

## Effects of organically enriched magnesite fertilizers on the soil ciliates of a spruce forest

E. Aescht<sup>1</sup> and W. Foissner<sup>2</sup>

<sup>1</sup> Oberösterreichisches Landesmuseum, Biologiezentrum, J.-W.-Klein-Str. 73, A-4040 Linz, Austria

<sup>2</sup> Universität Salzburg, Institut für Zoologie, Hellbrunnerstr. 34, A-5020 Salzburg, Austria

**Summary.** The effects of organically enriched magnesite fertilizers on the active soil ciliates of a declining spruce forest were investigated using a direct counting method. For revitalization 2000 kg ha<sup>-1</sup> biomag (= 90% magnesite and 10% dried fungal biomass) and 3000 kg ha<sup>-1</sup> bactusol (dried bacterial biomass) + 2000 kg ha<sup>-1</sup> biomag, respectively, were applied once in June 1987. Treatments were assigned in a completely randomized block design to 100 m<sup>2</sup> plots in an 80-y-old and a 40-y-old Norway spruce stand in Upper Austria; six replicates from the litter layer (0–3 cm) were investigated eight times during a 4-y-period. Fertilization caused a short-term increase in pH from 3 to 4.3; four years later, the pH differed by about 0.8 units from the control. None of the treatments substantially altered biomasses and species numbers of the ciliates, while their total abundances were significantly decreased by up to 38%. The dominances of *Avestina ludwigi*, *Rostrophryides australis*, and *Cyclidium muscicola* decreased after fertilization, whereas grossglocknerids and *Colpoda* spp. became more abundant indicating changes in the number and kind of fungi and bacteria. This is sustained by an increased catalase and protease activity and a decreased phosphatase and cellulolytic activity. These observations suggest that both fertilizers slightly enhanced decomposition (increased catalase and protease activity, decreased abundances of active ciliates due to an enhanced production of antiprotozoal substances) and improved soil conditions (pH-rise, increased individual and species numbers of K-selected ciliates). In general, the community structure of the ciliates and the soil enzyme activities were influenced more by the (“organic”) bactusol-biomag than by the (“mineral”) biomag application. The dominant and most frequent species, *Avestina ludwigi* and *Rostrophryides australis*, feed on certain fungi and are lost in the usual culture methods. Direct microscopy of fresh samples is thus a prerequisite for successful ecological work with soil protozoa.

**Key words:** Protozoa, soil ciliates, Norway spruce forest, organic fertilizer, magnesite fertilizer, soil enzymes

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### Introduction

Fertilization and liming are widely used to counteract soil acidification and forest decline associated with nutrient imbalances (Huettl 1989, Katzensteiner et al. 1992). Research focuses on revitalization and increased wood production of coniferous forest stands. . . . Microbiological and zoological investigations have also been intensified due to the growing recognition of the importance of soil organisms for decomposition and nutrient cycling

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Offprint requests to: W. Foissner

(Ellenberg et al. 1986, Funke 1986, Hoffmann 1986, Beck 1989, Schinner 1989, Schaefer 1991). Most studies deal with responses of the soil meso- and macrofauna to various lime and fertilizer applications (reviewed in Persson 1988, Hartmann et al. 1989, Irmeler & Heydemann 1989, Jans & Funke 1989, Grossmann et al. 1990, Funke 1986, 1991, Makeschin & Haberer 1991). These investigations show that individual numbers in acid-tolerant groups, such as enchytraeids and certain microarthropods, usually decrease, while individual numbers of acid-intolerant organisms, like earthworms, increase. The extent of these changes depends on the amount and composition of the substance applied.

The effects of forest fertilizers on the soil microflora and microfauna are still poorly understood. Most fertilizers increase the pH and change the microbial activity, i.e. cause a shift from acid-tolerant fungi to basophilic bacteria (e.g. Schinner et al. 1980, Schifferegger & Schinner 1986, Zelles et al. 1986, 1987, 1990, Kratz et al. 1991, Illmer & Schinner 1991, Badalucco et al. 1992). Bååth et al. (1980), however, report a strong decrease in the number of bacteria (and also fungi) after increasing the pH of a spruce forest soil with lime. Some studies show that the abundance of nematodes increases after liming (followed by a decline), while Hyvönen & Persson (1990) did not find marked effects, except that the numbers of root and fungal feeding nematodes decreased slightly.

With regard to soil protozoa, some investigations have been performed in fertilized coniferous forests of Czechoslovakia and southern Germany. The data were reviewed by Foissner (1987, 1993) and indicate that lime and fertilizers usually increase the individual and species numbers of the ciliates and testate amoebae in very acidic (pH < 4) forest soils. Ciliates react particularly quickly if the original pH of an acidified soil is restored by liming with  $\text{CaCO}_3$ : abundance and species richness were almost doubled within a few months (Funke 1986). A combined application of lime and nitrogen [ $5 \text{ Ca}(\text{NO}_3)_2\text{NH}_4\text{NO}_3$ ] decreased species and individual numbers. If, however, fertilization with  $5 \text{ Ca}(\text{NO}_3)_2\text{NH}_4\text{NO}_3$  is preceded by liming with  $\text{CaCO}_3$ , the positive and negative effects seem to counteract each other (Funke 1986, Lehle 1989, Lehle & Funke 1989). Rosa (1974) found a short-time increase of the ciliate abundance after application of NPK and lime. Unfortunately, Lehle's and Rosa's studies lack statistics and active and cystic individuals were not separated. Studies related to testate amoebae will be discussed in detail in a forthcoming paper.

The present study was undertaken in a large woodland, the Böhmerwald in Upper Austria, which shows marked signs of spruce forest decline, at least partially due to magnesium deficiency (Katzensteiner et al. 1992). Thus, recently designed organically enriched magnesite fertilizers were applied for revitalization, i.e. to increase the extremely low pH (about 3) without drastically changing soil life. Protozoa, with their short generation times, their high individual numbers, and their tolerance to low pH, were one of the indicator groups selected because, e.g., earthworms are poorly represented in such highly acidic environments (Schauermann 1985, Funke 1986). The present paper reports on the active ciliates which mainly colonize the uppermost litter layer and are thus directly affected by fertilizer application. To obtain information about the factors which might regulate the ciliate community, basic abiotic measures (pH, soil moisture) and a few soil enzymes, as an indication of microbial activity, were also studied.

