The soil macrofauna (Diplopoda, Isopoda, Lumbricidae and Chilopoda) near tree trunks in a beechwood on limestone: indications for stemflow induced changes in community structure

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Abstract

Due to stemflow water running down beech trees (*Fagus sylvatica* L.) pollutants (protons, heavy metals) accumulate in the vicinity of the trunk in beech forests in central Europe. This study investigates density, biomass, species composition and depth distribution of major soil macrofauna groups (Diplopoda, Isopoda, Lumbricidae, Chilopoda) near beech trees and distant to trees in a beechwood on limestone in northern Germany each season for 1 year. Litter accumulated in the vicinity of the trunk and these localities were more acidic (average pH of 0–3 cm soil depth near to trees 3.7, distant to trees 5.3 (KCl measurement)). Macrofauna species differentially responded to changed environmental conditions in the tree vicinity. Generally, the density of soil-inhabiting (endogeic) species was lower in the tree vicinity, whereas the density of species inhabiting predominantly the litter layer (epigeic species) was similar to or higher than that distant to trees. The most dramatic reduction occurred in the density of endogeic earthworm species which were almost absent in the tree vicinity, but the density of endogeic centipedes (Geophilomorpha) was also significantly lower in the tree vicinity. Canonical correspondence analysis showed that soil pH was an important environmental factor structuring the soil macrofauna community in the tree vicinity, whereas distant to trees soil pH was of minor importance and the faunal gradient was generally less pronounced. Depth distribution of animals indicated the retreat of most macrofauna species from deeper soil layers near the tree. Our results suggest that owing to damage of soil-inhabiting macrofauna, particularly earthworms, near to trees and concomitant reduction in bioturbation, soil humus type is changing from mull to moder.

1. Introduction

The effects of acidification due to increased input of protons from polluted air on the structure and function of the soil fauna community has been investigated frequently. Most investigations were performed in woodlands growing on non-calcareous parent rock with humus types of moder or mor (Abrahamsen et al., 1980; Bååth et al., 1980; Persson et al., 1989; Hågvar, 1990; Ohtonen et al., 1992; Rundgren, 1994; Wolters and Schaefer, 1994). In addition, most of these more acidic woodlands were planted with coniferous trees. Little is known of the effect of soil acidification on the soil fauna community of deciduous woodlands growing on alkaline soils. In contrast to the soil fauna community of woodlands with moder or mor, which is domi-

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nated by mesofauna species (particularly Collembola, Acari and Enchytraeidae), mull humus soils on calcareous parent rock are dominated by macrofauna species, e.g. earthworms, millipedes and isopods (e.g. Petersen and Luxton, 1982; Schaefer and Schauermann, 1990). This suggests that soil acidification may affect the soil fauna community of mull and moder soils very differently.

In base-rich deciduous woodlands, soil processes are affected strongly by the activity of the saprophagous soil fauna community, particularly by macrofauna species (Scheu, 1987; Schaefer, 1991). Alterations in the composition of the soil fauna community due to increased acid loading are therefore expected to have strong implications on soil processes in these ecosystems. In microcosm experiments it could be shown that litter fragmentation and bioturbation significantly reduced the adverse effects of increased acid precipitation on decomposition of beech leaf litter in a base rich mull soil (Scheu and Wolters, 1991a).

In beech (*Fagus sylvatica* L.) woodlands in Europe the effects of acid precipitation vary with distance from tree trunks. Owing to stem flow water running down beech trunks, particularly during winter, the soil around beech tree trunks is affected much more by acidity than the area distant to trunks (Jochheim, 1985; Koenies, 1985; Schäfer, 1988). The present study investigates these two contrasting environments to evaluate the impacts of increased acid loading on the composition of the soil fauna community in a calcareous mull beechwood near Göttingen, Germany (cf. Schaefer, 1990). Particular attention was paid to the soil macrofauna (Diplopoda, Isopoda, Lumbricidae, Chilopoda) because these species are considered to be important for the formation and persistence of this ecosystem (Schaefer, 1991). Earthworms were shown to be the major agents responsible for soil turnover and mixing of organic material with mineral soil in this woodland (Scheu, 1987; Scheu and Sprengel, 1989; Scheu and Wolters, 1991b). Litter fragmentation and formation of faecal pellets by diplopods and isopods is a precondition for mixing of organic materials with mineral soil by endogeic earthworms which are abundant in this beechwood (Scheu and Sprengel, 1989; Scheu, 1992). Centipedes were included in the analysis because they are the most important predatory animals in this ecosystem (Poser, 1988; Schaefer, 1990).

2. Study site

The study was performed in a beech forest (about 130 years old) located on the limestone plateau (420 m) east of Göttingen (northern Germany) known as Göttinger Wald (cf. Schaefer, 1990). The climate in Göttingen generally is atlantic but in some years the summers are dry, and harsh frost conditions may occur in some winters. Average temperature is 8.7°C and mean annual precipitation is 613 mm. The forest is considered to represent the climax stage of a temperate woodland ecosystem growing on calcareous mull soil characterised by high macrofauna activity (cf. Schaefer, 1990).

3. Materials and methods

In October 1987, January, April and July 1988 soil samples were taken at two different localities in the beechwood. Each season eight randomly distributed samples were taken distant to beech trunks (distance to nearest tree at least 2 m) and eight samples were taken close to beech trunks. Trunk samples were taken directly at the base of the trunk usually between two large roots entering the soil. At each trunk two samples were taken at opposite sides of the trunk. To ensure representative sampling, two samples were taken from each exposition (north, west, south, east). We did not selectively sample the area where most of the stemflow water enters the soil ('Baumfußtasche'; Koenies, 1985) but usually two or three of the eight samples taken each season came from near these localities.

