

# Hydrochemical and microbiological distinction and function of ombrotrophic peatland lagg as ecotone between *Sphagnum* peatland and forest catchment (Poleski National Park, eastern Poland)

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**Abstract** – The testate amoeba, ciliate and rotifera communities living in interstitial waters in peatbog in eastern Poland were studied. Sampling was done on a monthly basis from April to November 2007–2008. Microbial communities were examined in a transect including three sites: (1) pine forest (site located 5 m from the lagg/forest contact zone), (2) lagg, (3) open peatbog (the centre of the peatbog). At each of the sites, interstitial water was sampled by means of piezometric wells placed to a depth of 1 m. The species richness and abundance of protozoa and rotifers significantly differed between the studied stations, with the lowest numbers in the pine forest and the highest in the lagg. These differences between macro-habitats may be due to differences in environmental conditions. The distribution of samples in ordination space led to conclude that studied habitats are distributed along the falling gradient of pH and rising gradient of total organic carbon, water table depth and nitrate nitrogen. Assemblages of all three groups showed a strong compositional gradient correlated with water-table depth, conductivity and total phosphorus. However, species composition of ciliates and rotifers was explained by nitrate nitrogen and/or phosphates concentrations. The results suggest that lagg zone of a raised bog can fulfil the function of an ecotone zone, distinguished by a significant increase in biodiversity, abundance and species specificity of micro-organisms. It can also be a place of very efficient matter and energy flow in a peat bog ecosystem.

**Key words:** peatlands / lagg / ecotone / testate amoebae / ciliates / rotifers

## Introduction

Quantifying the diversity and distribution of protozoa (testate amoebae and ciliates) and rotifers in aquatic habitats is important to gain a better understanding of microbial food webs in these systems. However, limnologists have paid little attention to peatlands, compared with other aquatic ecosystems (Gilbert and Mitchell, 2006). Peatlands, and especially *Sphagnum*-dominated peatlands, were at one time erroneously believed to be devoid of microbial life. In reality, and despite the successful use of *Sphagnum* as surgical dressings, diapers, or menstrual pads, *Sphagnum* mosses and peatlands support a high diversity of micro-organisms (Gilbert *et al.*, 2000; Gilbert and Mitchell, 2006). In *Sphagnum*-dominated peatlands, the animal communities, especially invertebrate are sufficiently known (Borcard and Vaucher von Ballmoos, 1997).

By contrast, little or no attention is given to abundance and biomass of protozoans and rotifers, and their relationships to environmental parameters in these specific ecosystems. The ecology of peatland testate amoebae is studied along broad gradient from very wet to dry micro-sites where testate amoebae are often found to respond primarily to the depth of water table (Lamentowicz *et al.*, 2010; Jassey *et al.*, 2011; Payne, 2011). Although the relationship between testate amoebae and DWT-depth of water table and others variables are well documented, much less is known about ciliates and rotifers in peatlands. These micro-organisms are important consumers of pico- and nano-sized producers, as well as important food sources to others metazoan (Mieczan, 2010, 2012; Wilkinson and Mitchell, 2010; Bielańska-Grajner *et al.*, 2011). Wilkinson and Mitchell (2010) suggested that protozoa, even if only a minor fraction of the total microbial biomass, could be responsible for a large proportion of nutrient recycling in peatland communities. Metazoan grazing is important

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for recycling of nutrients and production of dissolved organic substrates for bacteria, but it is also a controlling factor for the protozoan community structure (Pierce and Turner, 1992; Mieczan, 2010, 2012; Wilkinson and Mitchell, 2010; Bielańska-Grajner *et al.*, 2011).

A raised bog is not a uniform ecosystem. Several zones can be distinguished within its area, differing with a number of physical, chemical and biological factors. The dominant area of a peatbogs is the open bog, mainly occupied by *Sphagnum* and other peat-forming vegetation. In the case of many peatbogs, the open bog is surrounded by forest, and more specifically a forest catchment, *i.e.*, an area of accumulation of all types of allochthonic materials. A raised bog also includes a zone separating the two areas. It is the laag area, *i.e.*, a transitional zone between the ecosystem of the open peatbogs and the peatbogs catchment. The investigated area is generally distinguished by occurrence of nitrophilous vegetation, *Cladietum marisci* and *Salix* shrubs (Herbichowa and Potocka, 2004). So far, studies concerning physical and chemical water parameters in the agricultural catchment – laag system were conducted only on the peatland at Lake Głębokie in the Mazurian Lakeland (Kruk, 2003). Due to a clear differentiation of chemical and biological conditions of the water in the horizontal arrangement, it seems that a similar differentiation should be expected in the case of testate amoebae, ciliates and rotifers. On the other hand, there are hardly any data concerning the horizontal distribution of protozoa and rotifers in interstitial waters. As the laag zone is recognised as an ecotone (the contact zone between two different ecosystems – in this case between pine forest and peatland), it was assumed that it should show significant differences between physical and chemical water parameters from adjacent habitats, and be distinguished by high species richness of protozoa and rotifers, including occurrence of species typical of the zone. According to di Castri *et al.* (1988), ecotones are transitional zones between relatively homogenous areas or patches and characterized by high structural and spatial diversity. They are zones in which environmental gradients are steepened, where rates of change in ecological patterns and processes are increased relatively to the surrounding.

The primary objectives of this paper were: (i) to determine selected physical and chemical water parameters in the transect: pine forest catchment – laag – open peatbog; (ii) to analyse the qualitative and quantitative structure of protozoa and rotifers in the horizontal forest catchment – laag – peatbog; (iii) to determine whether the laag waters differ in hydrochemical and microbiological terms from the waters of the forest catchment and the central part of the peatbog.

## Material and methods

### Study site

The study was performed in peatbog Durne Bagno located in the western part of the Polesie Lubelskie

(Eastern Poland, 51°N, 23°E). Its borders encompass the most precious parts of Poleski National Park, including lakes and floodplains, as well as swamps and peatlands, which survived until now in a relatively unaltered shape. It is one of the most natural region of Poland, which was not covered by the last glaciation. The Durne Bagno is peatbog of continental type with hummock-hollow structure. It occupies the clearly distinguishable oval-shaped depression in sandy deposits. The western part of the depression is rather shallow and its eastern part reaches the depth of 7–8.5 m (Bałaga, 2007). The monthly average air temperatures of January and July are –4.1 and 17.9 °C, respectively, and the average annual total rainfall is 551 mm. The first sampling area (pine forest) was characterized by the presence of *Pinus sylvestris* (L.), *Molinia coerulea* (L.) and *Calamagrostis epigeios* (L.) The second sampling area (laag) is a contact zone between forest and open peatland with mixed vegetation: *C. marisci* (All.), *Carex gracilis* Curt., *Sphagnum angustifolium* (C.C.O. Jensen ex Russow), *Sphagnum cuspidatum* Ehrh. ex Hoffm. and *Phragmites australis* (Cav. Trin. ex Steud). Currently, the open peatbog (third sampling area) is overgrown by sparse pine-birch forest, with pine predominant in the central, highest part. The proportion of birch is higher to the marginal belt of peatbog. The vegetation is dominated by graminoids such as *Eriophorum vaginatum* (L.), *Carex acutiformis* Ehrhart., *C. gracilis* Curt. and *S. angustifolium* (C.C.O. Jensen ex Russow), *S. cuspidatum* Ehrh. ex Hoffm., *Sphagnum flexuosum* Dozy & Molk., *Sphagnum magellanicum* Bird. and *Polytrichum* sp.

### Microbial communities sampling and identification

Microbial communities were examined in a transect including: (1) pine forest (site located 5 m from the laag/forest contact zone – PF), (2) laag (LG), (3) open peatbog (the centre of the peatland – OP) (Fig. 1). The samples were taken once a month from April to November 2007–2008. Collected data were presented in three seasons: spring (April, May and June), summer (July, August) and autumn (September, October and November). Mean values per season were presented in results due to the lack of significant differences between studied months.

