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## Soil faunal activity as measured by the bait-lamina test in monocultures of 14 tree species in the Siemianice common-garden experiment, Poland

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### ABSTRACT

In 1970–1971, 53 tree monoculture study plots were established (20 m × 20 m) in Siemianice (SW Poland) by clearcutting of an 81-year-old pine forest. The following 14 tree species were planted there with 3 or 6 replicates: *Abies alba*, *Acer pseudoplatanus*, *Acer platanoides*, *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, *Quercus robur*, *Tilia cordata*, *Pinus nigra*, *Quercus rubra* and *Pseudotsuga menziesii*. During 34 years of monitoring the soil chemistry, ground floral composition and litter decomposition rates differed strongly between some tree species. The aim of this study was to determine whether tree species also influenced soil faunal activity.

In June and October 2006, 50 bait-laminas were distributed in the center of each study plot and exposed for 42 and 33 days, respectively. The soil faunal activity levels in plots of the same tree species were similar but differed between monocultures, being particularly high in monocultures of *L. decidua* and *P. abies*. These differences cannot be directly attributed to the soil chemical characteristics. Soil faunal activity was significantly higher in summer than in autumn, although soil moisture was lower in summer (12% at the beginning and 4% at the end of the period) than in autumn (10% and 12%, respectively). The main factor affecting seasonal differences in soil faunal activity seems to be soil temperature, which was significantly higher in summer (mean 19.3 °C) than in autumn (mean 10.1 °C). Faunal activity differed also along the soil profile, with maximum at 0–4 cm depth.

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### 1. Introduction

Soil animals play a key role in ecosystem functioning, affecting litter decomposition as well as the activity of other animals and microorganisms. Comparisons of soil faunal structure and function between different ecosystems suffer from uncontrolled multiple effects, such as local climatic conditions, soil properties (substrate, structure, pH, nutrient content), the species composition of vegetation, and the regional species pools from which local communities can form. All these factors can influence the species composition, density and activity of soil animals.

The Siemianice common-garden experiment (Reich et al., 2005; Hobbie et al., 2006) provides a unique opportunity for soil faunal studies under controlled conditions. In 1970–1971, monocultures of 14 tree species were planted in 3 or 6 replicate plots there. This experimental design obviates the effect of environmental conditions such as climate, and minimizes the variability of other factors such as soil properties. It also allows the variation of a given effect to be examined using the replicates of particular tree species on several plots. In previous studies (Reich et al., 2005; Hobbie et al.,

2006, 2007; Dauer et al., 2007), many biogeochemical and structural parameters of the soil were found to differ greatly between monocultures. In the course of more than 30 years, the different tree species strongly affected the biogeochemistry of the litter/soil system and the forest litter decomposition rates, acting directly through the different chemical compositions of the litter, or indirectly through the effect of litter quality upon earthworms (Reich et al., 2005; Hobbie et al., 2006). The dynamics of organic matter in the soil (including mineral horizons) were also strongly influenced by the overstory trees (Hobbie et al., 2007). Hobbie et al. (2006) suggested that microbial decomposition rates are modified mostly by differences in lignin content, while Ca content in litter can influence the activity of earthworms. Although earthworms seem to play an important role in accelerating decomposition rates of deciduous trees' litter (Hobbie et al., 2006), many other detritivores may contribute as well. No other invertebrate taxon in the Siemianice experiment has been studied in that respect.

Systematic studies of soil fauna are very laborious, making it difficult to monitor many sites at the same time. A precise assessment of the role of different groups of soil animals requires the involvement of taxonomists with different specializations, because species may differ in feeding habits even within a single genus. Information limited to the density and biomass of taxa does not tell us their position in the food web or their role in soil functioning. Moreover,

