ingests microorganisms mainly with plant debris and only to a low extent with peat moorsh, and it may be expected that the total microbial biomass will increase in the area of its occurrence, especially when the possibility of the movement of this species is limited.

Primarily, nematodes feeding on bacteria and fungi, ingesting and digesting soil microorganisms, have a direct effect on the biomass and numbers of microflora (Trofymov and Coleman 1982). At the end of the experiment, densities of these two groups were lower in variants with 4 and 6 *L. rubellus*, as compared with the control (Fig. 15). This may explain the increase in the total biomass of microorganisms observed at the end of the experiment.

Microorganisms in the isolators with earthworms had a high metabolic activity, as indicated by a higher dehydrogenase level in the variants with 4 and 6 earthworms during the first two months of the experiment. This is indirectly confirmed by the rate of cellulose decomposition which was higher in the isolators with *L. rubellus* (Fig. 14). An increased decomposition rate of plant material in the presence of this species was also observed by Haimi and Huhta (1990), Haimi and Boucelham (1991), Ruz-Jerez *et al.* (1992), and Brown *et al.* 1995).

Cellulolytic microorganisms responsible for this process were more abundant, like in casts, in the isolators with different *L. rubellus* densities in the first two sampling periods. At the end of the experiment, their numbers in the isolators with earthworms declined, probably as a result of the depletion of food substrate.

5.3. THE EFFECT OF *L. RUBELLUS* ON THE CONTENT OF EXCHANGEABLE NUTRIENTS AND HUMUS COMPOSITION IN PEAT SOILS

As a result of digestive processes in the gut and microbial activity in casts, the concentrations of exchangeable potassium, magnesium, and phosphorus increased, and those of iron and calcium decreased in the casts (Fig. 10). *L. rubellus* has well developed calciferous glands. Their secretion neutralizes acid components of the diet (Piearce 1972). Calcium is resorbed in the hind portion of the gut to the vascular system, and retained in glands. A part of calcium is bound by complex organic substances in the gut content, by bacterial mucus, and by humic acids, this having a stabilizing effect on soil aggregates. As found by Shipitalo and Protz (1988), casts of *L. rubellus* are more durable than those of *L. terrestris* due to a higher content of organic matter.

Most authors noted an increase in total and exchangeable calcium in earthworm casts from mineral soils (Lunt and Jacobson 1944, Graff 1971, Czerwiński *et al.* 1974) and in laboratory cultures (Basker *et al.* 1993). Differences are likely to be a result of specific properties of peat moorsh. The content of exchangeable calcium in them is over five times higher than in mineral soils described in the cited papers. Selective feeding by *L. rubellus*, resorption in the gut, and formation of mineral-organic chelates reduce the concentration of calcium in casts. Basker *et al.* (1994) found that *L. rubellus* inhabiting soils rich in exchangeable calcium, potassium, and magnesium deposited casts with reduced concentrations of these cations, whereas in poor soils they observed increased concentrations of these nutrients.

It was previously found that pH of *L. rubellus* casts was higher than that of the soil inhabited by earthworms (Chmielewski and Makulec 1993). Under these conditions, a part of exchangeable iron can be transformed into insoluble forms. Also soil microorganisms proliferating in casts use much iron (Paul and Clark 1996). Consequently, the content of available iron in casts may be reduced.

The concentration of phosphate ion shows a particularly high increase in casts. Lunt and Jacobson (1944) found similar relations when analysing casts derived from different earthworm species in ploughed soils. Springett and Syers (1979) recorded 16.7 $\mu g\ g^{-1}$ soluble inorganic phosphorus in *L. rubellus* casts, as compared with 6.7 $\mu g\ g^{-1}$ in the control soil. Graff (1971) recorded an over 7-fold increase in the content of soluble phosphorus in casts from meadow soils.

Such a high saturation of casts with cations and anions important for plants can cause a negative geotropism in roots, their horizontal growth, or growing into *L. rubellus* casts from below (Syers and Springett 1983). On the other hand, however, there is a danger of leaching these nutrients to ground waters, especially when the soil sorption complex is weakly developed as it is often the case in ploughed soils (Le Bayon and Binet 2001).