## Materials and Methods

### *Site description and experimental design*

The study area is situated in the Upper Austrian part of the Böhmerwald (Bohemian Forest), close to the Czechoslovakian and Bavarian border (48°50'N, 14°00'E). The average yearly air temperature is 4.5 °C; yearly precipitation is about 1000 mm. Two Norway spruce stands (*Picea abies*), both growing on abandoned pastures, were investigated: an 80-y-old "old" stand (site Bärenstein), 1000 m above sea level, and a 40-y-old "young" stand (site Pfliegerwiese), 940 m above sea level. Undergrowth in the old stand consists mainly of *Vaccinium-Oxalis-Dryopteris*; the young stand almost lacks ground

**Table 1.** Composition of fertilizers (as used; bactusol and biomag have since been improved) and nutrient quantities applied to each plot

Fertilizer component	Bactusol (%)	Biomag (%)	Mo, my <sup>a</sup> (kg/100 m <sup>2</sup> )	Oo, oy <sup>a</sup> (kg/100 m <sup>2</sup> )
Organic material	60	7	1.40	19.4
Nitrogen	4–6 <sup>b</sup>	0.5–0.7 <sup>b</sup>	0.14	1.9
Phosphorus	3–5	0.1–0.2	0.04	1.5
Potassium	3–5	0.3–0.4	0.08	1.6
Magnesium	1–3	0.05–0.3	0.03	0.8
Calcium	6–9	0.3–0.5	0.10	1.9
Magnesite <sup>c</sup>	—	90	18.00	18.0

<sup>a</sup> Mo = “mineral” biomag treatment, old stand; my = “mineral” biomag treatment, young stand; Oo = “organic” bactusol-biomag treatment, old stand; oy = “organic” bactusol-biomag treatment, young stand

<sup>b</sup> organically bound; in addition <0.2–0.3% soluble nitrogen is contained

<sup>c</sup> 80% crude magnesite (MgCO<sub>3</sub>) and 10% caustic magnesite [CaMg(CO<sub>3</sub>)<sub>2</sub> + MgO]

vegetation. The soil type is podsol to gleyic cambisol on Eisgarner granite. The humus type is moder forming a 2 to 10 cm thick layer (Katzensteiner et al. 1992). The revitalization experiments were planned and conducted by the Institut für Forstökologie, Universität für Bodenkultur, Vienna (for details see Katzensteiner et al. 1992). Two types of fertilizers were applied: (i) bactusol (Biochemie GmbH, Kundl, Austria) is a fermentation by-product made from dried bacterial biomass; (ii) biomag (Tiroler Magnesit AG, Hochfilzen, Austria) consists of 80% crude magnesite (MgCO<sub>3</sub>), 10% caustic magnesite [CaMg(CO<sub>3</sub>)<sub>2</sub> + MgO], and 10% biosol (dried fungal biomass produced by Biochemie GmbH, Kundl, Austria). For each stand a pure biomag treatment (2000 kg ha<sup>-1</sup>) and a combined treatment of bactusol (3000 kg ha<sup>-1</sup>) + biomag (2000 kg ha<sup>-1</sup>) were compared with unfertilized controls. Treatments were assigned in a randomized block design to 100 m<sup>2</sup> plots with 11 replications (i.e. a total of 33 independent 100 m<sup>2</sup> plots) in the old stand and 9 replications (i.e. a total of 27 separated 100 m<sup>2</sup> plots) in the young stand (Katzensteiner et al. 1992). The composition and nutrient equivalents of the fertilizers are summarized in Table 1. The fertilizers were applied once in granular form in June 1987.

### *Sampling and counting procedures*

In our study each block contained three 100 m<sup>2</sup> plots (two fertilized, one untreated). Six blocks (replicates) were investigated on 6 consecutive days, which means that a total of 18 different plots were selected at random for each series (e.g., 10.–15. June 1987). Altogether 288 samples were investigated (8 series × 3 treatments × 6 replicates × 2 stands). The sampling dates and the months elapsed since fertilization are summarized in Table 2.

Eight subsamples per plot were taken from the upper 0–3 cm of the litter layer at random; each subsample comprised an area measuring about 3 × 3 cm collected with a spatula. The subsamples

**Table 2.** Sampling dates and months elapsed since fertilizer application (3. 6. 1987 old stand; 4.–6. 6. 1987 young stand)

Series	Date	Months
1	10. 06. – 21. 06. 1987	< 1
2	13. 07. – 25. 07. 1987	< 2
3	13. 10. – 24. 10. 1987	5
4	11. 05. – 22. 05. 1988	12
5	04. 10. – 15. 10. 1988	16
6	11. 10. – 23. 10. 1989	29
7	22. 10. – 02. 11. 1990	41
8	02. 05. – 13. 05. 1991	47