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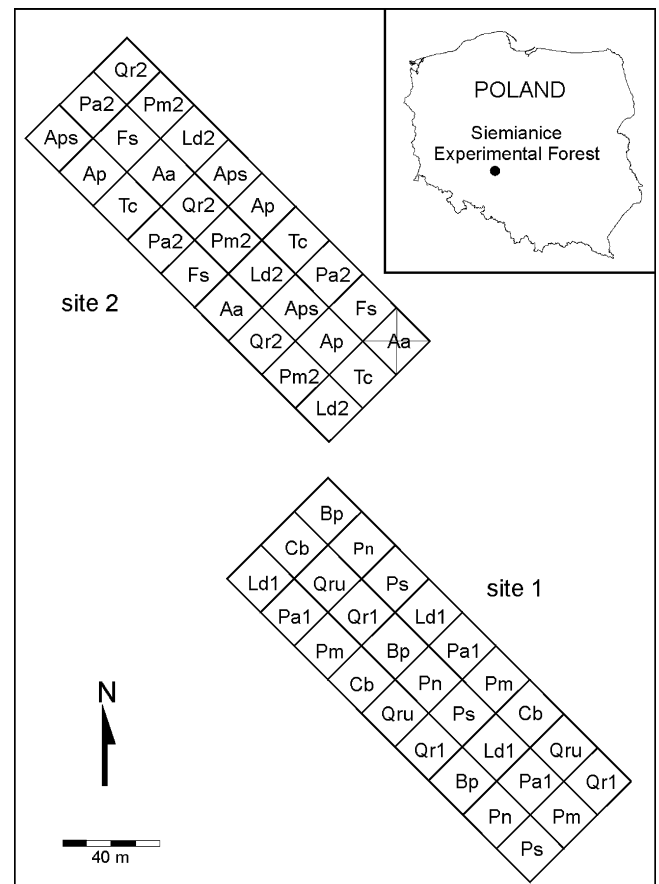
the spatial heterogeneity of soil and litter (Laskowski et al., 2003) requires sampling from many places at each study site. For some purposes, however, for example when functional effects rather than community structure are studied, it may be enough to compare soil faunal activity between sites, even without knowledge of species composition and density. This may be done with the use of bait-laminas, a method introduced by Von Törne (1990). The bait-lamina method estimates the feeding activity of soil animals, measured as the proportion of exposed baits removed by soil invertebrates. The test seems to be indicative of the activity of soil fauna (especially earthworms) and not of microflora, whereas other tests (cotton strip and wheat straw) are directly indicative of microbial activity (Kratz, 1998; Van Gestel et al., 2003). Because of its simplicity the bait-lamina method has recently been used frequently for different purposes, for example to study forest soil faunal activity under cold-moderate (Gongalsky et al., 2004) and tropical climatic conditions (Römbke et al., 2006), in grasslands (Spehn et al., 2000; Hamel et al., 2007), and in response to fertilization and liming (Geissen and Brümmer, 1999), different agricultural practices (Jacometti et al., 2007; Reinecke et al., 2008), metals contamination (Filzek et al., 2004; André et al., 2009) and pesticides (Reinecke et al., 2002). The bait-lamina method has been used in soil-ecological experiments at the landscape scale as well (Joschko et al., 2008). It has been proposed as an international standard test (Römbke et al., 2006). The numerous studies using bait-laminas have not yet provided a body of accessible data on the repeatability of results obtained in the field at the same site in consecutive trials, that is, on the robustness of the method when sources of variation are uncontrolled.

The goals of our study were to determine (by the bait-lamina method) whether tree species differently affect forest soil faunal activity, and to see whether the patterns observed are repeatable and can be attributed to the chemical properties of the soil.

## 2. Methods

### 2.1. Study site and experimental plots

The study was conducted in Siemianice, southwestern Poland (51°14.87'N; 18°06.35'E, alt. 150 m a.s.l.), in the Experimental Forest of the Academy of Agriculture of Poznań (Fig. 1). The climate of the region is transitional between maritime and continental, with 591 mm mean annual precipitation and 8.2 °C mean annual temperature. The soils are formed on sandy outwash overlying finer textured glacial deposits (Reich et al., 2005). The study plots were established in 1970–1971 by clearcutting of an 81-year-old pine forest (Szymański, 1982). The stumps were removed and the soil plowed to 60 cm depth. Two study sites (Site 1 and Site 2) were established, each divided into 27 plots of 400 m<sup>2</sup> (20 m × 20 m; Fig. 1). The study sites were fenced. The study plots were planted as monocultures with seedlings of 14 tree species (species abbreviations in parentheses). Eleven are native: *Abies alba* (Aa), *Acer platanoides* (Ap), *Acer pseudoplatanus* (Aps), *Betula pendula* (Bp), *Carpinus betulus* (Cb), *Fagus sylvatica* (Fs), *Larix decidua* (Ld), *Picea abies* (Pa), *Pinus sylvestris* (Ps), *Quercus robur* (Qr) and *Tilia cordata* (Tc). Three are exotics: *Pinus nigra* (Pn), *Quercus rubra* (Qru) and *Pseudotsuga menziesii* (Pm). Eight of them are deciduous trees and six are conifers. All species were planted in three replicate plots at one of the sites (except *A. alba* with two replicates), but four of them (*L. decidua*, *P. abies*, *P. menziesii* and *Q. robur*) were planted at both sites, giving six replicates of each. Those planted at Site 1 are denoted "1", and those planted at Site 2 are denoted "2" (e.g., Qr1 and Qr2). The trees were planted in a grid of 1 m × 1 m squares. The seedlings for the experiment were obtained from the Peplin nursery, except for *P. nigra* which was obtained from the Kraszkowice nursery (Szymański, 1982).



**Fig. 1.** The Siemianice common-garden experiment – location and spatial scheme of tree monocultures. One fir plot (Aa, crossed) was excluded from the experiment because of poor seedling survival. Species abbreviations: Aa, *Abies alba*; Ap, *Acer platanoides*; Aps, *Acer pseudoplatanus*; Bp, *Betula pendula*; Cb, *Carpinus betulus*; Fs, *Fagus sylvatica*; Ld, *Larix decidua*; Pa, *Picea abies*; Pm, *Pseudotsuga menziesii*; Pn, *Pinus nigra*; Ps, *Pinus sylvestris*; Qr, *Quercus robur*; Qru, *Quercus rubra*; Tc, *Tilia cordata*; 1, Site 1; 2, Site 2.

The mean pH of the A horizon was 4.3 before establishment of the experimental plots. Since then the soil pH and exchangeable base cations have diverged between species. The *A. platanoides*, *A. pseudoplatanus* and *T. cordata* plots now have the most basic soils, and the *P. sylvestris*, *P. nigra* and *L. decidua* plots the most acidic (Reich et al., 2005).