The soil cores (inner diameter 15 cm) were separated into three layers (litter, 0–3 cm soil depth and 3–6 cm soil depth) in the field and transferred to the laboratory. Soil animals were extracted by a modified Kempson apparatus (Schauermann, 1982) and Diplopoda, Isopoda, Lumbricidae and Chilopoda were determined to species level. Scientific names follow Blower (1985), Gruner (1966), Sims and Gerard (1985), Eason (1964) and Eason (1982) for Diplopoda, Isopoda, Lumbricidae, Geophilomorpha and Lithobiomorpha, respectively.

Abiotic factors were measured from soil cores (i.d. 5.5 cm) taken directly beneath the soil core for macrofauna extraction. The following factors were measured in each of the three soil layers: dry weight (24 h at
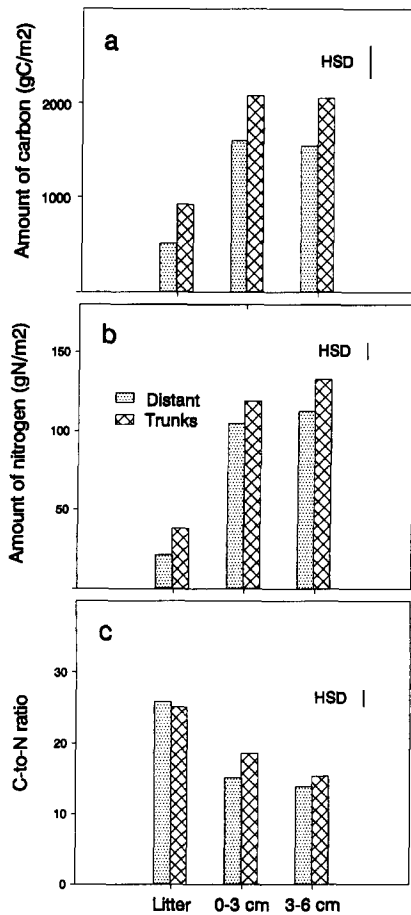
Fig. 1. Amount of carbon (a), nitrogen (b) and C:N ratio (c) in the litter layer, and at soil depths of 0–3 and 3–6 cm distant to trunks and close to trunks in a beechwood on limestone (annual means, $n = 32$; HSD, Tukey's honestly significant difference at $P < 0.05$).

head capsule and biomass in isopods (Strüve-Kusenberg, 1987) and in centipedes (Albert, 1983; Poser, 1988), width of the first tergite and biomass in glomerids, and diameter of mid-body and biomass for other diplopods (Sprengel, 1986).

3.2. Depth distribution

Depth distribution of soil animals was estimated using Usher's mean depth and depth deviation (Usher, 1970). For the litter layer a thickness of 3 cm was used uniformly for both localities studied because we focused on differences in colonisation of different soil layers (i.e. litter and mineral soil). Owing to the increased amount of litter close to beech trunks (see below) this procedure may have resulted in an underestimation of the degree of litter colonisation by soil animals in soil near the trees.

3.3. Statistical analysis

Data on the amount of C and N in soil layers and on C:N ratio were analysed by three-factor ANOVA. Factors were site (distant to trunks and close to trunks), layer (litter layer, 0–3 and 3–6 cm soil depth) and sampling date (October, January, April, July). Density and biomass of animal groups and pH at 0–3 cm soil

105°C), C content and N content (Carlo Erba Elemental Analyser, Milan, Italy). From contents of C and N the C:N ratio was calculated. In addition, soil pH (0.01 M KCl measurement; ratio between soil and KCl solution 1:10 (w/v)) in 0–3 cm soil depth was measured. From data on C and N contents and dry weight of soil layers the amount of C and N in each layer was calculated.

3.1. Biomass determination

Biomass of macrofauna species was determined according to regressions between cylindrical volume and biomass in lumbricids (Scheu, 1992), width of the
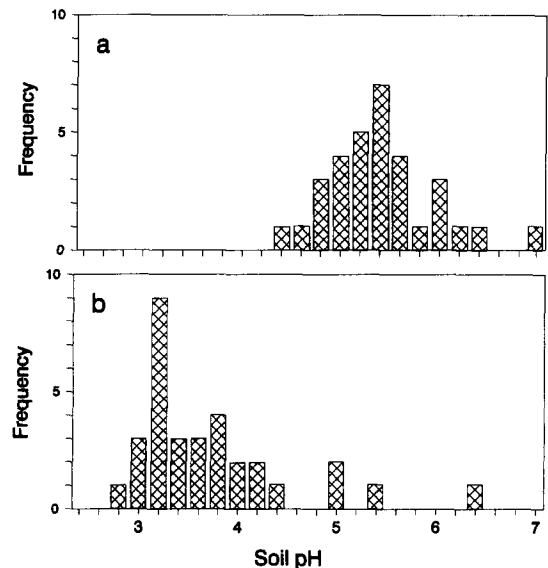

Fig. 2. Frequency diagram of soil pH at a soil depth of 0–3 cm distant to trunks (a) and close to trunks (b) in a beechwood on limestone.

Table 1

Density and biomass of diplopods, isopods, earthworms and centipedes near beech trunks and distant to trunks (annual means of samples taken in four seasons). Differences in density and biomass close to trunks in comparison with values distant to trunks are given as factors with F-values for the effect of site (distant to trunks and close to trunks)

	Density (ind. m^{-2})				Biomass (mg DW m^{-2})			
	Distant	Near	Factor	F-value	Distant	Near	Factor	F-value
Diplopoda	65	63	1.0	<0.1	583	300	0.5	1.9
Isopoda	236	261	1.1	0.1	139	172	1.2	0.2
Lumbricidae	198	65	0.3	30.3***	4954	381	0.1	28.0***
(a) Epigeic	53	60	1.1	0.1	273	357	1.3	0.4
(b) Endogeic	138	5	<0.1	164.7***	2503	13	<0.1	52.5***
(c) Anecique	7	1	0.1	6.4*	2177	12	<0.1	8.2**
Chilopoda	207	396	1.9	5.5*	284	793	2.8	14.4***
(a) Epigeic	141	378	2.7	9.0**	235	782	3.3	16.7***
(b) Endogeic	66	18	0.3	28.0***	48	11	0.2	17.8***

*$P<0.05$; **$P<0.01$; ***$P<0.001$.

depth were analysed by two-factor ANOVA with site and sampling date as factors. Depth distribution of animal groups was analysed by three-factor ANOVA with site, sampling date and soil layer (litter, 0–3 and 3–6 cm soil depth) as factors. Prior to the ANOVAs, data were inspected for homogeneity of variances (Bartlett test and F_{max} test). If necessary, data were log-transformed to approximate homogeneity of variances. As the effects of site and layer were focused on in this study, the effects of seasonal changes (effects of sampling date) are not reported.

Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) available in CANOCO (Ter Braak, 1988) were used to analyse the structure of the macrofauna community distant to beech trunks and close to beech trunks. DCA (detrending by segments) instead of CA was used because an arch effect (artificial correlation between first and second axis) occurred in ordinating the species data. Environmental factors included in CCA were: C and N contents and C:N ratio in the litter layer and at soil depths of 0–3 cm and 3–6 cm and soil pH at 0–3 cm. Of these variables, the C:N ratio in the litter layer and at 0–3 cm was excluded from further analysis because of T-values considerably below 2.1 (cf. Ter Braak, 1988). The amount of N in the three soil layers studied was also excluded because of multicollinearity with the amount of C in the respective layers. To test the significance of the relation between species and environmental variables in CCA the Monte Carlo Permutation Test avail-

able in CANOCO was used and the significance of the first ordination axis was tested.

4. Results

4.1. Abiotic factors

Generally, close to beech trunks the amount of C and N significantly exceeded that distant to trunks ($F=41.7$, $P<0.001$ and $F=16.1$, $P<0.001$ for the effect of site on the amount of C and N, respectively; Fig. 1). The amount of C in the litter layer, at 0–3 and 3–6 cm close to trunks exceeded that distant to trunks by factors of 1.8, 1.3 and 1.3, respectively. Respective factors for N were 1.8, 1.1 and 1.2. C:N ratio of litter and soil materials also differed between sites but differences depended on soil layer ($F=4.9$, $P<0.01$ for the interaction of site and layer). C:N ratios in the litter layer distant to trunks and close to trunks were similar, but close to trees at 0–3 ($P<0.05$) and 3–6 cm soil depth (NS) they were lower than corresponding values distant to trees.

Soil pH (0–3 cm soil depth) distant to trunks varied between 4.4 and 7.0 and was on average 5.3 (Fig. 2). In contrast, soil pH close to beech trunks varied between 2.8 and 6.4 and was on average 3.7. Differences between sites were highly significant ($F=96.9$, $P<0.001$).
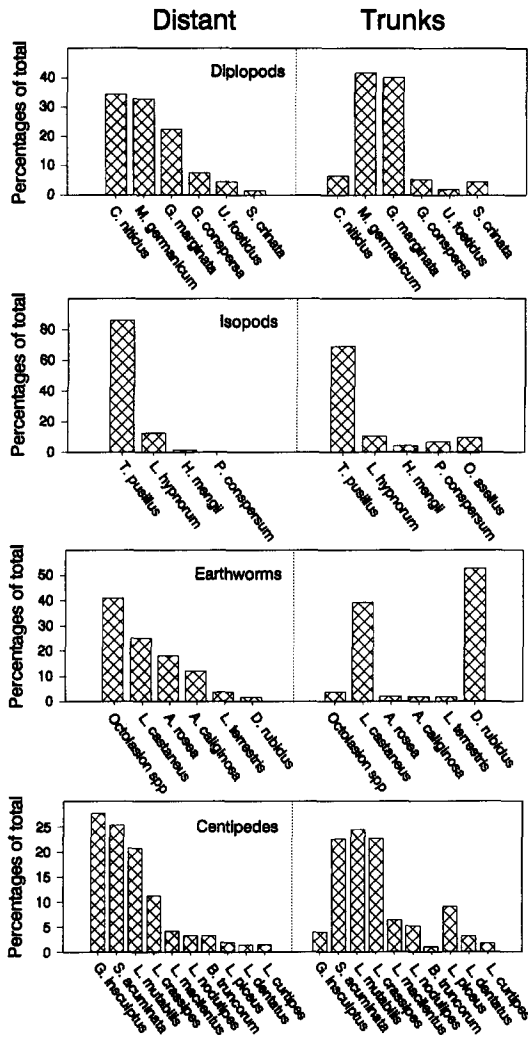
Fig. 3. Dominance structure (contribution of each species to total number of animals; annual means) of diplopods, isopods, earthworms and centipedes distant to tree trunks and close to trunks in a beechwood on limestone (for full species names see Appendix A).

4.2. Density and biomass

The mean annual density of saprophagous soil macroarthropods near beech trunks was very similar to that distant to trunks (Table 1). In contrast, lumbricids were significantly less abundant near trunks (33% of abundance distant to trunks). In terms of biomass the saprophagous macrofauna community distant to trunks (annual mean of 5676 mg dry weight (DW) m^{-2}) was dominated by earthworms (4954 mg DW m^{-2}). Con-

siderably lower biomass of the saprophagous macrofauna near trunks (15% of that distant to trunks) was mainly caused by lower density of lumbricids.

Earthworms of different ecological groups (cf. Bouché, 1977) responded differently to trunk vicinity. Density and biomass of epigeic species near trunks was similar to that distant to trunks, whereas the density and biomass of endogeic species was reduced dramatically to 4% and 0.5% of values distant to trunks, respectively. The anecique species *Lumbricus terrestris* was also less abundant close to beech trunks (90% less) and in particular, the biomass of this species appeared to be strongly reduced near to trees (to 0.6% of the values distant to trunks). It should be noted, however, that only specimens inhabiting the litter layer and the upper 6 cm of the mineral soil are considered in this study which underestimates numbers of deeper burrowing species like *Lumbricus terrestris*.