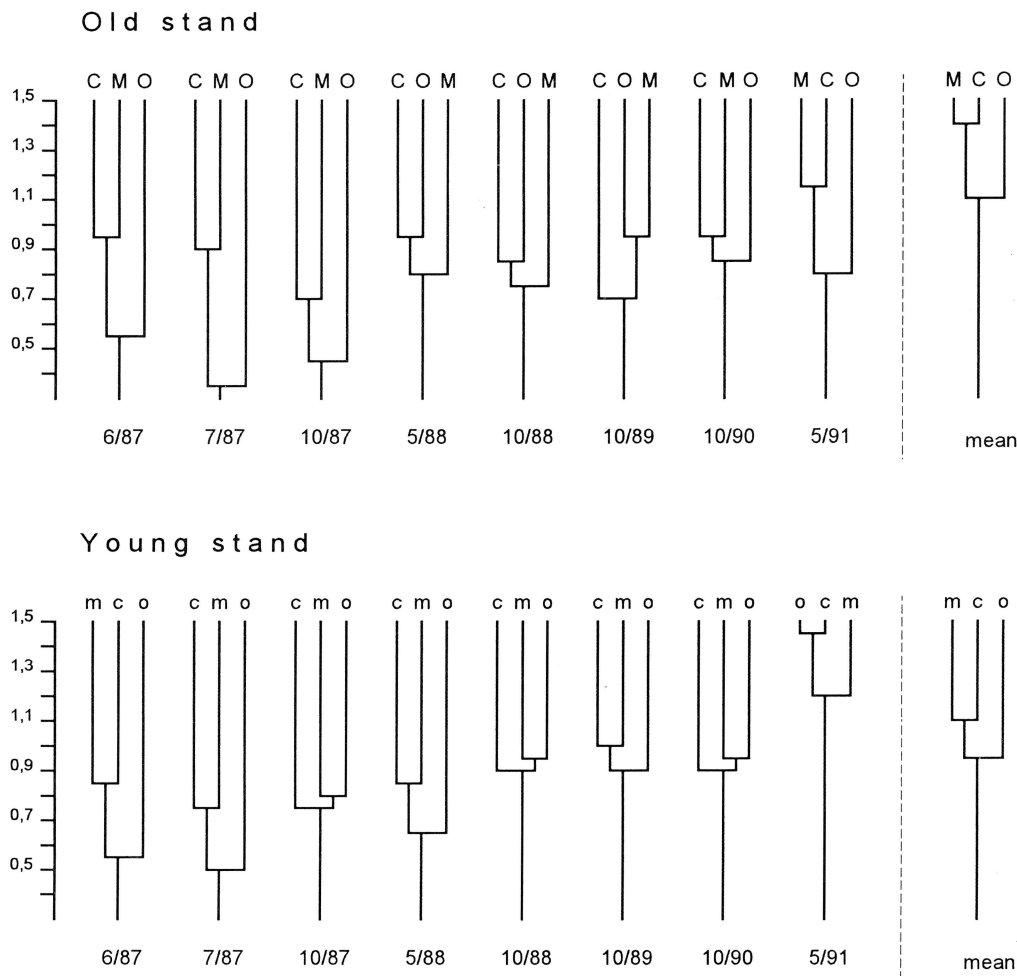
were thoroughly mixed in the laboratory and pooled. Direct counting according to Aesch & Foissner (1992) was used. Biomass for species was calculated as described in Foissner (1985); the values given by Foissner (1987) were frequently used.

### *Abiotic factors and soil enzymes*

Soil moisture and pH (glass electrode; 0.01 M CaCl<sub>2</sub>) were determined from oven-dried litter (50 g heated for about 10 hours at 105 °C). Alkaline phosphatase, catalase, cellulolytic ("cellulase"), and protease activities were measured from air-dried (about 6 weeks) pooled samples using standard procedures (Hoffmann 1968, Beck 1971, Hofmann 1979, Speier et al. 1980).

### *Statistics*

The data were examined with a two-way analysis of variance (block and treatment factor). Where necessary, values were square-root or  $\log t(x + 1)$  transformed to meet the assumptions of this procedure [normality was checked with the Kolmogorov-Smirnov test and homogeneity of variances



**Fig. 1.** Species and abundance similarity (Morisita index) of active soil ciliates in the litter layer (0–3 cm) of two spruce forest stands. C, c = control; M, m = biomass treatment; O, o = bactosol-biomag treatment



with the Cochran test (Sachs 1984)]. If a treatment effect was suggested, pairwise comparisons between the control and each treatment using least significant differences (LSD) were undertaken. The Spearman rank correlation coefficient was calculated according to Sachs (1984).

The Morisita (1959) index was used to measure species and abundance similarity. For brevity, clusters from Jaccard's, Renkonen's, and Bray & Curtis' indices are omitted because they are similar to those obtained with the more sharply discriminating Morisita index (Fig. 1). Clusters were constructed by the unweighted pair-group method with arithmetic means (UPGMA). The colpodid/polyhymenophoran ratio (C/P index) and the weighted coenotic index (WCI) were calculated according to Lüftenegger et al. (1985) and Wodarz et al. (1992). Both indices were used as quantitative general estimates of treatment effects. The C/P index describes the proportion of r- and K-selected ciliate species. The WCI is a single value that unifies total abundance, dominance structure, species richness, and ecological weightings (habitat preference and position of species in the r/K continuum). Spruce forest litter is characterized by low WCI values because active ciliates are abundant due to the reduced ciliatostasis (Foissner 1987, Petz & Foissner 1988). Thus, increasing index values indicate a more pronounced ciliatostasis, i.e. an enhanced production of antiprotozoal substances due to increased decomposition, or unnatural (disturbed) conditions.

**Table 3.** Effects of fertilizers on abiotic factors, soil enzymes, and soil ciliates in two spruce forest stands. Arithmetic means of all blocks sampled (= n) per treatment during the investigation period are shown and compared by a two-way analysis of variance and by least significant difference

Parameter	n	Co	Mo	Oo	cy	my	oy
<b>Abiotic factors</b>							
Soil moisture (% of dm)	48	60.0	59.1	61.7	58.3	59.1	59.9
pH (CaCl <sub>2</sub> )	48	2.8	3.6***	3.9***	3.0	3.8***	3.9***
<b>Soil enzymes</b>							
Catalase (mg O <sub>2</sub> g <sup>-1</sup> dm · 3 min <sup>-1</sup> )	7	20.8	24.7**	25.5**	20.6	21.6	24.2**
Phosphatase (mg phenol g <sup>-1</sup> dm · 3 h <sup>-1</sup> )	7	1.7	1.4 ×	1.3*	1.2	1.1	1.1
Protease (mg µg tyrosine g <sup>-1</sup> dm · 2 h <sup>-1</sup> )	7	1.2	1.2	1.5	1.1	1.3*	1.3*
Cellulase (mg glucose g <sup>-1</sup> dm · 23 h <sup>-1</sup> )	7	39.6	35.2*	33.4**	36.5	35.3	30.6
<b>Ciliophora</b>							
Individuals (g <sup>-1</sup> dm) <sup>a</sup>	48	641	395*	421*	241	212	220
CV		65	62	90	96	62	67
Total number of species	48	25	23	26	19	21	19
CV		44	46	34	31	26	23
Biomass (µg g <sup>-1</sup> dm) <sup>a</sup>	48	4.6	3.8	4.3	2.0	2.1	2.1
C/P index (abundance)	8	139	101	113	56	49	63
C/P index (species number)	8	3.9	3.5	3.1	4.1	4.1	5.5
Weighted coenotic index	8	5	25	14	51	67	92

<sup>a</sup> Multiply with 4154 and 4452 to get values per square meter in the old and young stand, respectively. Bulk density was determined by weighing 6 air-dried replicates (25 × 25 cm) per stand from the upper 0–3 cm of the litter layer.