### 2.2. Bait-laminas

Bait-laminas are plastic strips 120 mm long, 10 mm wide and 1.5 mm thick. Each strip has 16 biconical holes 1 mm in diameter, 5 mm apart. The holes are filled with a 1:4:3 paste of modified starch (distarch phosphate – E-1412), dried ground leaves of nettle (*Urtica dioica*), and water. Nettle leaves were used as bait because of their high nitrogen content (low C/N) and preference as food by soil animals (Helling and Larink, 1998). The prepared bait-laminas were air-dried, checked to ensure that the bait was secure in the holes, and wrapped in aluminum foil for transporting to the field. In the study plots the bait-laminas were exposed twice in 2006, in summer (June 13–July 25) and autumn (October 3–November 7). On both occasions 50 strips per plot were inserted vertically into the soil in the centers of the 53 plots, for a total of 2650 bait-laminas per season. The strips were arranged 10 cm apart in five parallel rows 20 cm apart. After those exposure periods the bait-laminas were removed, wrapped in aluminum foil, transported to the lab and scanned for documentation and subsequent examina-

tion. The number and positions of pierced holes in each lamina were recorded.

### 2.3. Soil moisture and temperature

At the beginning and end of the exposure period, 3 soil samples were taken from each study plot to 5 cm depth for moisture determination. On the first day of bait-lamina placement, 3 data loggers in total (HOBO H8, Onset Computer Corporation, USA) were buried at random places within the study area at 5 cm depth for hourly soil temperature recording during the whole period of bait-lamina exposure.

### 2.4. Data analysis

Since the periods of bait-lamina exposure differed between seasons (42 days in summer and 33 days in autumn), so we linearly interpolated the results for 4 weeks (28 days) (Reinecke et al., 2002, 2008). The mean of all 50 laminas (or a few less, if one or more laminas were lost or destroyed), from a given plot was taken as a single measurement. Thus we had 3 or 6 replications for every tree species (except for *A. alba* with 2 replicates; Fig. 1).

The effects of tree species, season and site on feeding activity in all monocultures studied (tree species nested in site) were analyzed using the GLM model with the Tukey post hoc test. Before analysis the data were  $\log_2(x+1)$ -transformed. Contrast analysis (planned comparison) was performed to check for the effect of tree taxonomic group (conifer vs. deciduous) on feeding activity.

The index of average depth of trophic activity at a plot was calculated as proposed by van Straalen (Gongalsky et al., 2004):

$$D = \frac{\sum n_i d_i}{N}$$

where  $D$  is average depth of trophic activity (mm),  $n_i$  is the number of holes pierced at depth  $i$  counted in all laminas,  $d_i$  is the depth (mm) of hole  $i$ , and  $N$  is the total number of pierced holes counted in all laminas and at all depths,  $N = \sum n_i$ . The statistical analysis was similar to that for feeding activity. The data were not transformed (all assumptions were fulfilled).

The relationship between bait-lamina piercing rate and the densities of invertebrates estimated from the same sites (Collembola and Enchytraeidae collected in 2004 and earthworms in 2008), was analyzed using Pearson correlations. Repeatability (Sokal and Rohlf, 1994) of bait-lamina activity estimates was evaluated as the Pearson product-moment correlation coefficient between standardized values of data collected at the same locations in two consecutive terms (Hayes and Jenkins, 1997). The analyses were done with STATISTICA Ver. 8 (StatSoft, Inc., Tulsa, OK, USA). Significance was assumed at 0.05.

## 3. Results

### 3.1. Soil moisture and temperature

The climate in the studied forest is characterized by low rainfall in summer. During the summer experiment, soil moisture dropped significantly from  $12.2 \pm 0.5\%$  (mean  $\pm$  SD) at the beginning to  $4.2 \pm 0.2\%$  at the end of the period ( $t = 14.81$ ,  $p < 0.0001$ ). In autumn the soil moisture remained relatively stable during the study, but the initial and final values differed significantly ( $9.1 \pm 0.5\%$  at the beginning,  $11.1 \pm 0.6\%$  at the end;  $t = -2.6$ ,  $p = 0.01$ ). Differences in soil moisture between summer and autumn were statistically significant ( $t = 4.4$ ,  $p < 0.0001$  and  $t = -10.9$ ,  $p < 0.0001$  for the start and end of each study period, respectively).

Soil temperature was measured continuously. In summer it increased from  $14.5^\circ\text{C}$  in June to  $21.6^\circ\text{C}$  at the end of the study period. During autumn the soil temperature decreased from  $14.3^\circ\text{C}$  at the beginning to  $6.9^\circ\text{C}$  at the end. The mean temperature during the summer experiment ( $19.1^\circ\text{C}$ ) was significantly higher ( $t = 17.2$ ,  $p < 0.0001$ ) than during the autumn ( $10.2^\circ\text{C}$ ).

### 3.2. Effect of tree species on soil faunal activity

Soil faunal activity differed between tree species (Fig. 2). Activity was highest under larch (*L. decidua*) and spruce (*P. abies*) in both seasons studied, and lowest under hornbeam (*C. betulus*) and Douglas fir (*P. menziesii*; Fig. 2). ANOVA revealed significant effects of season ( $F = 872.9$ ,  $p = 0.02$ ; summer > autumn) and tree species ( $F = 7.2$ ,  $p < 0.001$ ) on soil faunal activity. The effects of site and of interactions were not significant. While contrast analysis revealed greater soil fauna activity under coniferous than deciduous species ( $p < 0.0001$ ), post hoc tests indicated considerable overlap between tree types (Table 1).