Centipedes were generally more abundant near beech trunks than distant to trunks (factor 1.9; Table 1). The difference was even more pronounced in terms of biomass (increase by a factor of 2.8). Higher abundance of centipedes resulted from increased density of mainly the litter-inhabiting lithobiids and the litter-inhabiting scoleoplanid *Strigamia acuminata* (2.7 times the density distant to trunks), whereas the soil-inhabiting geophilid species were less abundant near beech trunks (30% of the density distant to trunks).

Table 2
Depth distribution of diplopods, isopods, earthworms and centipedes near beech trunks and distant to trunks (annual mean percentages per layer) with F-values for the interaction of site (distant to trunks and close to trunks) and layer (litter, 0–3 and 3–6 cm soil depth)

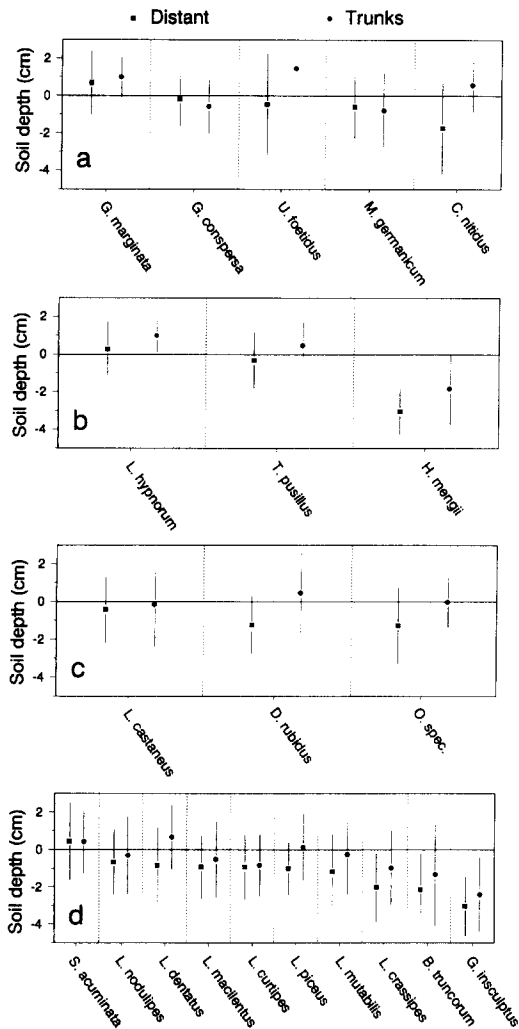|	Distant			Near			F-value
	Litter	0–3 cm	3–6 cm	Litter	0–3 cm	3–6 cm	
Diplopoda	43	34	22	53	39	8	0.6
Isopoda	47	56	6	71	24	6	3.7*
Lumbricidae							
(a) epigeic	42	48	10	70	23	7	3.4*
(b) endogeic	22	47	31	80	20	0	10.4***
Chilopoda							
(a) epigeic	31	58	11	45	47	8	5.1*
(b) endogeic	0	42	58	21	32	47	4.4*

*$P < 0.05$; ***$P < 0.001$.

Fig. 4. Depth distribution (Usher's mean depth with depth deviation; see Section 3) of diplopods (a), isopods (b), earthworms (c) and centipedes (d) distant to trunks and close to trunks in a beechwood on limestone (for full species names see Appendix A).

4.3. Dominance structure of Diplopoda, Isopoda, Lumbricidae and Chilopoda

The dominance structure in each of the macrofauna groups studied was strongly affected by tree vicinity, but alterations were most pronounced in earthworms (Fig. 3). In diplopods *Cylindroiulus nitidus* dominated distant to beech trunks, whereas close to trunks this species contributed only 6.4% to total diplopod density. The contribution of both *Mycogona germanicum* and *Glomeris marginata* to diplopod density was higher

near beech trunks (42% and 40 %, respectively) in comparison to localities distant to trunks (33% and 22%, respectively). The most significant change in isopods was the occurrence of a fifth species (*Oniscus asellus*) close to beech trunks which contributed 10% to total isopod density at this locality.

In earthworms, species of the endogenic genus *Octolasion* dominated distant to beech trees (the ratio between adult *Octolasion tyrtaeum* and *Octolasion cyaneum* shows that the former contributed most to the density of *Octolasion* species), whereas close to beech trunks *Octolasion* species contributed only 3.6% to total earthworm density. The contribution of the other two endogeic earthworm species (*Aporrectodea caliginosa* and *Aporrectodea rosea*) was also strongly reduced close to beech trunks and in contrast to localities distant to trunks where this earthworm group dominated (70.6% of total), endogeic species contributed only 7.6% to total earthworm density close to beech

Table 3

Faunal gradients near beech trunks and distant to trunks. Eigenvalues of the first and second ordination axes obtained by detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA). For CCA the species–environment correlation coefficients are also given

	Distant to trunks		Near trunks	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues DCA	0.22	0.12	0.33	0.26
Eigenvalues CCA	0.13	0.06	0.23	0.13
Correlation coefficients CCA	0.88	0.78	0.82	0.68

Table 4

Canonical coefficients and correlation coefficients of environmental variables (pH at 0–3 cm soil depth, amount of C in the litter layer (C lit), at 0–3 cm soil depth (C 0-3), at 3–6 cm soil depth (C 3-6) and C:N ratio at 3–6 cm soil depth (C:N 3-6)) with the first two axes in CCA ordination of the near beech trunk data (for details see text)