Abbreviations: C/P = colpodid/polyhymenophoran ratio; CV = coefficient of variation; Co = control, old stand; cy = control, young stand; dm = dry mass of soil; Mo = biomag treatment, old stand; my = biomag treatment, young stand; Oo = bactosol-biomag treatment, old stand; oy = bactosol-biomag treatment, young stand; x =  $P \leq 0.1$ ; \* =  $P \leq 0.05$ ; \*\* =  $P \leq 0.01$ ; \*\*\* =  $P \leq 0.001$

## Results

### *Abiotic factors and soil enzymes*

Fertilization brought about a highly significant increase in pH from about 3 to 4.3 in the first year. Although the pH of the fertilized plots was on average 0.8 units higher than in the control four years after fertilization, the range of 3.0–4.2 clearly demonstrates the prevailing extreme conditions in the spruce litter (Table 3). The initial differences between the biomag and bactosol-biomag treatment disappeared about two years after fertilization. Effects of fertilizers on the soil moisture were negligible. Fertilization increased the catalase and protease activity and decreased the phosphatase and cellulolytic activity; the mean differences of about 20% were statistically significant in half of the samples (Tab. 3). Some treatment effects still exist five years after fertilization.

### **Ciliates**

#### *Abundance, biomass, and species number*

In the untreated spruce litter abundances of active ciliates range from 120 to 1583 and 21 to 1106 individuals per g dry mass in the old and young stand, respectively; these extreme

**Table 4.** Effects of fertilizers on active soil ciliates. Arithmetic means of six replicates (blocks) per series are shown and compared by a two-way analysis of variance and by least significant difference

Series	Co	Mo	Oo	cy	my	oy
<b>Abundance</b> (Individuals g <sup>-1</sup> dm)						
6/87 <sup>a</sup>	909	710	519	121	176	275
7/87	341	335	211	87	140	153
10/87	1302	503**	445**	272	150	172
5/88	549	213	233	177	273*	289*
10/88	468	431	409	230	202	223
10/89	461	200*	156**	254	213	165
10/90	535	404	909	456	280	258
5/91	563	362*	488	389	258	225
<b>Biomass</b> (µg g <sup>-1</sup> dm)						
6/87	7.4	4.4	3.5	1.0	1.3	3.4
7/87	1.7	1.9	1.7	0.6	1.5	1.3
10/87	6.3	3.2	3.6	1.7	1.0	1.0
5/88	3.2	1.3	2.8	0.9	3.2*	2.1x
10/88	3.8	8.1	5.1	1.5	1.7	1.5
10/89	2.8	2.4	2.0	1.3	1.4	1.5
10/90	2.4	2.3	6.3	3.0	3.0	2.5
5/91	9.4	7.1	9.4	6.0	3.5	3.4
<b>Species number</b> (all replicates)						
6/87	35	31	31	18	21	21
7/87	10	10	17	11	15	12
10/87	22	22	24	16	16	17
5/88	20	14	21	19	21	20
10/88	29	28	33	15	18	17
10/89	22	23	23	16	17	17
10/90	12	13	16	23	26	24
5/91	40	41	42	30	31	26

<sup>a</sup> 1–2 weeks after fertilization

Abbreviations: Co = control, old stand; cy = control, young stand; dm = dry mass of soil; Mo = biomag treatment, old stand; my = biomag treatment, young stand; Oo = bactosol-biomag treatment, old stand; oy = bactosol-biomag treatment, young stand; x =  $P \leq 0.1$ ; \* =  $P \leq 0.05$ ; \*\* =  $P \leq 0.01$ .

values (not tabulated) are rather similar for all blocks. However, the total mean individual number from the control plots of the young stand is only about one third of the old ones, whereas the coefficient of variation is much higher (cp. cy and Co in Tab. 3). The mean biomass and species number in the young stand are 56% and 24%, respectively, lower than in the old one. Similar relations are obtained if values are transformed to square meters because bulk density is almost identical in the young and old stand (0.15 and 0.14 g cm<sup>-3</sup>, respectively). Minimal abundances in all plots were observed in July 1987, probably due to summer dryness (about 40% soil moisture; litter appeared virtually dry).

Statistically significant differences among treatments appeared four months after fertilization in the old stand (Tab. 4). Compared to the control, individual numbers were decreased by 61% and 66% in the biomag (Mo) and bactosol-biomag plots (Oo), respectively. This decrease is still recognizable four years after fertilization; the total mean individual numbers of both treatments differ by about 35% from the control (Tab. 3). The outlier in Oo in 10/90 results from an extraordinarily high abundance of a single species, *Rostrophryides australis*, in one of 6 blocks (Tab. 4). The reasons for this luxurious development are unknown. Consequently, the coefficient of variation is 90% in Oo and about 63% in Mo and Co.

In the young stand ciliate numbers were 45% to 147% higher in the treated than in the control plots during the first year after fertilization. While the abundances remained rather stable in the fertilized plots, those of the control increased considerably during the study period, particularly in 10/90 and 5/91, resulting in a high coefficient of variation over time (Tab. 3). Consequently, the mean abundances of all variants are almost the same in the young stand (Tab. 3).

The rather pronounced differences in ciliate abundances between control and treated plots are not reflected in biomasses and species numbers (Tab. 3, 4). This is due to certain shifts in the community structure, e.g. an increase of more voluminous *Colpoda* spp. in the fertilized plots.