During each sampling occasion three samples were collected from each site (peatbog, laag and pine forest). At each of the sites, free water (water between bryophytes on the surface) and interstitial water were sampled by means of piezometric wells placed to a depth of 1 m. Water collected in the piezometric wells during 2–4 min was then sampled by means of a syringe equipped with a rubber tube, and poured into plastic containers with a capacity of 100 mL. Next, the samples were preserved with Lugol's iodine, and stored in dark at a temperature of 4 °C. The abundance of testate amoebae, ciliates and rotifers and their community composition were determined using the Utermöhl's method. For rotifers 2 L samples were filtered through plankton net of 10 µm mesh size. Protozoa

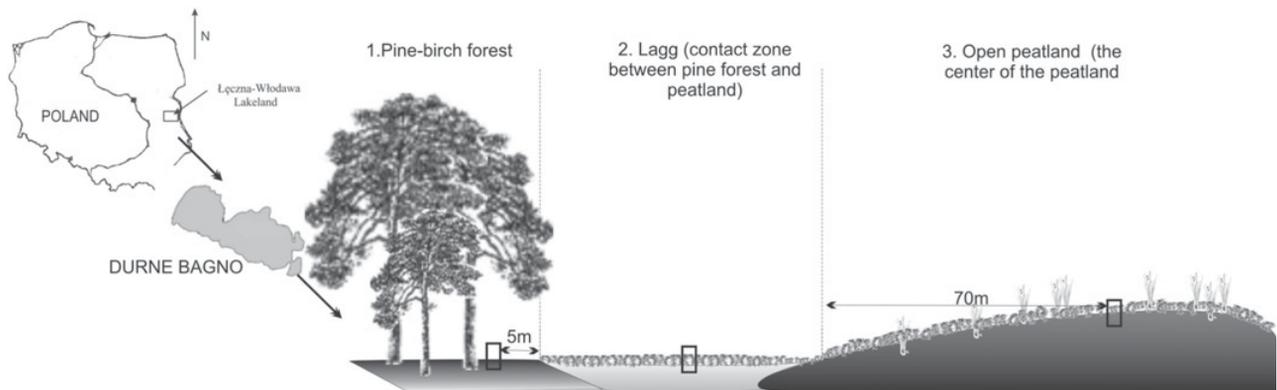


Fig. 1. Location of the sampling point.

(testate amoebae and ciliates) samples (whole sample = 500 mL) were sedimented for 24 h in cylinder, closed with parafilm, then the upper layer was gently removed. To determine the density, three samples were preserved with Logol's solution. Observation of live samples was used for the taxonomic and trophic identification. Ciliates are highly perishable, and the type of motility is a species-specific feature; for this reason, species determination and measurements were carried out on live material immediately after return to the laboratory and after silver impregnation (Augustin *et al.*, 1984). Morphological identifications were mainly based on works by Foissner and Berger (1996), Foissner *et al.* (1999), Charman *et al.* (2000) and Clarke (2003).

### Abiotic variables

Once a month, the water samples (volume of 500 mL) for chemical analyses were taken. Temperature, conductivity, pH and dissolved oxygen (DO) were determined *in situ* with a multiparametric probe, total organic carbon (TOC) was determined using the spectrophotometer PASTEL UV and the remaining factors (TP – total phosphorus, P-PO<sub>4</sub>, TN – total nitrate, NH<sub>4</sub>, N-NO<sub>3</sub>) were analysed in the laboratory (Golterman, 1969).

### Data analyses

Diversity analysis [Shannon Wiener diversity index (log<sub>10</sub>-based)] was performed using the Multivariate Statistical Package – MVSP (Kovach Computing Services, 2002).

The differences between physical and chemical water parameters among studied habitats were analysed by means of one-way ANOVA. Tukey's multiple range test (at  $P < 0.05$ ) was used to compare means when significant differences were found. The analysis was performed using PAST software. Spearman's rank correlation coefficients ( $R$ ) were calculated for pairs of environmental variables to recognize which of these variables are inter-correlated.

Detrended correspondence analysis (DCA) was used to measure and illustrate the variability gradients indicated

by testate amoebae, ciliates and rotifers. Variables whose level of significance exceeded 0.05 were plotted passively on the diagrams. As the length of the gradient was  $> 2$  standard deviations, canonical correspondence analysis (CCA) was used to explore the relationships between the abundance of taxonomic groups and environmental variables (ter Braak and Šmilauer, 2002). Automatic forward selection of environmental variables, Monte Carlo permutation test (999 permutations) was used to determine the most important variables (Lepš and Šmilauer, 2003). Variables whose level of significance exceeded 0.05 were plotted passively on the diagrams. On the resultant plot, the arrows representing the physico-chemical variables indicate the direction of maximum change of that variable, and the length of each arrow is proportional to the rate of change. The proportion of variance explained by environmental variables was quantified using variance partitioning. The analysis was repeated in all sampling areas and separately for each of studied habitat. The ordination analyses were performed by means of CANOCO 4.5 for Windows.

## Results

### Abiotic variables

The water level was highly variable among sites and samples, ranging 4–25 cm above the surface (ANOVA,  $F = 27.2$ ,  $P = 0.001$ ). Statistically significant differences between the investigated sites (pine forest, lagg and open peatbog) were found in pH, conductivity, nutrients and TOC (ANOVA,  $F = 26.22$ – $29.71$ ,  $P = 0.001$ ). Water pH fluctuated from 2.9 in open peatbog to 7.1 in pine forest. In turn, conductivity was significantly differentiated, attaining from  $32 \pm 6.1 \mu\text{S}\cdot\text{cm}^{-1}$  in open peatbog to  $487 \pm 82.7 \mu\text{S}\cdot\text{cm}^{-1}$  in pine forest. The highest conductivity occurred in spring and summer, but was decidedly lower in autumn. In all sites examined, the water temperature reached the highest value in summer ( $11.0$ – $17.0 \pm 2.9^\circ\text{C}$ ), and decreased in autumn ( $4.0$ – $11.0 \pm 1.9^\circ\text{C}$ ). The highest concentration of TOC occurred in the lagg ( $> 77 \pm 8 \text{mg}\cdot\text{C}\cdot\text{L}^{-1}$ , mean from three sites) and the lowest

**Table 1.** Physical and chemical characteristics of water in investigated peatbog (average values,  $\pm$  SE, for the period 2007–2008),  $n = 48$ .

Parameters/micro-habitat	Pine forest			Lagg			Open peatland		
	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn
Temp. (°C)	6.1 $\pm$ 1.0	11.0 $\pm$ 1.2	4.0 $\pm$ 0.7	9.1 $\pm$ 1.5	17.0 $\pm$ 2.9	9.0 $\pm$ 1.5	7.6 $\pm$ 1.3	17.0 $\pm$ 2.9	11.0 $\pm$ 1.9
pH	7.11 $\pm$ 1.2	5.8 $\pm$ 1.1	6.5 $\pm$ 0.9	4.77 $\pm$ 0.8	2.64 $\pm$ 0.6	4.1 $\pm$ 0.7	4.76 $\pm$ 0.8	2.9 $\pm$ 0.5	4.0 $\pm$ 0.6
Conductivity ( $\mu$ S.cm)	487 $\pm$ 82.7	154 $\pm$ 26.2	111 $\pm$ 19.9	145 $\pm$ 25.9	157 $\pm$ 26.6	97 $\pm$ 16.4	44 $\pm$ 7.5	49 $\pm$ 8.8	32 $\pm$ 6.1
O <sub>2</sub> (mgO <sub>2</sub> .L <sup>-1</sup> )	4.8 $\pm$ 0.8	7.3 $\pm$ 1.3	7.0 $\pm$ 1.2	9.7 $\pm$ 1.7	7.1 $\pm$ 1.3	8.2 $\pm$ 1.7	8.3 $\pm$ 1.6	8.4 $\pm$ 1.9	8.3 $\pm$ 1.6
TOC (mgC.L <sup>-1</sup> )	21 $\pm$ 3.8	23 $\pm$ 4.4	19 $\pm$ 3.4	120 $\pm$ 25.2	55 $\pm$ 9.4	58 $\pm$ 8.4	94 $\pm$ 16.7	69 $\pm$ 13.1	30 $\pm$ 5.1
TP (mgP.L <sup>-1</sup> )	0.336 $\pm$ 0.06	0.567 $\pm$ 0.09	0.345 $\pm$ 0.06	0.365 $\pm$ 0.06	0.321 $\pm$ 0.05	0.368 $\pm$ 0.07	0.33 $\pm$ 0.04	0.331 $\pm$ 0.03	0.332 $\pm$ 0.06
PO <sub>4</sub> (mg PO <sub>4</sub> .L <sup>-1</sup> )	0.34 $\pm$ 0.07	0.33 $\pm$ 0.06	0.348 $\pm$ 0.06	0.321 $\pm$ 0.04	0.203 $\pm$ 0.03	0.323 $\pm$ 0.05	0.224 $\pm$ 0.04	0.211 $\pm$ 0.04	0.224 $\pm$ 0.03
N-NO <sub>3</sub> (mg NO <sub>3</sub> .L <sup>-1</sup> )	0.128 $\pm$ 0.02	0.121 $\pm$ 0.02	0.127 $\pm$ 0.03	0.267 $\pm$ 0.06	0.26 $\pm$ 0.05	0.271 $\pm$ 0.06	0.124 $\pm$ 0.03	0.111 $\pm$ 0.02	0.128 $\pm$ 0.02
N-NH <sub>4</sub> (mgNH <sub>4</sub> .L <sup>-1</sup> )	1.11 $\pm$ 0.23	1.21 $\pm$ 0.27	2.211 $\pm$ 0.51	1.232 $\pm$ 0.28	1.13 $\pm$ 0.26	1.23 $\pm$ 0.24	1.123 $\pm$ 0.23	1.04 $\pm$ 0.22	1.112 $\pm$ 0.23
WL (cm)	4 $\pm$ 0.76	3 $\pm$ 0.57	4 $\pm$ 0.72	25 $\pm$ 5.2	9 $\pm$ 1.9	11 $\pm$ 2.1	11 $\pm$ 2.5	6 $\pm$ 1.3	11 $\pm$ 2.3