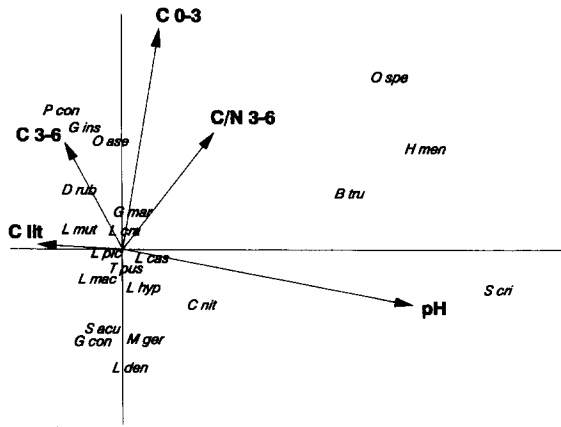|	Canonical coefficients		Correlation coefficients	
	Axis 1	Axis 2	Axis 1	Axis 2
pH	0.47	−0.05	0.80	−0.15
C lit	−0.16	−0.03	−0.25	0.02
C 0-3	0.11	0.24	0.10	0.64
C 3-6	−0.11	0.12	−0.17	0.35
C:N 3-6	0.10	0.15	0.29	0.39

Fig. 5. Biplot of diplopod, isopod, earthworm and centipede species close to beech trunks. Arrows indicate environmental gradients. C lit, amount of carbon in the litter layer; C 0-3, amount of carbon at 0–3 cm soil depth; C 3-6, amount of carbon at 3–6 cm soil depth; C/N 0-3, C:N ratio at 3–6 cm soil depth; pH, soil pH at 0–3 cm soil depth). Only species which were found in at least 3 independent samples were included in the analysis (for full species names see Appendix A).

trunks. In contrast to endogeic species, the contribution of epigeic species to total earthworm density near beech trunks strongly exceeded that distant to trunks. This was particularly the case with *Dendrodrilus rubidus*, which was least abundant distant to trunks but which flourished in the tree vicinity, contributing 49% to total earthworm density at this locality.

The most significant difference in the structure of the centipede community close to beech trunks was the lower abundance of *Geophilus insculptus*. This species dominated at localities distant to beech trees (27.6% of total) but contributed only 3.9% to total centipede density close to beech trunks. In contrast to *Geophilus insculptus*, the contribution of *Lithobius crassipes* to total centipede density close to beech trunks exceeded that distant to trunks.

4.4. Depth distribution

Each of the animal groups studied except diplopods were more concentrated in the upper soil profile near beech trunks than distant to trunks (Table 2). Isopods, epigeic and endogeic earthworms which were most abundant at 0–3 cm soil depth distant to trunks predominantly colonised the litter layer in trunk vicinity. Epigeic and endogeic centipedes were also more abundant

in the litter layer in trunk vicinity than distant to trunks.

Generally in each of the animal groups studied, the depth distribution of species was similar distant and close to trunks or animals were closer to the surface in the soil profile close to beech trunks (Fig. 4). Each of the isopod species which were present at both localities occurred more in the upper soil profile close to beech trunks. In earthworms this tendency to inhabit upper soil layers was most pronounced for *Dendrodrilus rubidus* and *Octolasion* species. In centipedes, six (*Lithobius dentatus*, *Lithobius piceus*, *Lithobius mutabilis*, *Lithobius cassipes*, *Brachygeophilus truncorum*, *Geophilus insculptus*) of the ten species lived more than 5 mm up in the soil profile close to beech trunks. None of the other species showed the opposite trend. In diplopods, *Cylindroiulus nitidus*, which predominantly colonised the upper mineral soil distant to trunks, colonised almost exclusively the litter layer in trunk vicinity.

4.5. Factors governing the structure of the macrofauna community

Eigenvalues of the first and second axes of DCA ordination were considerably higher near beech trunks than distant to trunks, indicating that the faunal gradient was more pronounced near beech trunks (Table 3). Including environmental variables in direct gradient analysis (CCA) caused the eigenvalues to drop considerably, indicating that the chosen environmental variables are not sufficient to explain the variance in species data. However, the first axis of the trunk area data was highly significant ($P < 0.01$; Monte Carlo test) and 73% of the variance in the species–environment data was explained by the first two axes.

The first axis of this data set represents mainly soil pH (0–3 cm soil depth), whereas the second axis represents mainly the amount of C at 0–3 cm soil depth. The amount of C in the litter layer, at 3–6 cm soil depth and the C:N ratio at 3–6 cm were of minor importance (Table 4, Fig. 5).

Canonical coefficients and correlation coefficients (cf. Ter Braak, 1988) show that soil pH was related best to species data (Table 4). Presumably, soil acidity is one of the important factors structuring the soil fauna community near beech trunks.

As indicated by their position in Fig. 5 the most acid tolerant species in lumbricids was *Dendrodrilus rubi-*

dus, whereas *Octolasion* species preferred localities higher in pH. Generally, most species living deeper in the soil (*Octolasion* spp., *Haplophthalmus mengii*, *Brachygeophilus truncorum*, *Stygioglomeris crinata*, *Cylindroiulus nitidus*; cf. Fig. 4) appeared to be more acid sensitive and preferentially occurred at localities of higher pH close to beech trunks. Most of the other species preferentially occurred at localities with intermediate pH and could therefore not be separated clearly along the first CCA axis.

5. Discussion

In recent years the effects of stemflow induced changes in beech forests have gained considerable attention because these changes were assumed to predict changes in the whole ecosystem caused by increased input of pollutants (Jochheim, 1985; Koenies, 1985; Schäfer, 1988; Kopeszki, 1991; Stöckli, 1991; Falkengren-Grerup and Björn, 1991). Studies on changes in density and composition of the soil fauna focused on mesofauna species (mainly Collembola and Acari; Kopeszki, 1991; Stöckli, 1991) and very little is known of stemflow induced changes in the soil macrofauna community. Although focusing on Collembola and Acari, Kopeszki (1991) also reported a decrease in density of myriapods near to trees to 10% of that distant to trunks. It is surprising that little information is available on changes in the soil macrofauna community because macrofauna species are important for the formation of mull–humus soils in forests on base-rich parent rock (Kubiëna, 1948; Bal, 1982; Scheu, 1987) and most of the macrofauna (i.e. earthworms, diplopods and isopods) species are known to be acid sensitive.