Earthworm casts contained more fulvic acids and less humin acids as compared with the upper layer of peat moorsh (Table 4). This is primarily a result of selective foraging by earthworms. *L. rubellus* feeds mainly on plant debris in various stages of decomposition, already containing fulvic acids and small amounts of peat moorsh in which humic acids prevail. It cannot be excluded, however, that these substances are also produced in earthworm guts and in casts with participation of microflora. Neuhauser and Hartenstein (1978) suggest that complex processes of polymerization of aromatic compounds occur in the guts of many earthworms, including production of soil humus, this being indicated by a high peroxidase activity, that is, enzymes determining these processes. Zraževskij (1957) found a 20–30% increase in the total humus content in *L. rubellus* casts, compared with its content in the soil, depending on the kind of the litter supplied for earthworms as food. Also in mineral meadow soils, over two-fold increase was found of the content of carbon and total nitrogen, and a 70% increase in the proportion of humin and fulvic acids in casts of this species as compared with the upper layer of the soil profile (Makulec and Kusińska 1995, 1997). These examples may imply that *L. rubellus* is one of the best species that can directly or indirectly influence and restore soil humus, especially in the surface layer, where casts are deposited. In this area, *L. rubellus* can replenish humus losses caused by biological oxidation of peat moorsh.

However, no changes were observed in the composition of soil humus after four months of the experiments in isolators with different earthworm densities. The development of humus is a slow and prolonged process, difficult to detect after such a short time, especially that peat moorsh is extremely rich in humus.

The increased activity of most microflora groups, intensive decomposition of plant material in the presence of *L. rubellus*, and movements of cations and anions from casts accounted for an increase in the concentration of exchangeable nutrients also in the soil of isolators (Fig. 19). *L. rubellus* penetrates the top layer of the soil profile, and the greatest changes occur in this layer. But because of a high demand for these nutrients by microorganisms and roots, the scale of these differences is smaller than in the casts. Anderson *et al.* (1983) found an over two-fold increase in concentrations of sodium, potassium, and calcium in extracts from forest soil in microcosms with *L. rubellus*.

Plant production is an indirect indicator of intensive release of exchangeable nutrients in soils colonized by earthworms. Atlavinyte (1975) observed an increase in barley yield by 78–96% after the introduction of 400–500 individuals m^{-2} of *A. caliginosa* into the soil. In microcosm experiments with three *L. rubellus* individuals, the biomass of birch seedlings after one year of the experiment was higher by 24%, and their leaves contained more nitrogen, as compared with the control variant (Haimi *et al.* 1992).

5.4. THE EFFECT OF *L. RUBELLUS* ON SOIL MICRO- AND MESOFAUNA

5.4.1. NEMATODA

Earthworms can affect soil nematode communities in various ways. They may reduce the abundance of their food resources such as microflora, or directly ingest and digest nematodes with plant residues and soil (Piearce and Phillips 1980). In the latter case, they can eliminate eggs, larvae and adults. Dash *et al*. (1980) observed this in tropical geophagous species. Also Hyvőnen *et al*. (1994) argue that a decrease in nematode abundance in the presence of *Dendrobaena octaedra* in forest soils was a direct effect of earthworm grazing.

Yeates (1981) found a 66% decline in numbers of free-living nematodes in mineral soils abundantly colonized by earthworms. Roessner (1986) investigated the effect of 8 Lumbricidae species, including *L. rubellus*, on soil nematodes by analysing their casts. He found almost total absence of plant parasites and a clear stimulation of bacterivorous nematodes. But as the present results show, these changes are not reflected in the soil inhabited by earthworms. The number of nematodes feeding on plants did not markedly change in the soil of isolators with *L. rubellus*, and often it was higher than in the control, and their proportions in the total community increased (Fig. 15). This may be a specific feature of meadow soil, associated with a great mass of roots in a large part of the soil profile. Moreover, large amounts of exchangeable nutrients and, possibly a better develoment of root systems, in the presence of *L. rubellus* provide suitable conditions for the development of this trophic group. Also the fact that *L. rubellus* most readily used already existing corridors and burrows causes that this group of nematodes is rather outside the area of its direct effects.

At the end of the first month of the experiment, the density of fungi significantly decreased, whereas the number of bacteria increased, as compared with the control (Fig. 11). These changes could be directly dependent on bacterivorous nematodes. Reduction of their densities in the variant with 4 and 6 earthworms probably enhanced bacterial proliferation in these combinations. On successive sampling dates, high bacterial densities were associated with low abundance of bacterivorous nematodes (Figs 11 and 15). Nematodes feeding on fungi were generally more abundant in the control variant as compared with the other variants, and their numbers and proportions steadily declined. Their response to fluctuations in food resources was markedly slower than in nematodes feeding on bacteria (Bouwman and Zwart 1994), hence the observed changes could have been a delayed effect of changes occurring between sampling dates.

5.4.2. COLLEMBOLA

Most authors emphasized that earthworm activity enhances an abundant occurrence of collembolans due to increasing the amount of free spaces and the content of particulate organic matter in the soil. Marinissen and Bok (1988) compared collembolan communities in soils of polders colonized by earthworms with those where earthworms were absent. They found that numbers of large species increased, and typically individuals of the remaining species were larger, in the soil with earthworms. But using similar food resources, modifying soil microflora, large sizes, and higher mobility of earthworms, they are predisposed to exert a strong competitive impact on the main mesofaunal groups.