concentration in pine forest ( $21 \pm 6$  mgC.L<sup>-1</sup>). The concentration of total organic carbon fluctuated between  $19 \pm 3.4$  mgC.L<sup>-1</sup> in autumn and  $120 \pm 25.2$  mgC.L<sup>-1</sup> in spring. Nutrients reached the highest values in the LG, and were the highest during the spring and autumn periods, and considerably lower in summer. Only PF had a higher concentration of nutrients in summer (Table 1). Only some pairs of environmental variables are strongly and significantly correlated (Table 2). Most of significant correlations were negative. The highest significant negative values of correlation coefficient were calculated for pH and temperature ( $r = -0.77$ ) and for dissolved oxygen and conductivity ( $r = -0.69$ ). The strongest positive correlation ( $r = 0.75$ ) showed pH with P-PO<sub>4</sub> ( $r = 0.75$ ), dissolved oxygen with TOC ( $r = 0.74$ ), WL with TOC ( $r = 0.67$ ) and WL with dissolved oxygen ( $r = 0.65$ ). In general, the correlation pattern among environmental variables fits well to the horizontal distribution of studied microhabitats. In scatter plots, pine forest sites are located at the highest end of pH, P-PO<sub>4</sub> and conductivity gradients; lagg sites are situated on the highest end of WL gradient and peatbog sites are in the middle of the gradient.

### Microbial communities – general results

A total of 44 testate amoebae taxa, 35 ciliate taxa and 75 of rotifers taxa occurred in the studied area. Species richness of protozoa and rotifers showed horizontal diversity. The highest numbers of taxa occurred in the LG (31, 13 and 45 taxa, respectively) and became much lower in the PF where merely 11 testate amoebae taxa, 5 ciliate taxa and 6 rotifers taxa were identified. The highest diversity was measured in the LG (Shannon–Wiener diversity index  $H = 2.2–2.5$ ), and the lowest diversity was observed in the PF ( $H = 0.75–0.83$ ) and a Gini-evenness measure of 0.60 in the PF, 0.61 in the OP and 0.78 in the LG. Micro-organisms densities were shown to be significantly different with site but not with time of year (Table 3). The numbers of testate amoebae and ciliates varied between 1.1 and  $5.3 \pm 0.6 \times 10^2$  cells.mL<sup>-1</sup> and between 18 and  $87 \pm 11$  cells.mL<sup>-1</sup>, respectively, with the highest mean numbers in the LG and the lowest in the PF. In all studied sites, the maximal abundance of testate amoebae was noted in spring (May) (from  $2.1 \pm 0.3 \times 10^2$  cells.mL<sup>-1</sup> in the PF to  $5.3 \pm 1.1 \times 10^2$  cells.mL<sup>-1</sup> in the LG) and the lowest in autumn; however, the differences were not significant. The highest abundances of ciliate communities were noted in spring and autumn (from  $46 \pm 12$  cells.mL<sup>-1</sup> in the PF to  $87 \pm 21$  cells.mL<sup>-1</sup> in the LG), whereas in summer we observed a remarkable decrease in ciliate abundance (from  $6 \pm 2$  cells.mL<sup>-1</sup> in the PF to  $27 \pm 6$  cells.mL<sup>-1</sup> in the LG). The numbers of rotifers ranged from  $111 \pm 16$  ind.mL<sup>-1</sup> in LG to  $65 \pm 11$  ind.mL<sup>-1</sup> in PF. In all the examined micro-habitats, the highest abundance of these micro-organisms occurred in summer and late autumn (from  $45 \pm 8$  cells.mL<sup>-1</sup> in the PF to  $111 \pm 13$  cells.mL<sup>-1</sup> in the LG), while the lowest values were recorded in late spring ( $14 \pm 4$  cells.mL<sup>-1</sup>). Distinct

**Table 2.** Non-parametric correlation matrix of measured environmental variables in pine forest-lagg-open peatbog transect.

	Temp.	pH	Conductivity	O <sub>2</sub>	TOC	TP	P-PO <sub>4</sub>	N-NO <sub>3</sub>	N-NH <sub>4</sub>	WL
Temp.	1	−0.77**	−0.29	0.38	0.40*	−0.35	−0.52**	0.16	−0.24	0.08
pH	−0.77**	1	0.33	−0.38*	−0.53**	0.47*	0.75**	−0.22	0.20	−0.39*
Conductivity	−0.29	0.34	1	−0.69**	−0.59**	0.26	0.42*	0.19	0.34	−0.26
O <sub>2</sub>	0.38	−0.38*	−0.69**	1	0.74**	−0.18	−0.21	0.21	−0.19	0.65**
TOC	0.40*	−0.53**	−0.59**	0.74**	1	−0.27	−0.37	0.37	−0.07	0.67**
TP	−0.35	0.47*	0.26	−0.18	−0.27	1	0.33	−0.05	0.52**	−0.18
P-PO <sub>4</sub>	−0.52**	0.75**	0.42**	−0.21	−0.37	0.33	1	0.27	0.35	−0.14
N-NO <sub>3</sub>	0.16	−0.22	0.19	0.21	0.37	−0.05	0.27	1	0.22	0.61**
N-NH <sub>4</sub>	−0.24	0.20	0.34	−0.19	−0.07	0.52**	0.35	0.22	1	0.01
WL	0.08	−0.39*	−0.26	0.65**	0.67**	−0.18	−0.14	0.61**	0.01	1

\*Correlations significant at the level  $P < 0.05$ ; \*\*Correlations significant at the level  $P < 0.01$ .

**Table 3.** Results of main effects ANOVA on density of testate amoebae, ciliates and rotifers, testing for the effect of the time (season) and the site (horizontal distribution).

	df	SS	MS	F	P
Density of testate amoebae					
Intercept	1	90.02	90.02	122.28	<b>&lt;0.001</b>
Site (Si)	2	22.05	11.03	14.97	<b>&lt;0.001</b>
Season (Se)	8	0.44	0.54	7.43	0.065
Si × Se	2	1.18	7.36	16.37	0.073
Density of ciliates					
Intercept	1	28.22	28.22	78.16	<b>&lt;0.001</b>
Site (Si)	2	5.92	2.95	50.95	<b>&lt;0.001</b>
Season (Se)	8	0.81	0.11	8.52	0.090
Si × Se	2	0.57	3.31	8.19	<b>0.037</b>
Density of rotifers					
Intercept	1	53.74	53.74	27.85	<b>&lt;0.001</b>
Site (Si)	2	17.76	19.32	5.81	<b>&lt;0.001</b>
Season (Se)	8	5.76	7.21	3.52	0.091
Si × Se	2	3.66	1.53	4.62	0.087