### Community structure

Altogether 64 species were found by direct counting, i.e. were active in the litter layer (Tab. 5). In terms of abundance and frequency, the control plots are dominated by *Avestina ludwigi* and *Rostrophryides australis*, rather small fungal feeders, and *Cyclidium muscicola*,

**Table 5.** Active ciliate species and their mean individual dominances (%; n = 48) in the upper (0–3 cm) litter layer of two spruce forest stands

Species	Co	Mo	Oo	cy	my	oy
<i>Arcuospathidium cultriforme</i> (Penard, 1922)	+	—	—	—	+	—
<i>Arcuospathidium muscorum</i> (Dragesco & Dragesco-Kernéis, 1979)	+	+	+	—	—	+
<i>Avestina ludwigi</i> Aesch. & Foissner, 1990	23	30	21	27	24	19
<i>Balantidioides dragescoi</i> Foissner, Adam & Foissner, 1982	+	—	—	—	—	—
<i>Blepharisma bimicronucleata</i> Villeneuve-Brachon, 1940	+	+	+	—	+	—
<i>Blepharisma hyalinum</i> Perty, 1849	+	+	+	—	—	—
<i>Bryometopus pseudochilodon</i> Kahl, 1932	+	—	—	+	—	—
<i>Bryophyllum loxophylliforme</i> Kahl, 1931	—	—	—	—	—	+
<i>Chilophrya terricola</i> Foissner, 1984	+	+	+	—	+	—
<i>Cirrophrya terricola</i> Foissner, 1987	+	—	—	—	—	—
<i>Colpoda aspera</i> Kahl, 1926	+	+	+	+	—	+
<i>Colpoda cucullus</i> Müller, 1773	+	1	1	+	1	1
<i>Colpoda henneguyi</i> Fabre-Domergue, 1889	—	+	+	—	—	—
<i>Colpoda inflata</i> (Stokes, 1885)	+	3	1	+	4	4
<i>Colpoda maupasi</i> Enriques, 1908	+	1	1	+	1	1

**Table 5.** (continued)

Species	Co	Mo	Oo	cy	my	oy
<i>Colpoda steinii</i> Maupas, 1883	+	1	1	1	5	11
<i>Cyclidium muscicola</i> Kahl, 1931	22	15	11	15	15	7
<i>Cyrtolophosis acuta</i> Kahl, 1926	+	+	+	3	2	3
<i>Cyrtolophosis mucicola</i> Stokes, 1885	3	+	1	+	+	+
<i>Dileptus alpinus</i> Kahl, 1932	+	+	+	+	—	+
<i>Dileptus anguillula</i> Kahl, 1931	+	+	+	+	—	+
<i>Dileptus gracilis</i> Kahl, 1931	+	+	+	—	+	—
<i>Dimacrocaryon amphileptoides</i> (Kahl, 1931)	+	+	+	+	+	+
<i>Drepanomonas exigua</i> Penard, 1922	+	—	+	—	—	—
<i>Drepanomonas revoluta</i> Penard, 1922	1	2	1	2	+	+
<i>Enchelydium polynucleatum</i> Foissner, 1984	+	+	—	+	+	—
<i>Epispathidium terricola</i> Foissner, 1987	+	+	+	+	+	+
<i>Frontonia depressa</i> (Stokes, 1886)	+	+	+	+	+	+
<i>Fuscheria terricola</i> Berger, Foissner & Adam, 1983	+	+	+	+	+	—
<i>Gonostomum affine</i> (Stein, 1859)	+	—	+	+	+	+
<i>Grossglockneria acuta</i> Foissner, 1980	1	2	4	1	2	5
<i>Halteria grandinella</i> (Müller, 1773)	+	—	+	—	—	—
<i>Hemisincirra filiformis</i> (Foissner, 1982)	—	+	—	—	—	—
<i>Hemisincirra gellerti</i> (Foissner, 1982)	+	+	+	+	+	+
<i>Hemisincirra gracilis</i> (Foissner, 1982)	+	+	+	+	+	—
<i>Hemisincirra inquieta</i> Hemberger, 1985	+	+	+	+	+	+
<i>Holosticha bergeri</i> Foissner, 1987	+	+	+	+	—	—
<i>Holosticha multistilata</i> Kahl, 1928	+	+	+	+	+	+
<i>Holosticha sigmoidea</i> Foissner, 1982	+	+	+	+	+	+
<i>Homalogastra setosa</i> Kahl, 1926	+	+	+	+	+	+
<i>Keronopsis wetzeli</i> Wenzel, 1953	+	—	—	—	+	—
<i>Lamtostyla</i> sp.	+	—	+	—	+	—
<i>Leptopharynx costatus</i> Mermod, 1914	1	2	2	2	3	3
<i>Microdiaphanosoma arcuatum</i> (Grandoni & Grandoni, 1934)	4	2	2	1	1	+
<i>Nivaliella plana</i> Foissner, 1980	+	+	+	2	1	+
<i>Opercularia arboricola</i> (Biegel, 1954)	+	+	1	2	1	+
<i>Oxytricha</i> sp.	—	+	—	—	+	—
<i>Paruroleptus notabilis</i> Foissner, 1982	+	+	+	+	—	+
<i>Platyophrya macrostoma</i> Foissner, 1980	—	—	+	—	—	—
<i>Platyophrya spumacola</i> Kahl, 1927	+	—	+	+	+	+
<i>Platyophrya vorax</i> Kahl, 1926	3	2	4	+	+	+
<i>Protospathidium bonnet</i> (Buitkamp, 1977)	+	+	—	—	—	—
<i>Pseudochilodonopsis mutabilis</i> Foissner, 1981	+	—	+	+	+	—
<i>Pseudocyrtolophosis alpestris</i> Foissner, 1980	—	+	+	+	+	+
<i>Pseudoholophrya terricola</i> Berger, Foissner & Adam, 1984	+	+	+	—	+	—
<i>Pseudoplatyophrya nana</i> (Kahl, 1926)	9	9	13	11	12	19
<i>Pseudoplatyophrya terricola</i> Foissner, 1985	+	—	+	+	+	+
<i>Rostrophryides australis</i> Blatterer & Foissner, 1988	21	17	16 <sup>a</sup>	22	15	14
<i>Satrophilus muscorum</i> (Kahl, 1931)	4	2	2	2	2	2
<i>Spathidium</i> sp.	+	+	+	+	+	+
<i>Spathidium spathula</i> (Müller, 1773)	+	+	+	+	+	+
<i>Tachysoma humicola</i> Gellért, 1957	+	+	+	+	+	+
<i>Tetrahymena rostrata</i> (Kahl, 1926)	+	+	+	—	+	—
<i>Vorticella astyliformis</i> Foissner, 1981	1	3	2	1	3	2