In mesocosms with *L. terrestris*, collembolans were significantly less abundant than in the control after two and three months of the experiment (Lagerlőf and Lofs-Holmin 1987). A considerably smaller species, *Dendrobaena octaedra*, slightly enhanced the development of springtails after 3 months in a lysimetric experiment, whereas it significantly reduced their numbers at F and G horizons of forest soil after 6 months of the experiment (McLean and Parkinson 1998). Also *L. rubellus* in forest soils reduced numbers of collembolans 3–5-times after 45 and 93 days of the experiment (Haimi and Boucelham 1991). It can thus be concluded that earthworms reduce collembolan abundance, but this effect can be observed only at high densities of the two groups, for example, at seasonal peak numbers, and also in the situation of limited mesofaunal movements as it is the case in field and laboratory experiments. The possible mechanism of this process is the reduction of fungal density and soil detritus – the primary source of food for collembolans, by earthworm activity (Petersen and Luxton 1982).

5.4.3. ENCHYTRAEIDAE

Healey (1980) stated that abundant occurrence of enchytraeids in acid soils was associated with the absence of earthworms, the main competitor for food. In the soils of drained peat fens in the Biebrza river valley, both families of oligochaetes form large densities with maxima in similar periods of the season (Makulec 1996). But in experimental studies, densities of enchytraeids most often decline in the presence of earthworms. Haimi and Boucelham (1991) found that numbers of *Cognettia sphagnetorum* were reduced by half after 45 weeks of culture in microcosms with *L. rubellus*. A similar effect of this species was also observed in an experiment conducted in a sedge-peat meadow (Makulec 1996). Lagerőlf of and Lofs-Holmin (1987) noted a significant decline in enchytraeid numbers after 2 and 3 months of culture in pots with *L. terrestris* as compared with the control variant. On the other hand, introduction of earthworm casts to mineral soils enchanced enchytraeid abundance (Makulec and Pilipiuk 2000).

No clear effect of earthworms on the total density of enchytraeids was found in the field experiment on peat meadows (Fig. 18). During the first two months of the experiment, numbers of enchytraeids were very high in isolators, often higher than in soils of very fertile peat meadows (Makulec 1996). These high densities could be maintained probably due to the limited access of predators to the isolators.

6.SUMMING UP AND CONCLUSIONS

To sum up, drained Biebrza fens were rapidly colonized by *L. rubellus*. Already in the first years after drainage they reached high densities and biomass (Makulec 1991). They showed preference for moderately and highly moorshed soils with high contents of nitrogen and phosphorus, low C/N, moderate porosity, and moderate moisture.

In the top layer of the peat moorsh, *L. rubellus* consumed large amounts of plant residues, and it deposited casts rich in fungi, cellulolytic organisms, and with a higher enzymatic activity than that of the soil (Figs 8 and 9). High concentrations of the analysed exchangeable nutrients and the reported literature data are indicative of a high metabolic activity of casts, and intensive mineralization processes. Concurrently, processes of the accumulation of organic matter, including the development of humus, take place (Table 4). At decreasing numbers of bacteria and actinomycetes, mostly fungi contributed to these processes. As a result of microbial metabolic activity, and due to processes occurring in earthworm guts, the content of fulvic acids, which are precursors of most stable forms of humus, increases in the casts. As *L. rubellus* deposits large amounts of casts (Table 2), this is an important source of "new" humus for peat moorsh. This process and a decrease in actinomycete abundance can slower the biological peat decomposition.

At high *L. rubellus* densities in the upper layer of peat moorsh, proportions of humification and mineralization processes in the total of soil organic matter transformations can differ from those occurring in casts. A pronounced increase in numbers of bacteria, microorganisms responsible for soil nitrogen transformation, and in some periods also actinomycetes and cellulolytic microorganisms, combined with a decrease in numbers of fungi, are indicative of a high mineralization rate of organic matter (Fig. 11). This is further confirmed by a high dehydrogenase activity, high rate of cellulose decomposition, and periodical increase in numbers of nematodes feeding on plants (Figs 14 and 15).

L. rubellus reduces densities of nematodes feeding on bacteria, and this enhances soil bacteria and, consequently, increases the accumulation of carbon and nitrogen in microbial biomass. When dead organic matter is in short supply, this situation can lead to a strong competition for essential nutrients and, as a result, to the exploitation of soil humus resources. Thus, within the drilosphere, high numbers of *L. rubellus* can indirectly contribute to reduction of humus in moorsh peat. The increase in numbers of actinomycetes in variants with different earthworm densities after 60 days of the experiment confirms this conclusion.