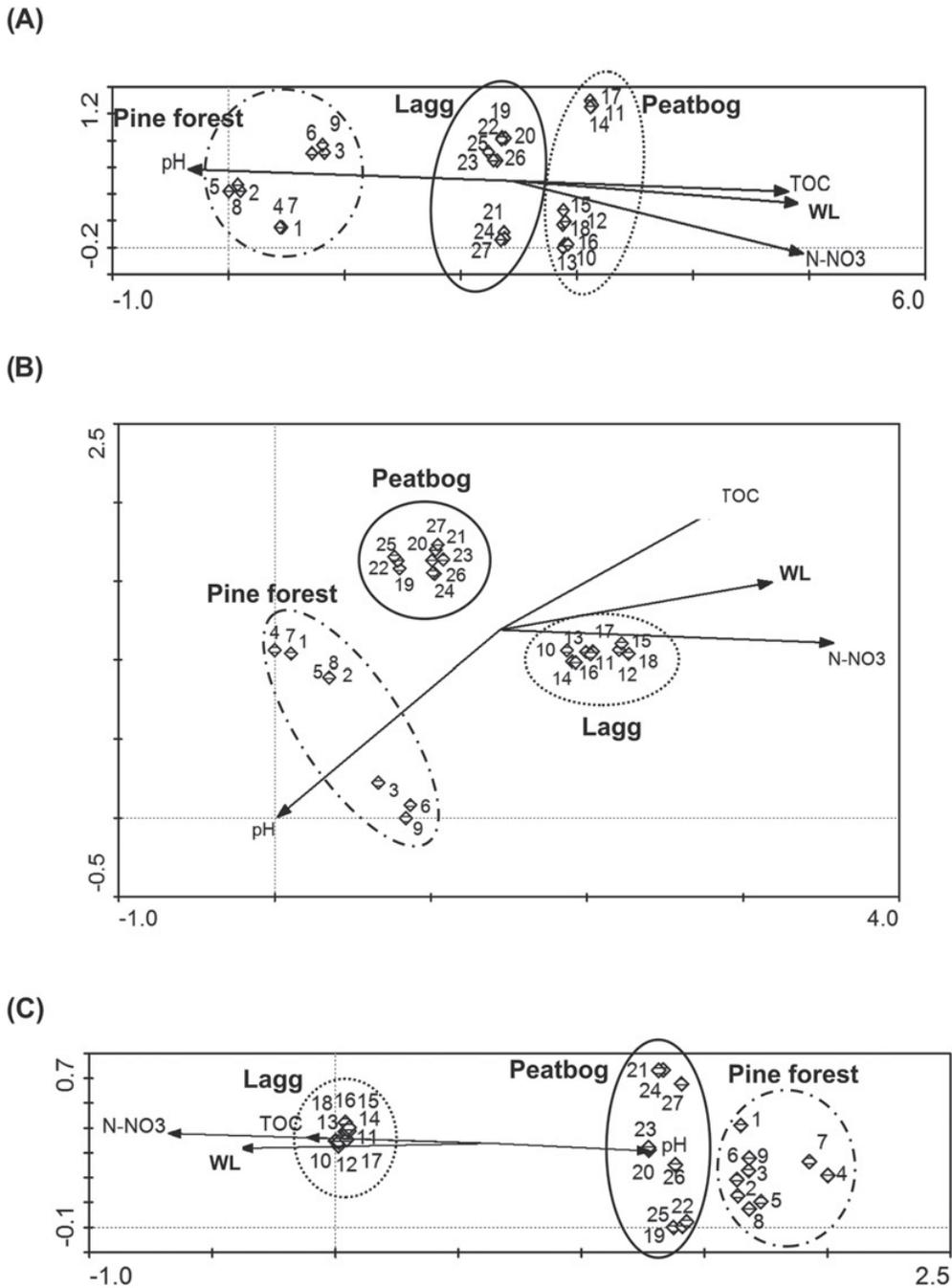
The significance of bold letters: \* significant at the level  $P < 0.05$ , \*\*significant at the level  $P < 0.01$ .

horizontal differences were noted in the domination structure of testate amoebae. The species distribution pattern also showed a higher variation in acid habitats (LG and OP), from wet assemblages (LG) with *Hyalosphenia papilio* to *Assulina muscorum* assemblages from drier microhabitats (PF). In the PF zone, only one species of testate amoeba typical of the zone occurred, namely *Diffugia leidyi*. In the LG, much more exclusive species occurred. They included: *Cryptodiffugia oviformis*, *Diffugia globulosa*, *Euglypha rotunda*, *Euglypha strigosa*, *Nebela collaris*, *Nebela flabellulum*, *Placocista spinosa* type, and *Trigonopyxis arcula* type. In the OP, no typical species were recorded. Also, the community composition of ciliates varied greatly from PF to OP. The most abundant species occurring in an environment with a very low pH (LG and OP) were *Colpidium colpoda* and *Chilodonella uncinata*, while *Euplotes* sp. was dominant in PF. Among ciliates, exclusive (typical) species for the PF were: *C. uncinata*, *Coleps spetai*, *Vorticella companula* and *Euplotes* sp. In the LG, a significant number of typical taxa were determined, not occurring at other sites. Those were: *Chlamydonella* sp., *Didinium* sp., *Lacrymaria olor*, *Paradileptus elephantinus*, *S. sensu lato*, *Paramecium putrinum*, *Aspidisca cicada*, *Oxytricha* sp., *Amphileptus claparedii*, *Amphileptus pleurosigma* and *Kahlilembus*

*attenuotus*. In the case of OP, only one exclusive species occurred, namely *Cyrtohymena muscorum*. The dominance structure of rotifers was very similar in all studied sites. Bdelloids were dominants and their percentage contribution to the rotifer communities varied from 60% to 80%. Additionally, in LG zone *Lecane lunaris* accounted for over 10% of total catch. In the investigated zones, no typical rotifers species were recorded.

### Unconstrained ordination (DCA)

DCA was generated for communities of testate amoebae, ciliates and rotifers and underlying environmental gradients (Figs. 2(A)–(C)). Biplots of DCA showed distribution of samples in ordination space of Axis 1 and Axis 2. Eigenvalue of ordination axes indicate that environmental gradient represented by Axis 1 the most strongly differentiated abundances of testate amoebae, ciliates and rotifers between studied habitats. Eigenvalue of Axis 1 exceeds 0.5 and amounted 0.769 for testate amoebae, 0.648 for ciliates and 0.523 for rotifers. In the biplots for ciliates, samples collected in pine forest are situated on the left side in ordination space; samples collected in lagg are situated on the right side of the diagram. In the biplots for testate



**Fig. 2.** Biplots of DCA for environmental variables and samples of (A) testate amoebae, (B) ciliates and (C) rotifers collected in three habitats. Samples collected in studied habitats are marked with an Arabic numeral: 1–9, Pine forest; 10–18, Lagg; 19–27, Peatbog.

amoebae, samples collected in the lagg are situated in the middle on the first ordination axis; samples collected in pine forest are situated on the left side in ordination space. The group of samples collected in peatbog lying between them. On the biplot for rotifers, the group of pine forest samples is placed on the right side of the ordination space, while samples from lagg are grouped at the left side of the diagram. The distribution of samples in ordination space led to conclude that studied habitats are distributed along the falling gradient of pH and rising gradient of TOC, WTD and N-NO<sub>3</sub>. Thus, the rotifers and ciliates displayed

the same principal gradient (PF-OP-LG) contrary to testate amoebae (PF-L-OP).

**Constrained ordination (CCA) – environmental gradient**

*Testate amoebae*

The CCA for spatial distribution of testate amoebae showed that all environmental variables together

**Table 4.** Results of the forward selection of environmental variables (Monte Carlo permutation test in CCA,  $P < 0.05$  are statistically significant and given in bold) for three studied group of organisms: testate amoebae, ciliates and rotifers.

Variable	Testate amoebae			Ciliates			Rotifers		
	$\lambda$	$F$	$P$	$\lambda$	$F$	$P$	$\lambda$	$F$	$P$
Temperature	0.02	0.52	0.806	0.01	0.60	0.756	0.01	1.14	0.362
pH	0.23	7.24	<b>0.002</b>	0.03	1.38	0.208	0.02	2.95	<b>0.012</b>
Conductivity	0.08	3.83	<b>0.002</b>	0.11	4.29	<b>0.004</b>	0.04	3.92	<b>0.004</b>
O <sub>2</sub>	0.01	0.36	0.910	0.01	0.73	0.636	0.01	1.31	0.258
WTD	0.20	7.83	<b>0.002</b>	0.04	1.91	0.084	0.04	4.34	<b>0.006</b>
TOC	0.015	0.55	0.776	0.01	0.38	0.908	0.01	1.56	0.152
N-NH <sub>4</sub>	0.01	0.87	0.524	0.01	0.31	0.942	0.01	0.66	0.732
N-NO <sub>3</sub>	0.02	0.39	0.898	0.21	7.33	<b>0.002</b>	0.24	18.56	<b>0.002</b>
TP	0.08	3.73	<b>0.004</b>	0.09	3.98	<b>0.002</b>	0.02	2.46	<b>0.016</b>
P-PO <sub>4</sub>	0.03	1.44	0.192	0.05	2.02	0.064	0.05	3.65	<b>0.006</b>