<sup>a</sup> The outlier from October 1990 is omitted

Abbreviations: Co = control, old stand; cy = control, young stand; Mo = biomag treatment, old stand; my = biomag treatment, young stand; n = number of blocks; Oo = bactosol-biomag treatment, old stand; oy = bactosol-biomag treatment, young stand; + = dominance <1%; — = not recorded

**Table 6.** Abundance, individual dominance, and frequency of relevant ciliate species in two spruce forest stands

Feeding group		Co	Mo	Oo	cy	my	oy	Difference to control (%) <sup>a</sup>			
								Mo	Oo	my	oy
<b>Fungal feeders</b>	ID <sup>b</sup>	55	58	62	62	53	58	5	13	-14	-6
<i>Avestina ludwigi</i>	Ind.	95	97	59	47	42	30	2	-38	-11	-36
	ID <sup>c</sup>	15	25	14	20	20	14	66	-5	2	-30
	F	94	86	81	94	83	81	-9	-14	-12	-14
<i>Rostrophryides australis</i>	Ind.	88	38	62	38	24	24	-57	-30	-37	-37
	ID <sup>c</sup>	14	10	15	16	11	11	-30	7	-28	-31
	F	100	92	96	88	83	90	-8	-4	-6	2
Grossglocknerids	Ind.	55	34	47	17	24	38	-38	-15	41	124
	ID <sup>c</sup>	9	9	11	7	11	17	0	30	59	144
	F	85	90	88	90	90	83	6	4	0	-8
<b>Bacterial feeders</b>	ID <sup>b</sup>	24	22	17	14	25	25	-8	-29	79	79
<i>Cyclidium</i>	Ind.	126	39	43	27	23	16	-69	-66	-15	-41
<i>muscolola</i>	ID <sup>c</sup>	20	10	10	11	11	7	-50	-48	-4	-35
	F	100	83	92	79	92	73	-17	-8	16	-8
<i>Colpoda</i> spp.	Ind.	19	23	29	13	25	21	21	53	92	62
	ID <sup>c</sup>	3	6	7	5	12	10	93	130	119	76
	F	38	44	58	33	58	71	17	56	75	112

<sup>a</sup> Co, cy = 100%

<sup>b</sup> sum of the arithmetic means

<sup>c</sup> calculated from the median

Abbreviations: Co = control, old stand; cy = control, young stand; F = frequency (%); ID = individual dominance (%); Ind. = individuals g<sup>-1</sup> dry mass of soil (median); Mo = biomag treatment, old stand; my = biomag treatment, young stand; Oo = bactosol-biomag treatment, old stand; oy = bactosol-biomag treatment, young stand

a tiny bacterial feeder. In contrast to the total abundances, the dominant and frequent species agree well in the young and old spruce stand (Tab. 3–6). This indicates that differences in soil development and plant cover, which is largely absent in the young stand, are more decisive for the quantity than for the quality of the ciliate community.

Fertilization changed the community structure; however, particular species were neither lost or gained. In the treated plots, especially in the “organic” variant, *Avestina ludwigi*, *Rostrophryides australis*, and *Cyclidium muscolola* showed decreased numbers and dominances, while those of the grossglocknerids, *Colpoda* spp., and peritrichs increased (Tab. 6; note also changes in frequency). This is reflected by the comparatively low similarity values of the Morisita index in the first two months after fertilization (Fig. 1). In contrast, total abundances were only affected four months after fertilizer application (Tab. 4). The “organic” bactosol-biomag treatment changed the community structure more distinctly than the “mineral” biomag fertilizer: Oo, oy separates from Co, cy/Mo, my in 9 of 16 clusters (56%), while Mo, my deviates from Co, cy/Oo, oy only 3 times (Fig. 1).

The high C/P indices clearly show that colpodid ciliates dominate in the acidic spruce litter with respect to abundance and species number, while polyhymenophorans (hypotrichs and heterotrichs) occur sparsely (Tab. 5). The latter is, however, partially caused by loss of specimens during counting because some species are very fragile. The polyhymenophoran ratio is slightly increased in the treated plots of the old stand (Tab. 3). All these small changes of the ciliate communities are more clearly expressed by the weighted coenotic indices which are distinctly lower in the control plots.

**Table 7.** Spearman rank correlations between ciliates (species number, abundance<sup>a</sup>, individual dominance) and some soil variables. First line = old stand; second line = young stand

Parameters (n)	Moisture (24)	pH (24)	Catalase (21)	Phosphatase (21)	Protease (21)	Cellulase (21)
Species number	+0.7624** +0.6498**	+0.0189 -0.0437	+0.1672 +0.1870	+0.5860* +0.5136*	+0.0464 -0.0539	-0.3523 -0.2851
Total abundance <sup>a</sup>	-0.0452 +0.6411*	-0.4957* -0.1472	-0.4182x +0.4636x	+0.3766x +0.6039*	-0.3714x -0.1104	-0.2532 -0.1104
<i>Avestina ludwigi</i> <sup>a</sup>	-0.6791** +0.3000	-0.4957* -0.3904x	-0.6143* +0.2909	-0.1338 +0.4727x	-0.3870x +0.6156*	-0.2429 +0.1649
<i>A. ludwigi</i> (ID%)	-0.8261** -0.0800	+0.0530 -0.1922	-0.4753x +0.1377	-0.3883x +0.0649	-0.2247 +0.7000**	-0.2104 +0.2753
<i>Rostrophryides australis</i> <sup>a</sup>	-0.2417 +0.3276	-0.4252x -0.3809x	-0.4896x +0.2805	+0.0442 +0.2506	-0.0468 +0.0909	+0.0948 +0.1286
Grossglocknerids <sup>a</sup>	+0.3000 +0.2035	-0.0165 +0.1704	+0.0182 -0.1221	+0.4519x +0.1338	-0.4545x -0.4403x	-0.4896x -0.3039
<i>Cyclidium muscicola</i> <sup>a</sup>	-0.1409 +0.3530x	-0.5470* -0.3139	-0.1961 +0.2532	+0.2442 +0.2649	-0.3065 -0.2299	+0.0364 +0.0377
<i>Colpoda</i> spp. <sup>a</sup>	+0.6713** +0.2087	+0.2417 +0.4583x	+0.3831x +0.0831	+0.5364* +0.1961	+0.0636 -0.0260	-0.4403x -0.2052