To examine the effect of site more fully, we conducted ANOVA separately for the species with 6 replicates (Ld, Pn, Pa and Qr). This revealed a significant effect of season ( $F = 211.8$ ,  $p = 0.04$ ) and of the site  $\times$  species interaction ( $F = 9.68$ ,  $p < 0.001$ ). Therefore, in all analyses (above and below) we treat the plots of the same species separately by site.

In spite of the overall difference in feeding activity levels between seasons, the patterns observed in all plots individually (not averaged for tree species) were quite similar in summer and autumn (Fig. 3). The highly significant correlation between the measurements taken at all individual plots in the two seasons ( $r = 0.63$ ,  $p < 0.0001$ ) indicates high repeatability of the estimates.

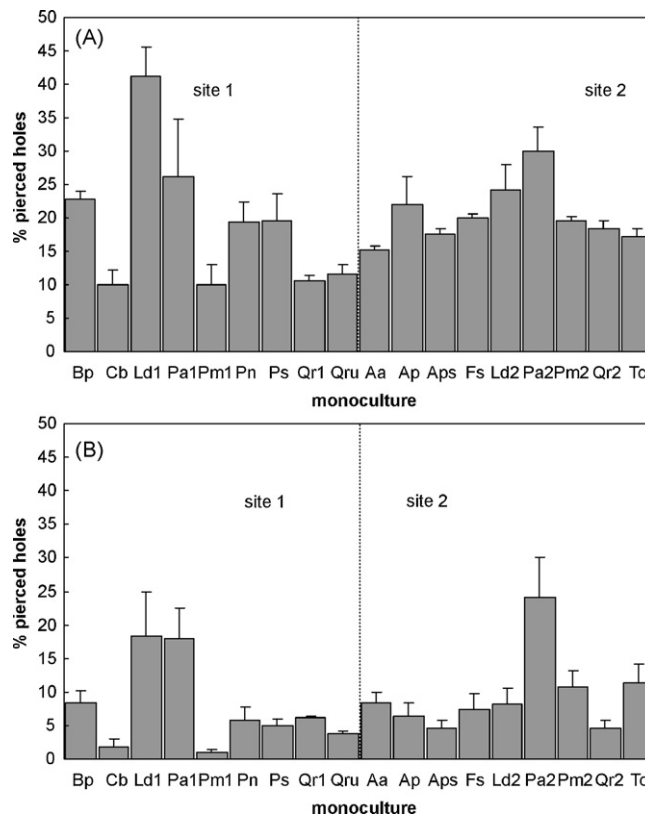


Fig. 2. Soil faunal activity (% of pierced holes in bait-laminas/28 days); (A) summer and (B) autumn. Bars – averages for monocultures  $\pm$  S.E. Vertical broken line separates monocultures planted at Site 1 from those planted at Site 2. Species abbreviations as in Fig. 1.

**Table 1**

Effect of tree species on soil faunal activity – mean number of pierced holes in bait-laminas/28 days in summer and autumn jointly. Groups of means that do not differ significantly according to the Tukey post hoc test are marked 'xx'. See Fig. 1 for explanation of species abbreviations.

Site	Tree species	Pierced holes		Homogeneous groups of means			
		Mean	±SD				
1	Pm1	0.88	0.95	xx			
1	Cb	0.95	0.83	xx	xx		
1	Qru	1.24	0.74	xx	xx	xx	
1	Qr1	1.34	0.41	xx	xx	xx	
2	Aps	1.78	1.17	xx	xx	xx	xx
2	Qr2	1.83	1.26	xx	xx	xx	xx
1	Ps	1.97	1.47	xx	xx	xx	xx
1	Pn	2.02	1.35	xx	xx	xx	xx
2	Aa	1.88	0.66	xx	xx	xx	xx
2	Ap	2.27	1.58		xx	xx	xx
2	Fs	2.18	1.19		xx	xx	xx
2	Tc	2.29	0.74		xx	xx	xx
1	Bp	2.49	1.32		xx	xx	xx
2	Ld2	2.60	1.61		xx	xx	xx
2	Pm2	2.42	0.88		xx	xx	xx
1	Pa1	3.52	1.87			xx	xx
2	Pa2	4.33	1.32				xx
1	Ld1	4.77	2.43				xx

### 3.3. Soil faunal activity along the soil profile

In both seasons the soil faunal activity was highest in surface layers of soil (0–4 cm). The vertical distribution of feeding activity differed between seasons. In summer, 52% of activity was located in the 0–2 cm layer, whereas in autumn as much as 74% of the activity was located there (Fig. 4). The mean depths of feeding activity differed between tree species (Fig. 4). The mean depth was shallowest in Pm1 both in summer (25.2 mm) and in autumn (12.0 mm). The mean activity level was deepest in summer in the Ld1 monoculture (37.3 mm), and in autumn in Pa2 (31.2 mm).