explained 65.3% of the total variance. However, Monte Carlo permutation test ( $P < 0.05$ ) showed the significance of WTD, conductivity, TP and pH in explaining the variability of testate amoebae in all habitats (Table 4). At the CCA biplots (Fig. 3(A)) samples are divided into three groups (habitats): pine forest, lagg and peatland. Axis 1 separated peatbog samples from lagg and pine forest. The species collected in pine forest (*Euglypha* sp., *Diffugia leidyi*, *N. flabellulum* and *N. collaris*) correspond with rising gradient of pH, TP and conductivity. Large group of species of testate amoebae (such as *Arcella catinus*, *Hyalosphenia elegans*, *Nebela bohémica*, *N. carinata*, *Nebela griseola*, *Nebela militaris*, *D. globulosa* and *E. strigosa*) are observed in habitats of higher water level (WTD) and correspond with lagg habitat. In the ordination biplot (Fig. 3(A)) species of testate amoebae (*Heleoptera petricola*, *Heleoptera sphagnii*, *Heleoptera rosea*, *Corythion dubium*, *Corythion-Trinema* type, *Cyclopyxis arcelloides*, *Euglypha ciliate* and *Euglypha compressa*) showed positive relation with rising gradient of TOC, O<sub>2</sub> and temperature and may correspond with peatland habitat (Fig. 3(B)).

#### Ciliates

The CCA showed that all environmental variables explained 60.8% of the total variance of ciliates in studied habitats. Only three variables (N-NO<sub>3</sub>, conductivity and TP) showed significant importance in Monte Carlo permutation test at  $P < 0.05$  (Table 4). Axis 1 correlate mostly with N-NO<sub>3</sub> and correspond with the group of species (*A. claparedii*, *A. pleurosigma*, *Codonella cratera*, *Paramecium* sp., *A. cicada* and *Didinium* sp.) commonly observed in lagg habitat. Axis 2 is mostly correlated with conductivity and TP. These variables may influence the presence of ciliate species: *C. uncinata*, *V. companula*, *Euplotes* sp. and correspond with pine forest habitat (Figs. 4(A) and (B)).

#### Rotifers

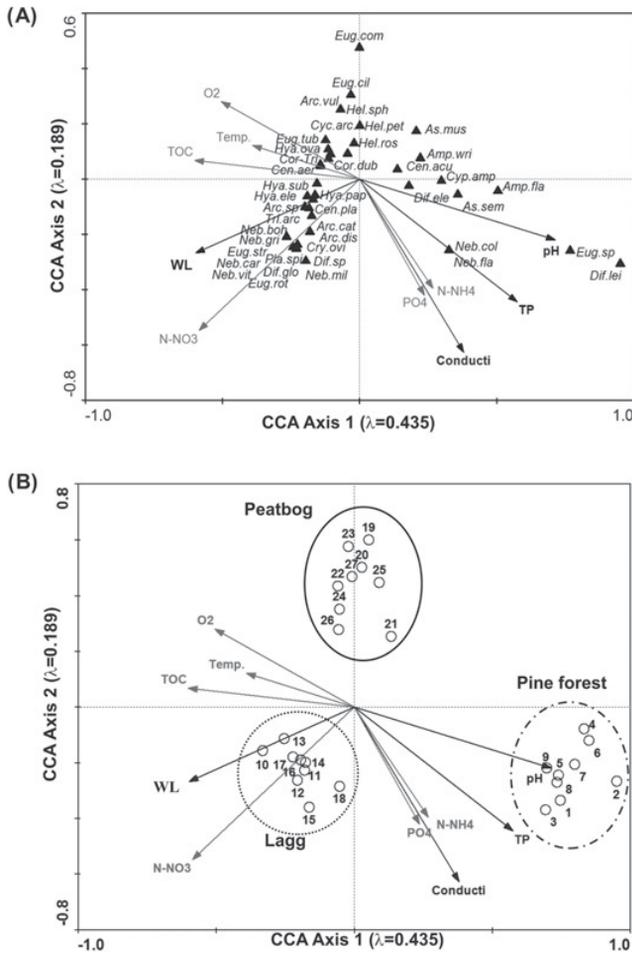
All environmental variables explained 78.4% of the total variability. Monte Carlo permutation test at  $P < 0.05$

showed the significance of six variables: pH, conductivity, WTD, TP, P-PO<sub>4</sub> and N-NO<sub>3</sub> in explaining the variability of rotifers in three studied habitats (Table 4). On the CCA biplots rotifers communities of studied habitats and species are visibly separated (Figs. 5(A) and (B)). Axis 1 correlates mostly with N-NO<sub>3</sub> and WTD. These environmental variables affect the abundance of rotifer species, *Lepadella* sp., *Keratella serrulata*, *Cohurella hindenburgi*, *Collotheca wiszniewski* and correspond with lagg habitat. Axis 2 is mostly correlated with conductivity, P-PO<sub>4</sub>, TP and pH. Two variables TP and pH showed the relation with rotifers species, *Lecane intrasinuata*, *Lecane flexilis*, *Lecane scutata* and *Rotaria sordida*, and may correspond with forest habitat.

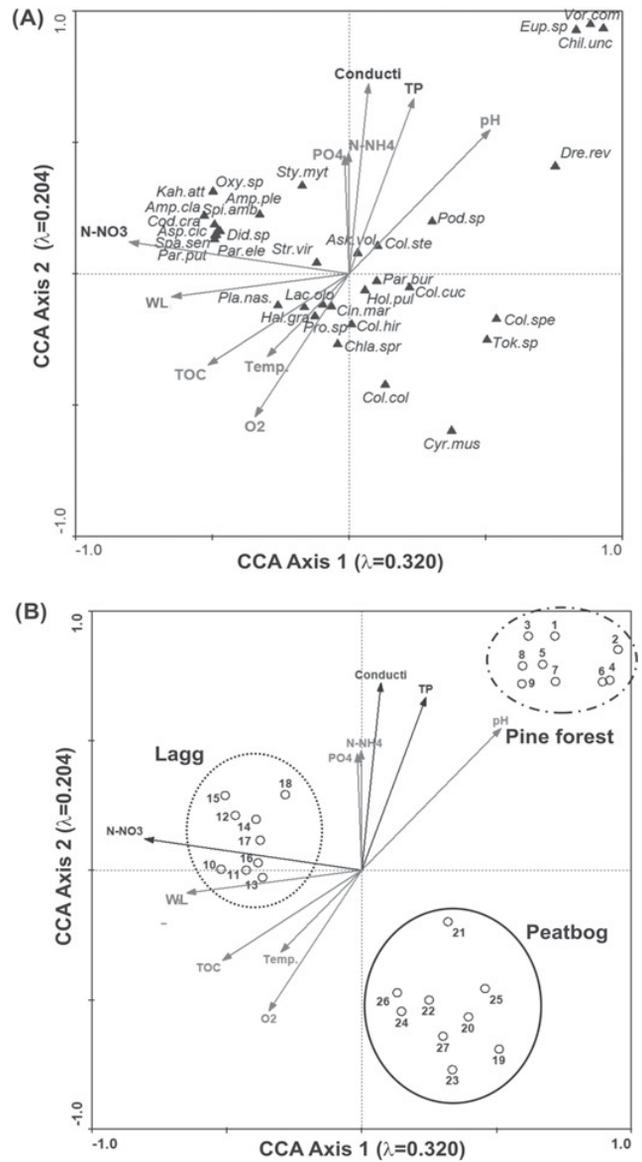
#### Seasonal variability in testate amoebae, ciliates and rotifers data

Analysis of testate amoebae, ciliates and rotifers data and environmental variables in all the studied habitats (CCA) revealed seasonal changes in species composition and environmental conditions (Figs. 6–8(A) and (B)). For pine forest habitat, the eigenvalue of first axis amounted 0.157 and for the second axis –0.103. These two axes captured 89.3% of the total variation of species data. The highest significant values of regression coefficients ( $P > 0.05$ ) showed conductivity and N-NO<sub>3</sub> along Axis 1 and pH and WL along Axis 2. Samples collected in studied seasons are clustered in three groups. Samples in April, July and October are clustered together; samples in June are grouped with samples in September and samples collected in May, August and November are clustered together (Fig. 6(A)). Ciliates, *Holosticha pullaster*, *V. companula* and *Podophyra* sp. were characteristic species in April, July and October (Fig. 6(B)). Testate amoebae, *H. petricola*, *H. rosea* and *H. sphagnii* and two ciliates species, *Coleps hirtus* and *C. spetai* were characteristic species in September. Rotifer species, *Lepadella patella* and ciliate *Strombidium viride* were characteristic species for samples collected in May and November.