<sup>a</sup> Individuals g<sup>-1</sup> dm

Abbreviations: dm = dry mass of soil; ID = individual dominance; n = number of arithmetic means of the series; x =  $P \leq 0.1$ ; \* =  $P \leq 0.05$ ; \*\* =  $P \leq 0.01$

### Correlations between ciliates, abiotic factors, and soil enzymes

The total individual and species number of active ciliates and the abundances of relevant species show slight correlations with some of the investigated abiotic factors and enzyme activities (Tab. 7). About 20% of the correlations were inconsistent, i.e. positive in the old stand, but negative in the young stand and vice versa. Consistent correlations in both stands exist between soil moisture and species richness (positive), pH and abundance of *Avestina ludwigi* and *Rostrophryides australis* (negative), phosphatase activity and total individual and species number (positive), and protease activity and abundances of grossglocknerid ciliates (negative).

## Discussion

### Ciliate communities in spruce forest litters

About 70 ciliate species can be expected in the litter layer of a spruce forest. This conclusion may be drawn — at least for Central Europe — from the few studies available, each however based on 100–300 samples taken over 1–4 years (Rosa 1974, Petz et al. 1988, Lehle 1989, present study). This figure is quite low compared to, e.g. grassland soils, where twice as many taxa have been found (Foissner 1987). Obviously, the acid and nutrient-imbalanced spruce forest litter is a rather poor biotope for ciliates, as it is for most other animals (e.g. Funke 1986, Schaefer 1991).

It is not yet possible to select a typical ciliate community of spruce forest litters, because taxonomic studies are incomplete and determinations often doubtful. Rosa (1974), for

instance, recorded *Glaucoma* spp. and *Colpidium* spp., which certainly do not occur in soil, but none of the autochthonous grossglocknerids. The data available and unpublished observations from our group suggest that the following species constitute a rather distinct community: *Avestina ludwigi* [misidentified as *Hausmanniella discoidea* by Petz & Foissner (1989a)], *Bryometopus sphagni*, *Chilophrya terricola*, *Dimacrocarion amphileptoides*, *Frontonia depressa*, *Grossglockneria acuta*, *Hemisincirra gellerti*, *Holosticha multistilata*, *H. sigmoidea*, *Keronopsis wetzeli*, *Nivaliella plana*, *Rostrophryides australis* [possibly misidentified as *Platyophrya spumacola* by Petz & Foissner (1989a)]. Some of these species are also rather frequent in acidic alpine mats (Foissner 1985) indicating that they prefer or tolerate a low pH.

*Rostrophryides australis* and *Avestina ludwigi*, the dominant species in the present study, have been described only recently (Blatterer & Foissner 1988, Aesch & Foissner 1990) and were not recorded by the workers cited above. This is not surprising since these species hardly grow with culture methods, i.e. can be best detected by direct microscopy of fresh samples. Both species feed on fungal propagules and obviously tolerate a very low pH, well documented by the negative correlation between pH and abundances (Tab. 7), and profit from the high fungal resources which develop under such extreme conditions.

Irrigation studies by Petz & Foissner (1989b) and our data (Tab. 7) suggest that soil humidity is not a major factor for the abundance of soil protozoa (as has been widely believed; see references in Foissner 1987), at least in spruce forest ecosystems. The individual number and dominance of *Avestina ludwigi* even show a negative correlation with the soil moisture content, indicating that it prefers comparatively dry litter and is well adapted to soil desiccation (Tab. 7; Aesch & Foissner 1990). Certain ciliate species, however, need a higher soil moisture content, which is indicated by the rather strong positive correlation between species richness and soil humidity (Tab. 7; Petz & Foissner 1989b).

Some effects of phosphorus-related processes on soil ciliates are indicated by their proportionally increasing individual and species numbers with phosphatase activity (Tab. 7) and the  $P_2O_5$  level in alpine soils (Foissner 1985). Some other correlations are also remarkable, e.g. the inverse relations between certain bacterivorous ciliates (*Cyclidium muscicola* and *Colpoda* spp.) and the cellulolytic activity, and between fungal feeders (*Avestina ludwigi* and grossglocknerids) and the protease activity in the old stand (Tab. 7). Certainly, the parameters measured are not sufficient to explain all observed changes in the community structure of ciliates. There are distinct indications, however, that they are related to changes in the number and quality of food organisms (see also next section).

### Fertilizer effects

The moder and mor soils of coniferous forests are usually acidic and nutrient-imbalanced due to an acid soil parent material, organic acids produced during decomposition of the needle litter, and acid deposition. Such unfavourable conditions limit the soil life, particularly bacterial and earthworm activity, and consequently inhibit decomposition, which results in the accumulation of litter, and reduces the availability of plant nutrients. The main purposes of forest fertilization and/or liming are thus to revitalize the declining forests and to improve wood production by increasing the low pH, enhancing decomposition rates, and balancing mineral nutrition. This demands slow and cautious, but sustainable changes of the soil microflora and fauna to avoid rapid decomposition and mineral leaching (Schaefer 1991). There are some indications that the fertilizers used in this study met these goals:

(i) The pH rose from about 3 to 4 in the treated plots. Despite prevailing strongly acidic conditions, this pH shift is sufficient to increase earthworm abundance (unpubl. observations) and nitrogen mineralization rates and to improve nutrient availability for the spruce trees (Katzensteiner et al. 1992).