Among the effects on the vertical distribution of activity (season, site, tree species nested in site) only tree species ( $F=2.52$ ,  $p=0.04$ ) and the season  $\times$  species interaction ( $F=2.22$ ,  $p=0.01$ ) were significant. Because of this interaction, further analyses were done separately for each season.

In summer only the effect of tree species was significant ( $F=5.44$ ,  $p<0.0001$ ). While contrast analysis showed significant differences

in the mean depth of faunal activity between coniferous and deciduous stands ( $p=0.02$ ), post hoc tests indicated considerable overlap between tree types (Table 2). In autumn, the effect of tree species (nested in site) ( $F=3.53$ ,  $p<0.001$ , post hoc test results given in Table 3) were significant, but with no difference between coniferous and deciduous stands.

The mean depth of faunal activity appeared to differ between seasons (30.8 mm in summer and 21.4 mm in autumn; Fig. 4), but the averages were not significantly different.

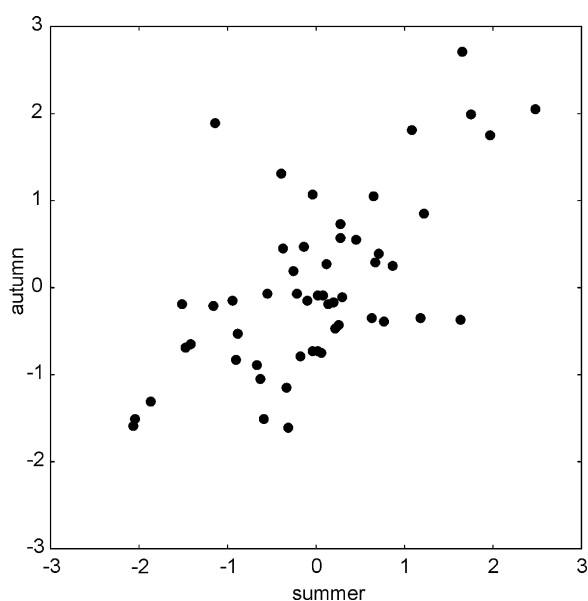
### 3.4. Soil faunal density

We did not measure soil faunal density at the time of bait-lamina testing. Quantitative information on the abundance and dynamics of the soil biota in the Siemianice monocultures is available only for earthworms (Reich et al., 2005; Hobbie et al., 2006), and in our unpublished data for Enchytraeidae and Collembola in a subset of 12 plots (two plots with *Tilia*, *Larix*, *P. sylvestris* and *Q. robur*, and single plots with *Picea*, *Betula*, *Carpinus* and *Q. rubra*; sampled in 2004; Fig. 5) and for earthworms in 21 plots (six with *Larix* and *Q. robur*, and three with *Picea*, *P. sylvestris* and *Tilia*; sampled in 2008). No significant correlation was found between faunal density (Enchytraeidae and Collembola) and bait-lamina activity.

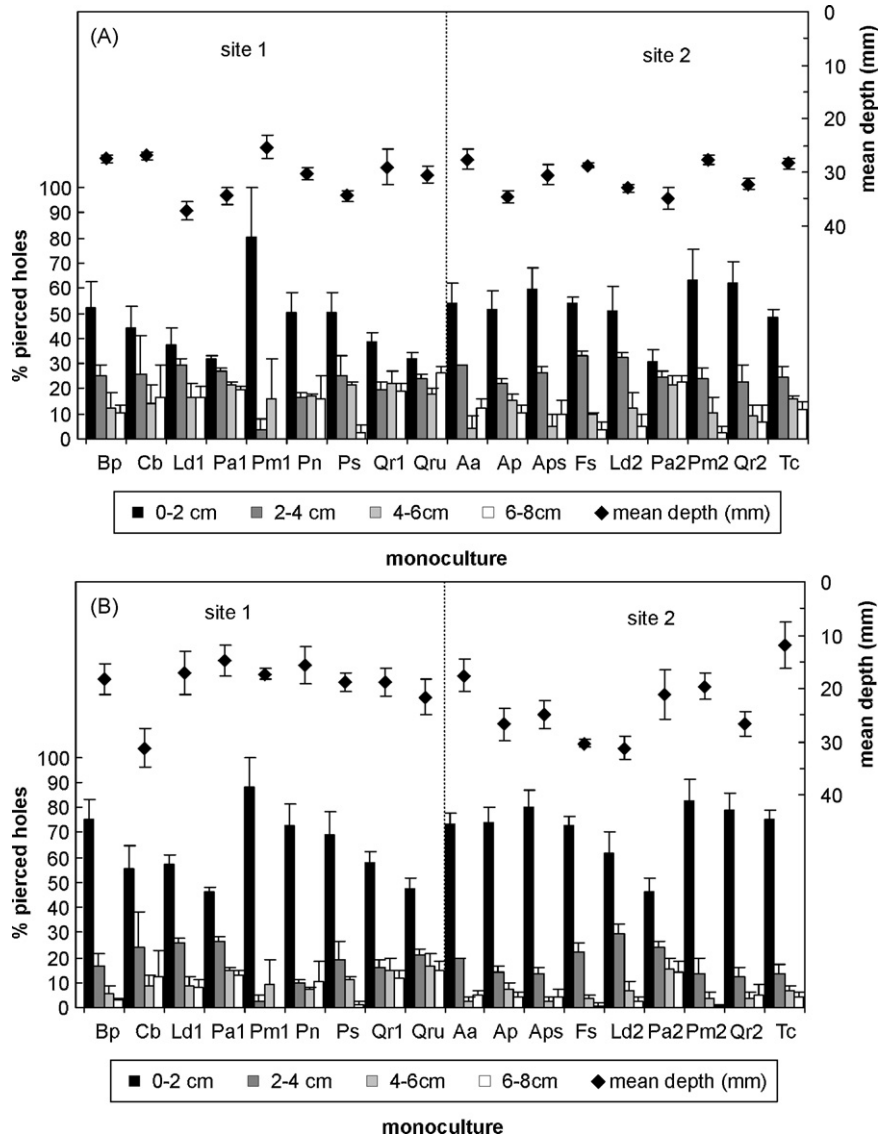
Earthworm densities in 2008 ranged from 0 to 56 ind.m<sup>-2</sup>, being generally higher in deciduous (26.7 and 24.0 ind.m<sup>-2</sup> for Qr and Tc) than in coniferous plots (8.7, 6.7, 1.3 ind.m<sup>-2</sup>, for Pa, Ps, Ld, respectively) although the differences were not significant (ANOVA).