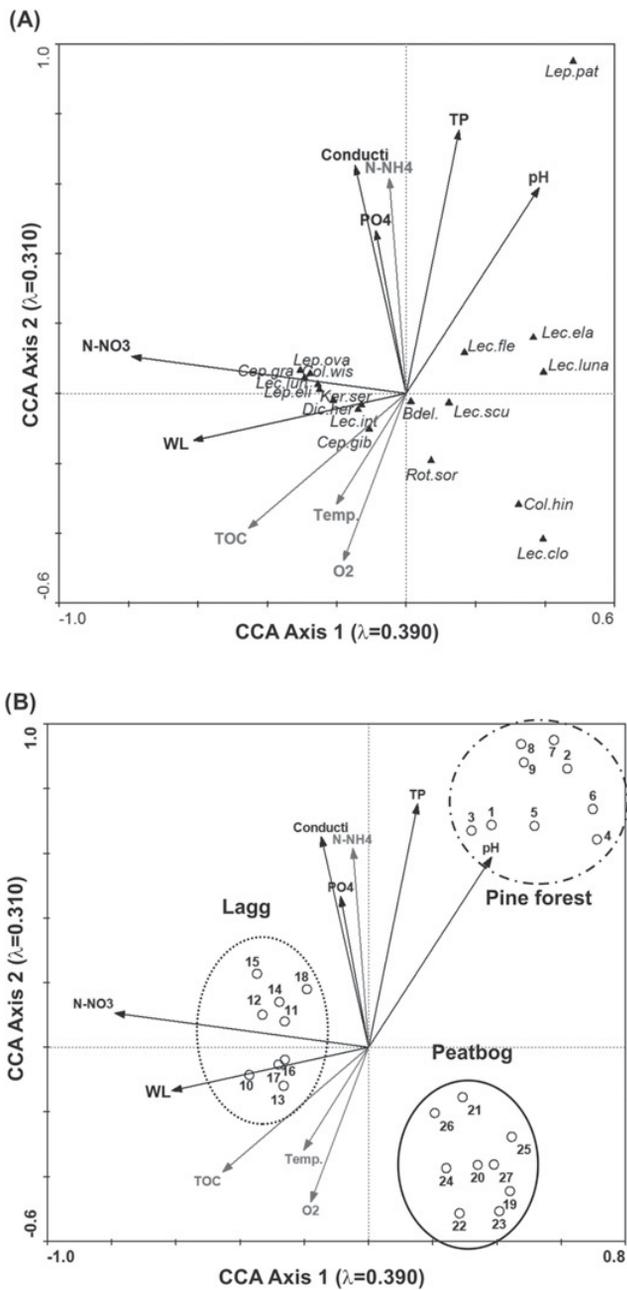
For lagg habitat, first and second axis explained 77.5% of total variability of species data. Eigenvalue of Axis 1



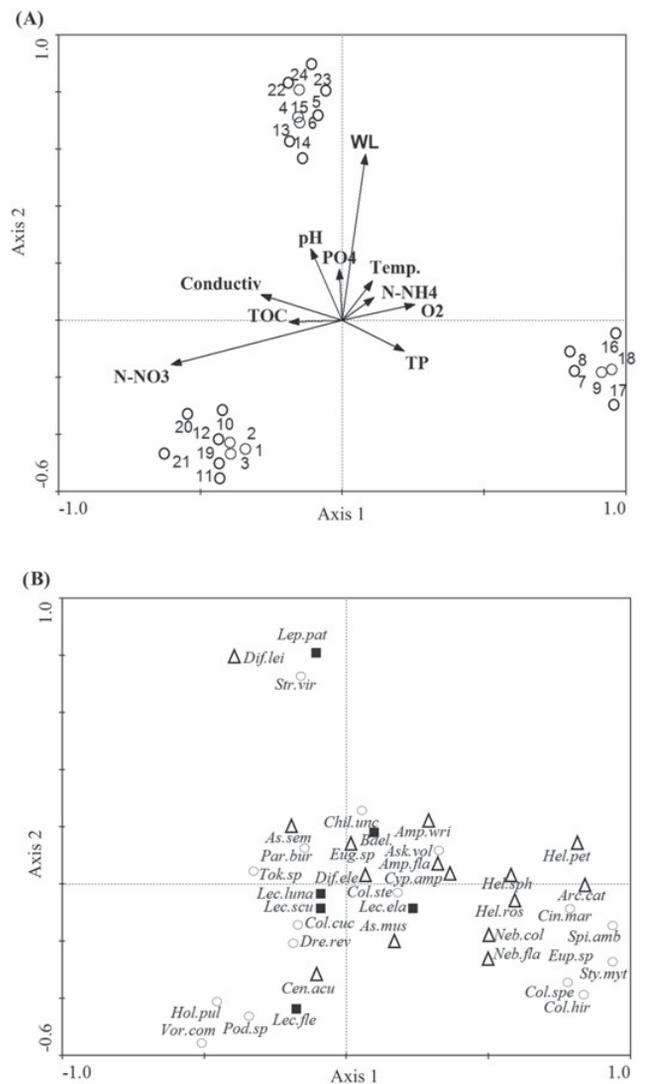
**Fig. 3.** Biplots of CCA of testate amoebae (A) species, (B) samples. Arrows marked as bold indicate significant parameters in Monte Carlo permutation test at  $P < 0.05$ . Samples collected in studied habitats are marked with an Arabic numeral: 1–9, Pine forest; 10–18, Lagg; 19–27, Peatbog. Species codes: Amp.fla, *Amphitrema flavum*; Amp.wri, *Amphitrema wrightianum*; Arc.cat, *Arcella catinus* type; Arc.dis, *Arcella disoides* type; Arc. sp, *Arcella* sp.; Arc. vul, *Arcella vulgaris*; Ass. mus, *Assulina muscorum*; Ass. sem, *Assulina seminulum*; Cen.acu, *Centropyxis aculeata* type; Cen.aer, *Centropyxis aerophila*; Cen.pla, *Centropyxis platystoma* type; Cor.dub, *Corythion dubioides*; Cor.Tri, *Corythion-Trinema* type; Cry.ovi, *Cryptodiffugia oviformis*; Cyc.arc, *Cyclopyxis arcelloides* type; Cyp.amp, *Cyphoderia ampulla*; Dif.ele, *Diffugia elegans*; Dif.glo, *Diffugia globulosa*; Dif.lei, *Diffugia leidy*; Dif.sp, *Diffugia* sp.; Eug.cil, *Euglypha ciliata*; Eug.com, *Euglypha compressa*; Eug.rot, *Euglypha rotunda* type; Eug.sp, *Euglypha* sp.; Eug.str, *Euglypha strigosa*; Eug.tub, *Euglypha tuberculata* type; Hel.pet, *Heleoptera petricola*; Hel.ros, *Heleoptera rosea*; Hel.sph, *Heleoptera sphagnii*; Hya.ele, *Hyalosphenia elegans*; Hya.ova, *Hyalosphenia ovalis*; Hya.pap, *Hyalosphenia papilio*; Hya.sub, *Hyalosphenia subflava*; Neb.boh, *Nebela bohemica*; Neb.car, *Nebela carinata*; Neb.col, *Nebela collaris*; Neb fla, *Nebela flabellulum*; Neb.gri, *Nebela griseola* type; Neb.mil, *Nebela militaris*; Neb.vit, *Nebela vitrea* type; Pla.spi, *Placocista spinosa* type; Tri.arc, *Trigonopyxis arcuata* type.