From studies on the structure of the soil fauna community in mull and moder soils (e.g. Petersen and Luxton, 1982; Schaefer and Schauermann, 1990) it is expected that an increase in acid loading will result in an increase in density of mesofaunal groups, e.g. collembolans, enchytraeids and oribatids, whereas the density of macrofauna species will decrease. However, investigations on the response of mesofaunal groups to increased input of protons are ambiguous. Bååth et al. (1980) reported a decrease in density of enchytraeids, little response of mites but an increase in density of collembolans in artificially acidified plots in a conif-

erous forest. In contrast, in stemflow affected localities in beech forests, Kopeszki (1991) found a decrease in density of collembolans and mites. However, investigating density and species composition of collembolans near to trees in the Göttinger Wald, Wolters (1985) reported a 1.6-fold increase in density near to trees but he also reported that the density of certain species was reduced. Presumably, differences in the numerical response of collembolans in total to tree vicinity are related to sensitivity of the Collembola species present to acidification (and increased loading by heavy metals; Hågvar, 1990). Results of the present study indicate a more conclusive response of macrofauna species to elevated soil acidification and to changes in other environmental factors near to trees of the studied beechwood on limestone.

As indicated by CCA, soil pH was the main factor correlating with the structure of the soil macrofauna community near to trees. In contrast, at localities distant to trunks the studied environmental factors were of minor importance and the gradient in species data was less pronounced. Generally, soil macrofauna species responded differently to distance from the tree. The density of centipedes near to trees markedly exceeded that distant to trunks, and due to high density of large lithobiids and the scoleoplanid *Strigamia acuminata*, biomass of centipedes near to trees was exceptionally high. In contrast to these centipede species, which predominantly colonise the litter layer, density of the endogeic centipede species (particularly *Geophilus insculptus* but also *Brachygeophilus truncorum*) was strongly reduced near to trees, on average to 30% of that distant to trunks. Similarly, the density of each of the endogeic earthworm species present (*A. caliginosa*, *A. rosea*, *Octolasion* spp.) was dramatically reduced, on average to 4% of that distant to trunks. It is interesting to note that the diplopod species *Mycogona germanicum* dominated close to trees. This species is known to be the only diplopod colonising moder-type beech forests in northern Germany (Ellenberg et al., 1986).

Epigeic earthworm species, particularly *Dendrodrilus rubidus* (and *Dendrobaena octaedra*), is known to tolerate moderate soil acidity and often dominates in moder- and mor-type forest soils (e.g. Nordström and Rundgren, 1973; Terhivuo, 1989). The lower number of earthworms in the mineral soil close to beech trunks presumably was caused by increased acid loading, but

heavy metals which also accumulate near to trees (Koenies, 1985; Schäfer, 1988) may also have contributed to the decline in soil-inhabiting earthworms. It is well documented that low pH conditions adversely affect the endogeic earthworm species present in the beechwood studied (e.g. Edwards and Lofty, 1977) but Bengtsson et al. (1986) showed that the combination of low pH and heavy metal pollution is most detrimental for earthworm development.

The increase in density of lithobiid centipedes near to trees presumably was caused by an increase in habitat space (amount of litter in the litter layer) and an accompanied increase in the density of prey species (e.g. Collembola; see above). However, saprophagous soil macroarthropods did not respond with an increase in density near to trees even though food substrate (litter material) was more abundant at this locality. In addition, due to the stemflow input, the soil close to beech trunks is moister and therefore presumably more favourable for litter-inhabiting macrofauna species. Benecke (1979) calculated that 14% of the precipitation in beech forests runs down beech trees, resulting periodically in exceptionally wet conditions close to beech trunks. More humid conditions in the litter layer may also have contributed to the preferential colonisation of this layer by soil animals. Inclusion of soil moisture presumably could have improved the CCA eigenvalues and made them less different from those of the DCA analysis. Differences in habitat structure (e.g. packing of the litter layer, density of roots) near to trees and distant to tree trunks may also have contributed to the observed differences in the soil animal community structure at these localities.

The higher amount of litter in the litter layer may have resulted from reduced decomposition rates due to increased proton and heavy metal loading. However, it may also have resulted from additional litter material deposited during windy periods or a low density of soil-inhabiting earthworms responsible for the removal of litter into the mineral soil (bioturbation). Pop (1987) assumed that the accumulation of litter in Romanian beech forests resulted from the disappearance of earthworms due to pollution with sulphur and heavy metals. Investigating changes in the structure of organic layers due to increased input of protons in a beech–oak–hornbeam forest in northern Germany, Von Buch (1981) concluded that the formation of moder at higher proton loadings resulted from reduced bioturbation activity of

Lumbricus terrestris. We also observed moder-type humus forms at various locations near to trees in the beechwood studied, which is situated on limestone. Similar observations in other beechwoods on different parent rock were reported by Jochheim (1985), Koenies (1985) and Schäfer (1988). From the results of laboratory experiments, it has been concluded that bioturbation by endogeic earthworms is important in the maintenance of mull-structured beechwood ecosystems (Scheu, 1987; Scheu and Wolters, 1991b).

Investigating the soil fauna at localities close to cut beech trees we also found a reduced density of soil-inhabiting earthworms and increased amount of carbon in the litter layer in comparison with sites distant to stumps (Poser, 1990; Scheu, 1990). Soil pH close to stumps was on average between that at the base of beech trees and at localities distant to trees. Investigating the reversibility of stemflow induced soil acidification in Swedish beech forests, Falkengren-Grerup and Björn (1991) found some improvement in soil proton loading during 15 years after felling but acidification was shown to last for more than 25 years. This indicates that detrimental conditions for soil-inhabiting macrofauna at stemflow affected sites in beechwoods last for several decades which should be studied in more detail in further investigations.