The field experiment only slightly disturbed soil functioning , thus the effects of *L. rubellus* activity found in this study can be considered as occurring also in undisturbed peat moorsh. This situation is possible in the periods of spring and autumn peak numbers, when *L. rubellus* population attains densities of 200–400 individuals m^{-2}. But because of the high mobility of this species and its active searching for places of organic matter concentration, these effects can last for a relatively short time, and they may be similar to those found after 30 days of the experiment.

The complexity of interactions among the main components of edaphon, and their effects on major soil processes need further investigations under conditions as close to natural as possible.

- *L. rubellus* colonizes drained soils of peat meadows merely within 3–5 years after drainage, and rapidly becomes the dominant species in terms of its density and biomass.
- This species is most abundant in peat moorsh with high contents of nitrogen and total phosphorus, low C/N, moderate porosity, and moderate moisture.
- Compared with the soil, *L. rubellus* casts are centres of more intensive development of fungi and cellulolytic microflora and less intensive development of bacteria and actinomycetes. As a result of microbial activity and processes in earthworm guts, they contain more exchangeable phosphorus, magnesium, and manganese, and less calcium and iron. In casts, mineralization of organic matter occurs concurrently with humus formation.
- Through modifying the composition and abundance of microflora, nematodes and mesofauna, high *L. rubellus* densities (400–600 ind. m^{-2}) in drained peat soils can speed up the mineralization of dead organic matter, increase competition for most important nutrients, and indirectly contribute to the biological decomposition of moorsh.

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7. SUMMARY

All the studies were conducted in natural and drained peat meadows located in the Biebrza river valley (Fig. 1). Field observations were focused on successional changes occurring in Lumbricidae communities with time after drainage. The experimental study was aimed at estimating the role and importance of *L. rubellus*, the dominant species in peat soils, to the composition and abundance of microflora and also micro- and mesofauna in the context of organic matter mineralization and humification.

In the soils of drained peats, 2–6 earthworm species were found (Table 1). *L. rubellus* appeared already 3–5 years after drainage, and it rapidly became the dominant species reaching high numbers and biomass (Figs 3, 4, and 6). It showed preference for moderately or highly moorshed soils with high contents of total nitrogen and phosphorus, low C/N, moderate porosity, and moderate moisture (Figs 5 and 7).

This species deposited large amounts of casts (Table 2) that contained more fungi and cellulolytic microorganisms, whereas less bacteria and actinomycetes than the upper soil layer (Fig. 8). Casts were also characterized by a higher urease activity (Fig. 9), higher content of fulvic acids, and higher concentrations of exchangeable phosphorus, magnesium, and potassium (Tables 3 and 4, Fig. 10). The contents of iron and calcium ions were lower in casts.

The field experiment was conducted for 4 months in a meadow on alder peat (Figs 1 and 2). Soil cores 100 cm^2 in surface area and 15 cm deep were taken from the meadow, placed in isolators made of steelon mesh screen, and returned to the place from which they were taken. *L. rubellus* was introduced to the isolators in different densities: 2, 4, and 6 individuals. The control variant was without earthworms. Samples were taken after 30, 60, and 120 days of the experiment.

It has been found that at high *L. rubellus* densities, numbers of bacteria, ammonifying microorganisms, microorganisms utilising mineral nitrogen, and temporarily also numbers of actinomycetes and cellulolytic microorganisms increased, whereas numbers of soil fungi decreased (Fig. 11, Table 5). Also soil enzymatic activity, total microbial biomass, and the rate of cellulose decomposition increased (Figs 12, 13, and 14).

Moreover, *L. rubellus* had a significant effect on the composition and abundance of Nematoda. Within a short time, their total numbers, mostly numbers of nematodes feeding on bacteria, decreased (Fig. 15). Also numbers and proportions of fungivorous nematodes slightly declined (Fig. 16). Nematodes feeding on plants were least affected by this species, and in some periods their densities were higher than in the control variant. The ratio of nematodes feeding on bacteria to nematodes feeding on fungi was higher in the soil with earthworms than in the control (Table 6).

In the periods of high Collembola densities in peat soils, high *L. rubellus* densities reduced their numbers (Fig. 16), probably as a result of competition for food. *L. rubellus* had no noticeable effect on numbers of Enchytraeidae (Fig. 18).

In the soil of isolators with earthworms, a significant increase was found in the contents of exchangeable phosphorus and magnesium, whereas a decrease in the concentration of iron (Fig. 19, Table 7). No changes were found in the contents of potassium, calcium, and manganese ions.

By modifying the composition and abundance of microflora, nematodes and mesofauna, high *L. rubellus* densities (above 200 individuals m^{-2}) can increase the rate of organic matter mineralization, intensify competition for nutrients, especially for nitrogen, and indirectly they contribute to the biological decomposition of moorsh in soils of drained peat meadows.

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