### 3.5. Effect of soil properties upon faunal activity

To investigate the relationship between soil properties and faunal activity, the correlations between bait-lamina piercing in the monocultures ( $n=14$ ) and any soil/litter variables reported in previous publications (averages for monocultures were calculated). The array of variables we examined included initial litter content of nutrients N, Ca, K, Mg, P (mg g<sup>-1</sup>), C:N ratio, fractions of initial litter organic matter (cell solubles, cellulose, hemicellulose, lignin; mg g<sup>-1</sup> ash-free dry mass) and of ash (mg g<sup>-1</sup> litter) (Hobbie et al., 2006), litter production (kg ha<sup>-1</sup> year<sup>-1</sup>), turnover rate constant  $k$  (year<sup>-1</sup>), soil CO<sub>2</sub> flux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), pH O horizon, pH 0–20 cm, cation exchange capacity (mequiv. kg<sup>-1</sup>) of O horizon and 0–20 cm, base saturation (%) of O-horizon and 0–20 cm,



**Fig. 3.** Correlation between soil faunal activities in summer and autumn. Dots represent log-transformed standardized bait-lamina activity values (% pierced holes) for individual plots ( $r=0.63$ ,  $p=0.000001$ ).



**Fig. 4.** Faunal activity (% of pierced holes in bait-laminas/28 days) along soil profile (left axis), and mean depth (mm) of faunal activity (right axis). (A) Summer and (B) autumn. Vertical broken line separates monocultures planted at Site 1 from those planted at Site 2. Bars – % pierced holes in bait-laminas at 4 depths in soil profile, av.  $\pm$  S.E. Diamonds – mean ( $\pm$ S.E.) depth of faunal activity in particular monocultures. Species abbreviations as in Fig. 1.

**Table 2**  
Mean depth of feeding activity (mm) in summer test. Groups of means that do not differ significantly according to the Tukey post hoc test are marked 'xx'. See Fig. 1 for explanation of species abbreviations.

Site	Tree species	Depth		Homogeneous groups of means			
		Mean	SD				
1	Pm1	25.2	3.9	xx			
1	Cb	26.9	1.3	xx	xx		
1	Bp	27.6	1.1	xx	xx	xx	
2	Aa	27.6	2.5	xx	xx	xx	xx
2	Pm2	27.7	1.3	xx	xx	xx	
2	Tc	28.4	1.6	xx	xx	xx	
2	Fs	28.8	0.7	xx	xx	xx	
1	Qr1	29.0	5.5	xx	xx	xx	
1	Pn	30.3	2.2	xx	xx	xx	xx
1	Qru	30.5	2.7	xx	xx	xx	xx
2	Aps	30.5	3.1	xx	xx	xx	xx
2	Qr2	32.2	1.6	xx	xx	xx	xx
2	Ld2	33.1	1.1	xx	xx	xx	xx
1	Ps	34.4	1.8		xx	xx	xx
1	Pa1	34.4	2.7		xx	xx	xx
2	Ap	34.7	1.9		xx	xx	xx
2	Pa2	34.9	3.4			xx	xx
1	Ld1	37.3	3.1				xx

**Table 3**

Mean depth of feeding activity (mm) in autumn test. Groups of means that do not differ significantly according to the Tukey post hoc test are marked 'xx'. See Fig. 1 for explanation of species abbreviations.

Site	Tree species	Depth		Homogeneous groups of means		
		Mean	SD			
1	Pm1	12.0	7.6	xx		
2	Pm2	14.7	5.1	xx	xx	
2	Aps	15.5	6.0	xx	xx	xx
2	Qr2	17.2	7.0	xx	xx	xx
2	Fs	17.3	1.8	xx	xx	xx
1	Bp	17.5	5.3	xx	xx	xx
2	Ap	18.2	4.9	xx	xx	xx
2	Tc	18.8	3.1	xx	xx	xx
2	Aa	18.9	3.7	xx	xx	xx
1	Ps	19.6	4.1	xx	xx	xx
1	Pn	21.1	7.9	xx	xx	xx
2	Ld2	21.6	5.8	xx	xx	xx
1	Ld1	25.0	4.5	xx	xx	xx
1	Qr1	26.7	4.1	xx	xx	xx
1	Cb	26.8	5.5	xx	xx	xx
1	Pa1	30.3	1.1		xx	xx
1	Qru	31.2	3.9			xx
2	Pa2	31.2	6.2			xx