In conclusion, our results support the hypothesis of Ulrich (1987) that the decomposer community retreats from the mineral soil at elevated soil proton loading which results in the formation of a refuge of the decomposer community in organic soil layers. Because nutrients are mineralised predominantly in these layers tree roots also concentrate there and are exposed to more fluctuating environmental conditions, particularly in soil moisture, which may result in a destabilisation of the ecosystem. Our findings indicate that the concentration of the decomposer community in the litter layer results from a dieback of acid-sensitive soil-inhabiting macrofauna species, mainly earthworms responsible for bioturbation, and their part in the recycling of nutrients is left to species adapted to the more variable environmental conditions in organic layers. There is an urgent need for experimental manipulations of soil pH in more alkaline beech forests to confirm causal relationships.

Acknowledgements

Appendix A

Species list.

Diplopoda: *Cylindroiulus nitidus*; *Glomeris marginata*; *Glomeris conspersa*; *Mycogona germanicum*; *Stygioglomeris crinata*; *Unciger foetidus*.

Isopoda: *Haplophthalmus mengii*; *Ligidium hypnorum*; *Oniscus asellus*; *Porcellium conspersum*; *Trichoniscus pusillus*.

Lumbricidae: *Aporrectodea caliginosa*; *Aporrectodea rosea*; *Dendrodrilus rubidus*; *Lumbricus castaneus*; *Lumbricus terrestris*; *Octolasion tyrtaeum*; *Octolasion cyaneum*.

Chilopoda: *Brachygeophilus truncorum*; *Geophilus insculptus*; *Lithobius crassipes*; *Lithobius curtipes*; *Lithobius dentatus*; *Lithobius macilentus*; *Lithobius mutabilis*; *Lithobius nodulipes*; *Lithobius piceus*; *Strigamia acuminata*.

References

Abrahamsen, G., Hovland, J. and Hågvar, S., 1980. Effects of artificial acid rain and liming on soil organisms and the decomposition of organic matter. In: T.C. Hutchinson and M. Hadas (Editors), Effects of Acid Precipitation on Terrestrial Ecosystems. Plenum Press, New York, pp. 341–362.

Albert, A.M., 1983. Life cycle of Lithobiidae—with a discussion of the r- and K-selection theory. Oecologia, 56: 272–279.

Bååth, E., Berg, B., Lohm, U., Lundgren, B., Lundkvist, H., Rosswall, T., Söderström, B. and Wirén, A., 1980. Effects of experimental acidification and liming on soil organisms and decomposition in a Scots pine forest. Pedobiologia, 20: 85–100.

Bal, L., 1982. Zoological Ripening of Soils. Centre for Agricultural Publishing and Documents, Wageningen.

Benecke, P., 1979. Der Wasserumsatz eines Buchen- und Fichtenwaldökosystems im Hochsolling. Thesis, University of Göttingen.

Bengtsson, G., Gunnarsson, T. and Rundgren, S., 1986. Effects of metal pollution on the earthworm *Dendrobaena rubida* (Sav.) in acidified soils. Water, Air Soil Pollut., 28: 361–383.

Blower, J.G., 1985. Millipedes. Synopses of the British fauna 35, Brill/Backhuys, London.

Bouché, M.B., 1977. Strategies lombriciennes. In: U. Lohm and T. Persson (Editors), Soil Organisms as Components of Ecosystems. Ecol. Bull. (Stockholm), 25: 122–132.

Eason, E.H., 1964. Centipedes of the British Isles. Warne, London.

Eason, E.H., 1982. A review of the northwest European species of Lithobiomorpha with a revised key to their identification. Zool. J. Linn. Soc. London, 74: 9–33.

Edwards, C.A. and Lofty, J.R., 1977. Biology of Earthworms, 2nd edn. Chapman and Hall, London.

Ellenberg, H., Mayer, R. and Schauermann, J., 1986. Ökosystemforschung-Ergebnisse des Sollingprojektes. Ulmer, Stuttgart.

Falkengren-Grerup, U. and Björn, L., 1991. Reversibility of stemflow-induced soil acidification in Swedish beech forests. Environ. Pollut., 74: 31–37.

Gruner, H.E., 1966. Die Tierwelt Deutschlands: Krebstiere oder Crustacea. 5: Isopoda, Vol. 2. Fischer, Jena.

Hågvar, S., 1990. Reactions to soil acidification in microarthropods: Is competition a key factor? Biol. Fertil. Soils, 9: 178–181.

Jochheim, H., 1985. Der Einfluß des Stammablaufwassers auf den chemischen Bodenzustand und die Vegetationsdecke in Altbuchenbeständen verschiedener Waldgesellschaften. Ph.D. Thesis, University of Kassel.

Koenies, H., 1985. Über die Eigenart der Mikrostandorte im Fußbereich der Altbuchen unter besonderer Berücksichtigung der Schwermetallgehalte in der organischen Auflage und im Oberboden. Ber. Forschungszentrums Waldökosysteme, A9: 1–288.

Kopeszki, H., 1991. Abundanz und Abbauleistung der Mesofauna (Collembolen) als Kriterien für die Bodenzustandsdiagnose im Wiener Buchenwald. Zool. Anz., 227: 136–159.

Kubiëna, W.L., 1948. Entwicklungslehre des Bodens. Springer, Wien.

Nordström, S. and Rundgren, S., 1973. Associations of lumbricids in Southern Sweden. Pedobiologia, 13: 301–326.

Ohtonen, R., Ohtonen, A., Luotonen, H. and Markkola, A.M., 1992. Enchytraeid and nematode numbers in urban, polluted Scots pine (*Pinus sylvestris*) stands in relation to other soil biological parameters. Biol. Fertil. Soils, 13: 50–54.