**Fig. 4.** Biplots of CCA of ciliates (A) species and (B) samples. Arrows marked as bold indicate significant parameters in Monte Carlo permutation test at  $P < 0.05$ . Samples collected in studied habitats are marked with an Arabic numeral: 1–9, Pine forest; 10–18, Lagg; 19–27, Peatbog. Species codes: Chil.unc, *Chilodonella uncinata*; Chla.spr, *Chlamydonella-spr*; Col.ste, *Colpoda steinii*; Col.cuc, *Colpoda cucullus*; Col.col, *Colpidium colpoda*; Ask.vol, *Askenasia volvox*; Did.sp, *Didinium* sp.; Lac.olo, *Lacrymaria olor*; Par.ele, *Paradileptus elephantinus*; Pla.nas, *Plagiopyla nasuta*; Spa.sen, *Spathidium sensu lato*; Spi-amb, *Spirostomum ambiguum*; Par.bur, *Paramecium bursaria*; Par.put, *Paramecium putrinum*; Cin.mar, *Cinetochilum margaritaceum*; Asp.cic, *Aspidisca cicada*; Eup.sp, *Euplotes* sp.; Hol.pul, *Holosticha pullaster*; Oxy.sp, *Oxytricha* sp.; Sty.myt, *Stylonychia mytilus-Komplex*; Cod.cra, *Codonella cratera*; Hal.gra, *Halteria gradinella*; Str.vir, *Strombidium viride*; Vor.com, *Vorticella companula*; Amp.cla, *Amphileptus claparedii*; Amp.ple, *Amphileptus pleurosigma*; Col.hia, *Coleps hirtus*; Col.spe, *Coleps spetai*; Pro.sp, *Prorodon* sp.; Dre.rez, *Drepanomonas rezoluta*; Tok.sp, *Tokophrya* sp.; Pod.sp, *Podophrya* sp.; Cry.mus, *Cyrtohymena muscorum*; Kah.att, *Kahlilembus attenuatus*.

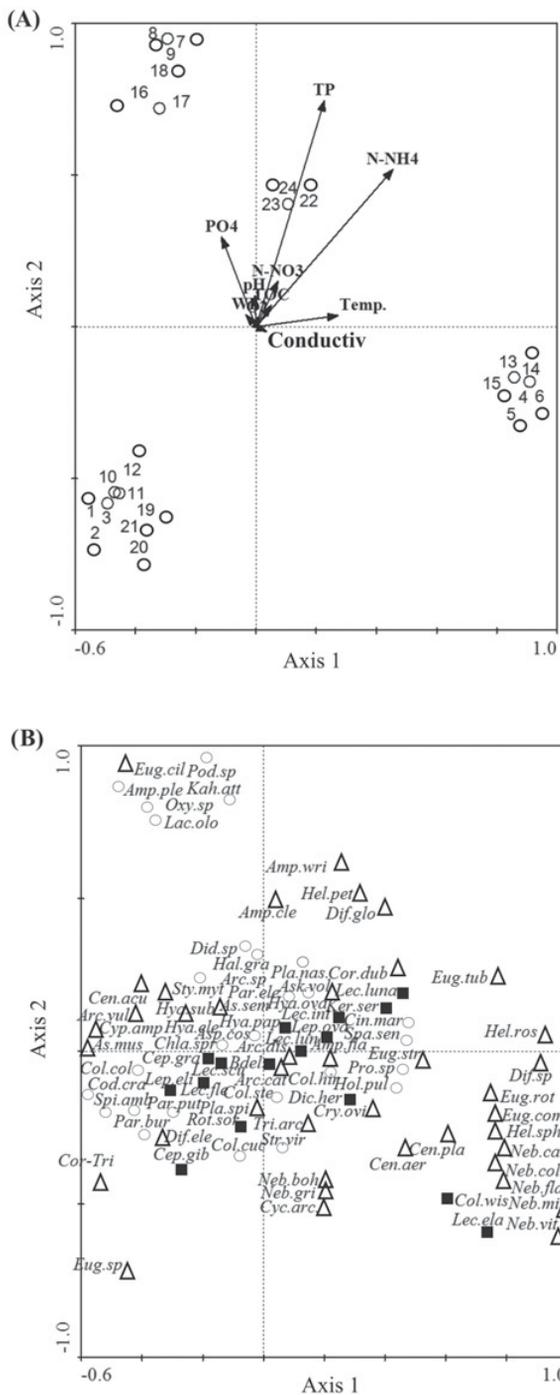


**Fig. 5.** Biplots of CCA of rotifers (A) species and (B) samples. Arrows marked bold indicate significant parameters in Monte Carlo permutation test at  $P < 0.05$ . Samples collected in studied habitats are marked with an Arabic numeral: 1–9, Pine forest; 10–18, Lagg; 19–27, Peatbog. Species codes: Bdel, *Bdelloida*; Cep.gib, *Cephalodella gibba*; Cep.gibb, *Cephalodella gibboides*; Cep.gra, *Cephalodella gracilis*; Col.wis, *Collotheca wiszniewski*; Col.hin, *Colurella hindenburgi*; Dic.her, *Dicranophorus hercules*; Ker.ser, *Keratella serrulata*; Lec.clo, *Lecane closterocerca*; Lec.ela, *Lecane elasma*; Lec.fle, *Lecane flexilis*; Lec.int, *Lecane intrasinuata*; Lec.lun, *Lecane luna*; Lec.luna, *Lecane lunaris*; Lec.scu, *Lecane scutata*; Lep.eli, *Lepadella eliptica*; Lep.ova, *Lepadella ovalis*; Lep.pat, *Lepadella patella*; Rot.sor, *Rotaria sordida*.



**Fig. 6.** Biplots of CCA of testate amoebae, ciliates and rotifers data in pine forest. (A) Seasons and environmental variables plot; (B) species and environmental variables plot. Environmental variables are the same as in part (A) but are not shown for clarity. Empty circles, ciliates; empty triangle, testate amoebae; filled square, rotifers. Samples collected in studied months are marked with an Arabic numeral: 1–3 April; 4–6 May; 7–9 June; 10–12 July; 13–15 August; 16–18 September; 19–21 October; 22–24 November. Abbreviations of species names are the same as in Figures 3–5.

amounted to 0.063 and for Axis 2, 0.035. Temperature and N-NH<sub>4</sub> showed the highest significant values of regression coefficients along Axis 1. Along Axis 2 the highest values of regression coefficient showed TP and N-NH<sub>4</sub>. In the ordination diagram, four groups of samples can be observed. Samples collected in May and August are clustered together. Samples in April are combined with July and October; samples in June and September are clustered together; samples in November are placed separately (Fig. 7(A)). Testate amoebae, *E. rotunda* and *E. compressa* are characteristic species for samples collected in May and



**Fig. 7.** Biplots of CCA of testate amoebae, ciliates and rotifers data in lagg. (A) Seasons and environmental variables plot; (B) species and environmental variables plot. Environmental variables are the same as in (A) but are not shown for clarity. Empty circles, ciliates; empty triangle, testate amoebae; filled square, rotifers. Samples collected in studied months are marked with an Arabic numeral: 1–3 April; 4–6 May; 7–9 June; 10–12 July; 13–15 August; 16–18 September; 19–21 October; 22–24 November. Abbreviations of species names are the same as in Figures 3–5.

August; *Euglypha* sp. and *Corythion-Trienema* type are typical for April and October samples. Testate amoebae *Amphitrema wrightianum* and *H. petricola* and ciliate *A. clapedii* are characteristic species for November samples. Ciliates, *A. pleurosigma*, *Oxytricha* sp. and *Podophyra* sp. are characteristic species for samples collected in June and September (Fig. 7(B)).

For open peatbog habitat, first and second ordination axis explained 84.2% of total species variability. Eigenvalue of Axis 1 amounted to 0.077 and Axis 2, 0.030. Regression coefficients showed the highest significant values for TOC and N-NH<sub>4</sub> along Axis 1 and for TP and O<sub>2</sub> along Axis 2. On the ordination plot, similarly to lagg habitat, samples collected in studied seasons are divided into four groups. Samples in April and July are clustered together; sample collected in May are grouped with samples in August; samples in June, September and November are clustered together and samples in October are put separately (Fig. 8(A)). Testate amoebae, *H. rosea* and *H. sphagnii* were characteristic for October samples. Rotifers, *K. serrulata*, *Lecane closterocerca*, *L. luna* and *Lepadella elliptica* were typical for samples collected in April and July. Testate amoebae, *Corythion-Trinema* type and *Hyalosphenia subflava*, ciliate *L. olor* and rotifer species *C. hindenburgi* were characteristic species for June (Fig. 8(B)).

The CCA on individual environmental variables revealed that the proportion of testate amoebae, ciliates and rotifers data explained by each of variable and the significance varied strongly among variables and among three studied habitats (Table 5). In the separate CCAs on “pine forest”, “lagg” and “open peatbog” samples, N-NH<sub>4</sub>, N-NO<sub>3</sub>, and WL were significant. The highest proportion of variance in pine forest habitat explained pH, TOC and N-NH<sub>4</sub>; in lagg, temperature and TP and in open peatbog – conductivity and N-NO<sub>3</sub>.