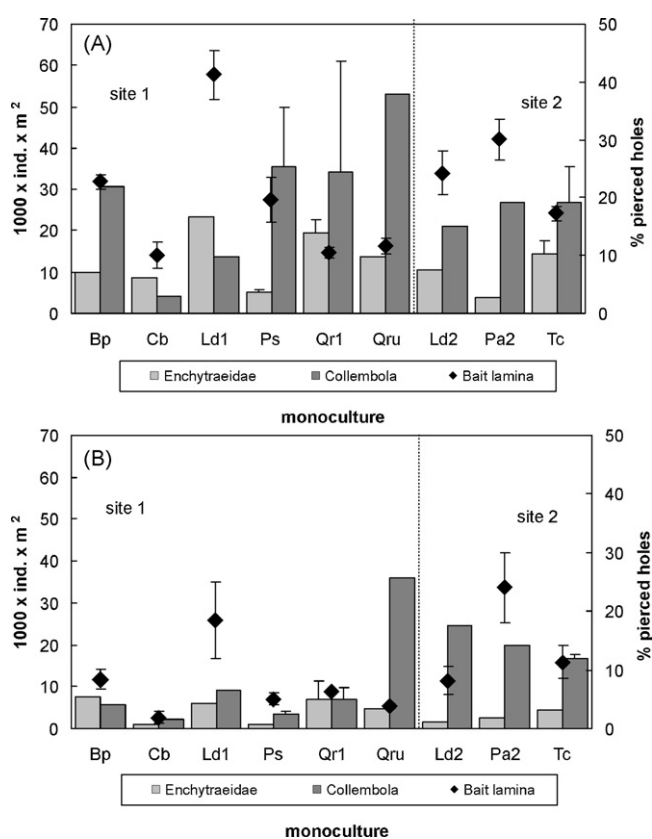
earthworm biomass ( $\text{g m}^{-2}$ ) (Reich et al., 2005), A-horizon cumulative respiration ( $\text{g C kg}^{-1}$  soil C), A-horizon microbial biomass ( $\text{g C kg}^{-1}$  soil C), net N mineralization ( $\text{g N m}^{-2} \text{ year}^{-1}$ ), net nitrification ( $\text{g N m}^{-2} \text{ year}^{-1}$ ), and nitrification:mineralization ratio (Hobbie et al., 2007). The Pearson product-moment correlation coefficients were not significant for any of the 26 cases analyzed.

**4. Discussion**

Most studies of soil faunal structure and function have involved multiple factors, making it difficult to draw conclusions about the causal relations between environmental conditions and soil faunal activity. The design of the Siemianice common-garden experiment avoids some of these problems: the monocultures were planted on plots close to each other, so that the climatic, geological and biogeographical conditions should be essentially uniform. However, in spite of the effort to homogenize the soil substrate by deep plowing before the trees were planted, the soil properties of Site 1, based entirely on sandy substrate, differ slightly from those of Site 2, fragments of which contain high amounts of clay and moraine deposits (Reich et al., 2005).

It has been demonstrated that the 14 tree species studied did affect soil properties through variation of litter quality, litter quantity, and soil nutrient uptake, associated with differences in abundance of earthworms (Reich et al., 2005). Our results show that overall soil faunal activity is also related to the overstorey tree species, as confirmed by ANOVA and post hoc tests, but that there is quite substantial variation between plots within monocultures (Fig. 2 and Table 1). On the other hand, the patterns of variation of activity indices between particular plots in summer and autumn were quite similar, in spite of the seasonal differences. Repeatability can be measured in various ways, for example as an intraclass correlation coefficient (Sokal and Rohlf, 1994), or, particularly when the averages of repeated measurements differ, as a simple product-moment Pearson correlation coefficient, based on standardized values or residuals (Hayes and Jenkins, 1997). Repeatability evaluated in this way proved to be highly significant (Fig. 3). This finding confirms the robustness of the method; on the other hand, the high repeatability of measurements from individual plots, taken together with relatively high within-monoculture variation, may suggest that another uncontrolled factor, presumably small scale spatial variation (Laskowski et al., 2003) contributed to the overall pattern observed.

Soil temperature and moisture are critical factors regulating biological activity in soils (Han et al., 2007). In our experiment the soil temperatures rose from  $15^{\circ}\text{C}$  to  $20^{\circ}\text{C}$  during the summer experiment, and fell from  $15^{\circ}\text{C}$  to  $5^{\circ}\text{C}$  during the autumn test. As the activity of invertebrates depends on temperature, the lower temperatures in autumn may be the primary explanation for lower faunal activity at that time. Another important factor is soil moisture, which, together with the temperature changes, may



**Fig. 5.** Soil faunal abundances in selected plots (bars: authors' unpublished data; sampled in 2004; data for Ps, Qr, Tc – averages of two plots  $\pm$  S.E.) and soil faunal activity (diamonds; bait-lamina test, averages of 3 plots for each monoculture  $\pm$  S.E.) in 2006 experiment (this study). (A) Spring and (B) autumn. Other symbols as in Fig. 2.

have affected the vertical distribution of soil faunal feeding activity. In summer, with lower soil moisture and higher temperature, the fauna migrated down the soil profile (mean depth of feeding activity at 30.8 mm; Fig. 4), while in autumn, with more rain and lower temperature, the animals were active mostly in shallower strata (mean activity depth 21.4 mm, Fig. 4).