Persson, T., Lundkvist, H., Wirén, A., Hyvönen, R. and Wessén, B., 1989. Effects of acidification and liming on carbon and nitrogen mineralization and soil organisms in mor humus. Water, Air Soil Pollut., 45: 77–96.

Petersen, H. and Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition process. Oikos, 39: 288–388.

Pop, V.V., 1987. Ecological consequences of the diappearance of lumbricids in the course of pollution in a beech forest in the Ampoi Valley (Apuseni Mountains) [Romania]. Stud. Cercet. Biol. Ser. Biol. Anim., 39: 88–92.

Poser, G., 1988. Chilopoden als Praedatoren in einem Laubwald. Pedobiologia, 31: 261–281.

Poser, G., 1990. Die Hundertfüßer (Myriapoda, Chilopoda) eines Kalkbuchenwaldes: Populationsökologie, Nahrungsbiologie und Gemeinschaftsstruktur. Ber. Forschungszentrums Waldökosysteme, A 71: 1–213.

Rundgren, S., 1994. Earthworms and soil acidification: Liming of acidified coniferous forest soils in Southern Sweden. Pedobiologia, 38: 519–529.

Schaefer, M., 1990. The soil fauna of a beech forest on limestone: Trophic structure and energy budget. Oecologia, 82: 128–136.

Schaefer, M., 1991. Secondary production and decomposition. In: E. Röhrig and B. Ulrich (Editors), Temperate Deciduous Forests. Ecosystems of the world 7. Elsevier, Amsterdam, pp. 175–218.

Schaefer, M. and Schauermann, J., 1990. The soil fauna of beech forests: Comparison between a mull and a moder soil. Pedobiologia, 34: 299–314.

Schäfer, H., 1988. Auswirkungen der Deposition von Luftschadstoffen auf die Streuzersetzung in Waldökosystemen—Eine Fallstudie an den durch Stammablaufwasser stark säure- und schwermetallbelasteten Baumfuß-Bodenbereichen alter Buchen. Ber. Forschungszentrums Waldökosysteme, A 37: 1–244.

Schauermann, J., 1982. Verbesserte Extraktion der Bodenfauna im Vielfachgerät nach Kempson und Macfadyen. Kurzmitteilungen aus dem SFB, 135-1: 47–52.

Scheu, S., 1987. The role of substrate feeding earthworms (Lumbricidae) for bioturbation in a beechwood soil. Oecologia, 72: 192–196.

Scheu, S., 1990. Die saprophage Makrofauna (Diplopoda, Isopoda und Lumbricidae) in Lebensräumen auf Kalkgestein: Sukzession und Stoffumsatz. Ber. Forschungszentrums Waldökosysteme, A 57: 1–302.

Scheu, S., 1992. Changes in the lumbricid coenosis during secondary succession from a wheat field to a beechwood on limestone. Soil Biol. Biochem., 24: 1641–1646.

Scheu, S. and Sprengel, T., 1989. Die Rolle der endogäischen Regenwürmer im Ökosystem Kalkbuchenwald und ihre Wechselwirkung mit saprophagen Makroarthropoden. Verh. Ges. Ökol., 17: 237–243.

Scheu, S. and Wolters, V., 1991a. Buffering of the effect of acid rain on decomposition of C-14-labelled beech leaf litter by saprophagous macroinvertebrates. Biol. Fertil. Soils, 11: 285–289.

Scheu, S. and Wolters, V., 1991b. The influence of fragmentation and bioturbation on the decomposition of C-14-labelled beech leaf litter. Soil Biol. Biochem., 23: 1029–1034.

Sims, R.W. and Gerard, B.M., 1985. Earthworms. Synopses of the British Fauna 31, Brill/Backhuys, London.

Sprengel, T., 1986. Die Doppelfüßer (Diplopoda) eines Kalkbuchenwaldes und ihre Funktion beim Abbau der Laubstreu. Ph.D. Thesis, University of Göttingen.

Stöckli, H., 1991. Influence of stemflow upon the decomposing system in two beech stands. Rev. Ecol. Biol. Sol, 28: 265–286.

Strüve-Kusenberg, R., 1987. Die Asseln eines Kalkbuchenwaldes. Ph.D. Thesis, University of Göttingen.

Ter Braak, C.J.F., 1988. CANOCO—A FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principle components analysis and redundancy analysis. Tech. Rep., TNO Institute, Wageningen, Netherlands.

Terhivuo, J., 1989. The Lumbricidae (Oligochaeta) of southern Finland: Species assemblages, numbers, biomass and respiration. Ann. Zool. Fenn., 26: 1–23.

Ulrich, B., 1987. Stability, elasticity, and resilience of terrestrial ecosystems with respect to matter balance. In: E.D. Schulze and H. Zwölfer (Editors), Potentials and Limitations of Ecosystem Analysis. Ecological Studies 61. Springer, Berlin, pp. 11–49.

Usher, M.B., 1970. Seasonal and vertical distribution of soil arthropods: Collembola. Pedobiologia, 38: 224–236.

Von Buch, M.-W., 1981. Einfluß von Schwefelimmissionen auf Waldhumusformen am Beispiel eines Buchenmischwaldes südlich von Hannover. In: B. Ulrich and J. Pankrath (Editors), Effects of Accumulation of Air Pollutants in Forest Ecosystems. Reidel, Dordrecht, pp. 247–255.

Wolters, V., 1985. Untersuchungen zur Habitatbindung und Nahrungsbiologie der Springschwänze (Collembola) eines Laubwaldes unter besonderer Berücksichtigung ihrer Funktion in der Zersetzerkette. Ph.D. Thesis, University of Göttingen.

Wolters, V. and Schaefer, M., 1994. Effects of acid deposition on soil organisms and decomposition processes. In: D.L. Godbold and A. Hüttermann (Editors), Effects of Acid Rain on Forest Processes. Wiley, New York, pp. 83–127.