(ii) Both treatments affected the community structure of ciliates and the activity of extracellular microbial enzymes. Catalase, which increased after fertilization, is produced

by nearly all bacteria and fungi to prevent accumulation of the highly toxic hydrogen peroxide during periods of higher respiration (Frankenberger & Dick 1983, Schlegel 1985). The hydrolysis of proteins to amino acids by proteases, which also increased after fertilization, is an important process in the nitrogen cycle; in an acid environment proteases are mainly produced by fungi (Frankenberger & Dick 1983, Schinner 1989). A shift in the fungal composition and/or activity is also indicated by changes in the mycophagous ciliate community: the grossglocknerids, which feed exclusively by perforation lysis on fungal cells (walls are breached by discrete holes and the cell content is ingested), became more dominant, particularly shortly after fertilization, whereas *Avestina ludwigi* and *Rostrophryides australis*, which feed by general lysis (fungal propagules are ruptured inside digestive vacuoles), decreased (Tab. 5, 6). Field experiments by Petz & Foissner (1989a) similarly showed that the effects of pesticides on mycophagous ciliates are complex and may be inverse: the fungicide mancozeb decreased the dominance of a grossglocknerid species, but increased *Avestina ludwigi* (misidentified as *Hausmanniella discoidea*), while *Rostrophryides australis* (possibly misidentified as *Platyophrya spumacola*) was unaffected. In contrast, the insecticide lindane caused an increase of the grossglocknerids, but a strong decrease (up to extinction) of *Avestina ludwigi* three months after application.

The average phosphatase and cellulolytic activity decreased slightly in the treated plots. Phosphatase and cellulase are known to be subject to catabolite repression, i.e. less of these enzymes are produced as long as easily decomposable phosphate or carbon sources, as contained in the fertilizers applied, are available; whereas more stable substrates, like spruce needles, remain intact (Schinner et al. 1980, Schlegel 1985, Hoffmann 1986, Häussling & Marschner 1989). Other explanations of the reduced phosphatase activity may be the sorption of the enzyme to an increased amount of organic colloids and/or degradation by the increased protease activity (cp. Kandeler 1990).

In the first two months after fertilization, however, significantly higher amounts of alkaline phosphatase, which is produced exclusively by bacteria (Frankenberger & Dick 1983, Häussling & Marschner 1989), were measured suggesting a short-time increase of bacterial activity. A shift in the bacterial composition and/or activity is also indicated by changes in the dominance structure of certain bacterivorous ciliates: *Cyclidium muscicola* decreased in number, while *Colpoda* spp. increased (Tab. 5, 6). *Cyclidium*, with its large paroral membrane area, is well adapted to collect small particles, e.g. bacteria about 0.3 µm in diameter, whereas *Colpoda* spp. ingest also longer bacterial rods (Fenchel 1986, Foissner 1987). Moreover, the feeding organelles of *Colpoda* spp. are small compared to the cell size, thus high concentrations of bacteria are required for growth.

(iii) K-selected polyhymenophorans needing a more stable environment increased slightly in the fertilized plots of the old stand as indicated by decreased C/P indices (Tab. 3). The abundance of the active ciliates declined suggesting enhanced decomposition, i.e. an increased production of antiprotozoal substances<sup>1</sup>. These effects are less evident, but nevertheless recognizable in the young stand too. It should, however, be mentioned that we could not prove an increased litter decomposition measuring the cellulolytic activity (see above) and using litter bags [method of Herlitzius (1983)]. The considerable increase of active ciliates in the control plots of the young stand during the four years of investigation could have been caused by a reduced amount of antiprotozoal substances related to an increased needle loss of the unfertilized trees.

Taken altogether, the fertilizers applied caused only slight changes in the ciliate community and several micro- and mesofaunal groups (unpubl. results); likewise, soil enzyme activities were only slightly affected. Thus a fertilization shock, as mentioned in other studies (e.g. Funke 1986, Lehle 1989), did not occur. Inconspicuous differences in total abundance were found between the two treatments applied (Tab. 3). However, the community analysis shows

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<sup>1</sup> This refers to the concept of ciliatostasis, i.e. that certain organic substances accumulate in older (evolved) soils, but are largely absent in "young" litter, and inhibit ciliate excystment and growth (Foissner 1987, Petz & Foissner 1988).



that the ciliates were more affected by the combined bactosol-biomag application (Fig. 1). The same applies to the pH and some soil enzymes and corresponds to the silvicultural investigations, which show an enhanced increment and a more healthy appearance of the bactosol-biomag treated spruce trees (Katzensteiner et al. 1992). Whether the main factor is the quantity or quality of the fertilizers cannot be answered from our investigation.

**Note.** Trade names and company names are included for the benefit of the reader and do not imply endorsement or preferential treatment of the products by the authors.

## Acknowledgements

We thank Univ.-Prof. Dr. H. Adam, the head of the Institute of Zoology, University of Salzburg, for institutional support and the owner of the forests (Stift Schlägl) for making the study area available. The enzyme analyses were performed in the laboratory of Dr. T. Peer by Mrs. M. Traunmüller (Univ. Salzburg). Thanks to Mr. E. Strobl for improving the English. Financial support was given by the Biochemie GmbH, Kundl, Austria.

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*Pedobiologia* **37**, 335 (1993)  
Gustav Fischer Verlag Jena

## Book Review

McMichael, B. L. and Persson, H. (eds.): **Plant roots and their environment**. Proceedings of an ISRR-symposium, August 21st–25th, 1988, Uppsala, Sweden. Developments in agricultural and managed-forest ecology 24, 649 pages, Elsevier Science Publishers, Amsterdam and New York, 1991. ISBN 0-444-89104-8.

This volume compiles in 650 pages the results of an ISRR-symposium which took place in 1988 (!) in Uppsala, Sweden. 83 pages cover a broad range of different aspects of root science. They deal with plant nutrition and root morphology; influence of water, soil types, agrotechnics and fertilization on root function and root distribution; the role of genetic variants; the impact of heavy metals and acid deposition. They also deal with laboratory experiments and field observations from agriculture and forestry, compiling different methods and demonstrating computer modelling of processes. Many papers give (1988) quite new data of experiments and investigations, some give very old data, i.e. from 1960. There are some nice reviews about special topics and original papers comprise just 4 pages. Many papers are of interest not only for root specialists but also for researchers from other fields of soil science and soil biology. Unfortunately papers about interactions within the rhizosphere, and about the role of other organisms like bacteria and soil animals in the root environment, are completely lacking, except for 9 papers about aspects of mycorrhiza. Another negative aspect is the long period between the conference and the publishing date (3 years), at though there are the technical opportunities available today for a quite short publishing period. Unfortunately it needed another 3 years to obtain a copy for reviewing. I do not think the volume provides a synthesis of our knowledge of plant roots, as claimed by the editors. But without doubt the book will be an important literature source in the field of root science.

O. Larink, Braunschweig, Germany