It seems obvious that the soil faunal feeding activity index determined by the bait-lamina method should correspond with the density of particular groups of invertebrates. However, outside of the artificial conditions of laboratory studies it is hard to find evidence for such a relationship (Gongalsky et al., 2003). However, in a comparison of forest monocultures of several tree species (*P. sylvestris*, *L. decidua*, *Q. robur*, *P. abies*, *B. pendula*) in the Niepołomice Forest, Ł. Sobczyk (unpublished Ph.D. thesis) found a significant correlation between enchytraeid density and bait-lamina piercing rate. Some laboratory results suggest that bait-lamina perforation can be attributed mostly to earthworms and enchytraeids, while springtails and mites do not make a significant contribution (Van Gestel et al., 2003; Gongalsky et al., 2008). Helling and Larink (1998) found that enchytraeids (*Enchytraeus minutus*, *E. lacteus*) showed feeding activity similar to that of *Folsomia candida* (Collembola), with the activity of other springtail species (*Onychiurus fimatus*) significantly lower.

The pattern of earthworm densities observed in 2008 does agree in general with that described by Reich et al. (2005) and Hobbie et al. (2006) on the basis of previous studies conducted between 1995 and 2002 (Reich et al., 2005). The abundances of Enchytraeidae and Collembola in 2004 demonstrated substantial variation among the monocultures studied, both in summer and autumn (Fig. 5). The densities of soil invertebrates and the bait-lamina activity indices appear unrelated, however as no significant correlation with bait-lamina activity indices was found for either taxon.

As the faunal density estimates are shifted in time by 2 years (in one direction or the other) from the bait-lamina experiment, any comparisons between trends should be treated with caution, though the relative abundances of soil invertebrates may be assumed not to have changed greatly during that period. It is also possible that other groups of fauna contributed to bait-lamina piercing. European terrestrial oligochaetes (earthworms and enchytraeids) are in general detritivores, but other terrestrial mesofauna are more diverse in their feeding habits. Springtails, for example, can feed on detritus, fungi, plants, etc., while some of them are highly specialized (Nakamori and Suzuki, 2005). Various feeding strategies ranging from omnivory to narrow specialization are found among mites and nematodes. Interactions between species in the field may also affect their feeding preferences.

All this makes it difficult to link the bait-lamina indices of overall faunal activity with particular groups of animals (Gongalsky et al., 2003). On the other hand, the spatial and temporal patterns of bait-lamina-estimated faunal activity do not contradict other findings on soil faunal abundance in the experimental plots: the lower number of bait-lamina perforations in autumn than in summer fits the significantly lower density of enchytraeids and collembolans in autumn than in spring samples taken in 2004 (Fig. 5). The soil faunal activity noted in the hornbeam plots in both studied seasons agrees with the densities of enchytraeids and springtails in those plots; all were lowest in that monoculture (Fig. 5). The lower density of soil fauna in autumn was caused by the heat and dryness of summer in southwestern Poland, which probably affected the survival of animals in sandy soils containing little organic matter in the Siemianice Forest. A similar phenomenon has been described from work in mixed grassland (Hamel et al., 2007). The lower density of soil animals together with lower autumn temperatures reduced the feeding activity in autumn.

It is well documented that the trees altered the biogeochemical properties of the litter/soil system in the Siemianice monocul-

tures, in a species-specific manner (Reich et al., 2005; Hobbie et al., 2006, 2007; Dauer et al., 2007). One can speculate that some of these characteristics may have affected the abundance and activity of soil fauna, as was previously demonstrated for Ca content and earthworm activity (Hobbie et al., 2006). In none of 26 cases examined was a significant correlation found. Only at a more general level, the coniferous species tended to contrast with deciduous ones both in faunal activity (this study) and in soil pH (Reich et al., 2005).

Thus it is still unresolved whether some mechanism other than altered litter and soil chemistry can explain the significant effect of overstory tree species on soil faunal activity. It is unlikely that the general properties of litter/soil changed much during the few years that lapsed between the soil chemistry studies and bait-lamina experiment. Rather, the values averaged over the whole area of the monocultures may have masked the local spatial variation of all litter/soil characteristics.

The relatively high activity values from larch and spruce monocultures might be attributable to the thicker litter layer and/or denser grass cover, which could maintain more moisture, and for longer, than under other tree species; such conditions are favorable for soil fauna. If so, this would suggest that abiotic factors most affect the activity of fauna as measured here.

The effect of the taxonomic composition of soil faunal communities cannot be properly evaluated unless the taxa most actively feeding on baits in particular habitats are identified. Nevertheless, our results reveal differences in the feeding activity of detritivores, which may be regarded as an index of the overall impact of soil fauna on forest ecosystem processes (e.g., litter decomposition rate, energy and nutrient flow) due to differential effects of dominant tree species. Such a finding would be difficult to obtain relying solely on analysis of the taxonomic composition and population density of the soil communities.

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