## Discussion

### Physical and chemical parameters

Physical and chemical water parameters showed high differentiation in investigated macro-habitats. The waters of the forest catchment area were distinguished by much higher pH values than those of the lagg and open peatbog zones. The results are significantly different than those presented by Kruk (2003), dealing with studies on a similar horizontal transect of a raised bog. The studies concerned the agricultural catchment-lagg-open bog transect. The author determined significant similarity of reaction of the waters of the agricultural catchment and the lagg area. Probably transported ions, namely Ca<sup>2+</sup> from the agriculture catchment are subjected to changes of water parameters. However, the periodical inflow of water from agriculture catchment alkalize this zone and, as a result, threaten the ecological system of bog, what is realized by increasing lagg area at the cost of bog area and by the decay of ombrotrophic



**Table 5.** Summary of CCA on testate amoebae, ciliates, rotifers and environmental variables from pine forest-lagg-open peatbog transect and significance of individual variables taken alone.

Variable	Overall CCA		Pine forest		Lagg		Open peatbog	
	%	<i>P</i> value	%	<i>P</i> value	%	<i>P</i> value	%	<i>P</i> value
Temp.	25.4	0.19	10.6	0.49	25.7	0.72	7.8	0.21
pH	4.7	0.31	11.1	0.34	9.9	0.16	12.7	0.07
Conductivity	1.4	0.28	2.8	0.55	6.6	0.33	40.1	0.54
O <sub>2</sub>	2.7	0.10	2.6	0.02	5.7	0.31	0.5	0.13
TOC	4.9	0.15	18.7	0.19	6.8	0.25	5.5	0.66
TP	2.5	0.16	2.2	0.65	21.4	0.32	3.1	0.58
PO <sub>4</sub>	0.2	0.07	6.3	0.34	10.7	0.26	3.6	0.78
N-NO <sub>3</sub>	7.6	0.14	10.6	0.01	6.8	0.01	29.5	0.01
N-NH <sub>4</sub>	0.1	0.03	11.1	0.01	4.3	0.01	4.5	0.01
WL	6.3	0.06	8.2	0.01	14.9	0.01	6.9	0.01

Likewise the study carried out by Warner *et al.* (2007) determined a seasonal change in testate amoebae assemblages. In the present study, the highest abundance occurred during spring and could have resulted from higher water level and acidity. During the spring period, those characteristic species of environments with considerable moisture were recorded in high numbers (*e.g.*, *H. elegans*, *H. sphagnii* and *Arcella vulgaris*). Spring or summer peaks have also been noted by Heal (1964) and Gilbert *et al.* (1998). Testate amoebae occurring in a given peatbog complex were mainly represented by: Arcellidae and Hyalosphenidae. Among species belonging to genus *Arcella*, the highest numbers were reached by *Arcella discooides*, and among genus *Hyalosphenia*, three species predominated: *H. elegans*, *Hyalosphenia ovalis* and *H. papilio*. The taxa are described as the so-called  $\alpha$ -hydrophiles, and predominate in habitats with significant humidity. A similar dominance structure was determined among others in peatlands of northern Russia (Bobrov *et al.*, 1999). In the forest catchment zone, only one species of testate amoeba typical of the zone occurred, namely *D. leidyi*. In the lagg zone, much more exclusive species occurred. They included: *C. oviformis*, *D. globulosa*, *Diffflugia* sp., *E. rotunda*, *E. strigosa*, *N. collaris*, *N. flabellulum*, *P. spinosa* and *T. arcula*. In the open peatbog zone, no typical species were recorded. The structure is characteristic for habitats of the type, and was earlier described by other researchers (Lamentowicz and Mitchell, 2005; Mieczan, 2009b).

The number of identified taxa and abundance of ciliates is comparable with other studies examining the surface water of peatbogs (Grolière, 1975, 1977, 1978; Mieczan, 2009a). The similarities between these surveys are not surprising, and support previous studies in illustrating the cosmopolitan distribution of many ciliates (Finlay, 1980). The three investigated sites had different ciliate assemblages with respect to species composition, total numbers, as well as distribution of particular dominating species. Similar to species richness, also numbers of ciliates were significantly higher in the lagg zone in comparison with other zones. The differentiation probably resulted from fertility of the microhabitat (contents of nutrients). Their concentrations indirectly condition

occurrence of protozoa by affecting abundance of bacteria. Bacteria constitute the main source of alimentation for ciliates in various types of hydrogenic ecosystems (Mieczan, 2007, 2009a). Maximum densities of ciliates have often been observed during mid or late spring (Mieczan, 2007). In addition to high late-spring densities, the concentrations of ciliates reached a peak in autumn. Spring and autumn peaks of ciliates coincided with the higher concentrations of total organic carbon and/or nutrients in three studied macro-habitats. In early spring and autumn, the sites were characterized by the presence of a considerable amount of decaying plant materials. Such a type of environment could enhance a massive development of bacteria and therefore bacterivorous ciliates. The highest contribution among ciliates was reached by species belonging to Colpodea, with *Colpoda steinii* occurring in the highest numbers. The species was observed both in mosses and in surface layers of soils (Foissner and Berger, 1996; Bamforth *et al.*, 2001). According to some authors (Foissner *et al.*, 1994), the species usually occurs in oligo- and beta-mesosaprobe environments. Grolière (1975, 1977, 1978) recorded the species on *Sphagnum* peatlands in France. Strüdel-Kypke and Schönborn (1999) observed its occurrence on glass plates exposed in dystrophic lakes in Germany. Among ciliates, exclusive (typical) species for the pine forest were: *C. uncinata*, *C. spetai*, *V. companula* and *Euplotes* sp. In the lagg zone, a significant number of typical taxa were determined, not occurring at other sites. Those were: *Chlamydonella* sp., *Didinium* sp., *L. olor*, *P. elephantinus*, *Spathidium sensu lato*, *P. putrinum*, *A. cicada*, *Oxytricha* sp., *A. cleparedii*, *A. pleurosigma* and *K. attenuotus*. In the case of the open peatland, only one exclusive species occurred, namely *C. muscorum*.

The species diversity and abundance of rotifers varied greatly from pine forest to open peatbog zone. This trend is probably related to differences in moisture content and pH, both of which are lower in open peatbog than lagg. The present study has revealed a remarkable relationship between the abundance of rotifers and ciliates. The decrease in abundance of ciliates in summer coincided with the peak of rotifer abundance. This may be due to both thermal preferences and conditions for feeding.

Among rotifers, in all the studied habitats, bdelloids were the most abundant. Most of the dominant species of rotifers were characterized by a broad range of pH tolerance. *L. lunaris* is known to be tolerant to a broad range of pH (Pejler and Berzins, 1993). Also *L. intrasinuata* is a characteristic species for peatlands, especially for microsites dominated by *Sphagnum* mosses (Bateman and Davis, 1980; Warner and Asada, 2006). Their dominance in aquatic ecosystems with a low pH has been reported by many researchers (Bateman and Davis, 1980; Petz, 1987; Warner and Asada, 2006). *Sphagnum* acidifies its habitat, so rotifer diversity is limited to the species that tolerate a low pH (Berzins and Pejler, 1987). Similar relationships were observed in different types of peatlands in eastern Poland (Bieleńska-Grajner *et al.*, 2011). Such a high tolerance may be associated with their mode of reproduction, *i.e.*, obligatory parthenogenesis (Berzins and Pejler, 1987), and – consequently – with its colonization strategy (Pejler and Berzins, 1993). Some authors suggest that the level of total dissolved carbon may be a significant factor affecting animal communities in peatbogs (Mieczan, 2009a). It also seems that concentrations of nutrients may significantly influence the communities of rotifers. In this study, we detected a significant positive correlation between rotifers abundance and the concentration of phosphates and nitrates. It seems that nutrients have an indirect influence on the abundance of protozoans and small metazoa, through the control of food abundance (mainly bacteria, fungi, or other protists). Data on relations between testate amoebae, ciliate and rotifer communities in *Sphagnum* peatlands and water chemistry parameters are, however, still insufficient.

The issues referring to mutual relations between the open peatland and its rim zone, *i.e.*, lagg, constitute a marginal subject in “peatbogs literature”. However, the role of the lagg zone in transformations of *Sphagnum* peatbogs deserves special attention due to its simultaneous buffer and transfer functions. The lagg zone of a raised bog can fulfil the function of an ecotone zone, distinguished by a significant increase in biodiversity, abundance and species specificity of micro-organisms. It can also be a place of very efficient matter and energy flow in a peatbog ecosystem.

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