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Response of different decomposer communities to the manipulation of moisture availability: potential effects of changing precipitation patterns

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Abstract

The potential impacts of changes in precipitation patterns associated with global climate change on the relationship between soil community diversity and litter decomposition were investigated. For a period of ca. 5 months, two decomposer communities in litterbags (1000 and 45 µm mesh size) containing spruce litter were subjected to two irrigation treatments: constant and fluctuating (drying/rewetting) moisture conditions. The latter were expected to induce moisture stress on the decomposer communities. The two mesh sizes were used to exclude different faunal components from the decomposer communities. The 1000 µm mesh excluded only the macrofauna, whereas the 45 µm mesh excluded both the macro- and mesofauna. In the short-term perspective of the present study, mesofauna abundance showed no response to imposed fluctuating moisture conditions. Irrespective of the presence of mesofauna, mass loss, microbial biomass and the control mechanisms, regulating carbon mineralization appeared unaffected by fluctuating moisture conditions. The reduction in the functional/structural diversity of the decomposer communities in the 45 µm litterbags resulted in strongly increased Nematoda abundance but it did not alter the response of Nematoda to fluctuating moisture conditions. Processes in the nitrogen (N)-cycle and mass loss were sensitive indicators of changes in the structural and functional complexity of decomposer communities. However, a negative effect of fluctuating moisture conditions on extractable N was coupled to the presence of mesofauna. Extremes in rainfall patterns, generated by climate change, may have a negative impact on the availability of nutrients, particularly N, for plants. This effect could be amplified by an additional impoverishment in the structural and functional complexity of the respective decomposer communities.

Keywords: functional diversity, microbial biomass, precipitation patterns, soil fauna, soil processes, spruce litter

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Introduction

Considerable changes in precipitation patterns are predicted to occur during the present century (Arnell, 1999; McCarthy *et al*., 2001). Several authors have demonstrated the potential impact of these changes on soil organisms (e.g. Briones *et al*., 1997; Wolters *et al*., 2000). Most of the studies investigating the influence of moisture conditions on the decomposer community have focused on contrasting but stable moisture levels (e.g. Huhta *et al*., 1998b; Sulkava *et al*., 1996). There is evidence, however, that fluctuations in substrate moisture may have a greater impact on soil processes by negatively affecting the decomposer microorganisms. Schimel and Gulledge (1998) suggested that increased frequency of episodic drying and rewetting of soil associated with climate change could alter the populations of cellulytic and lignolytic fungi. They also

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suggested that the corresponding decrease in litter decomposition may be greater than that predicted by simply the changes in soil and litter moisture. A similar sensitivity to fluctuations in substrate moisture could be expected from components of the nitrogen (N)-cycle, which is considered to be one of the nutrient cycling pathways most heavily dependent upon biological activities (Swift *et al.*, 1998).

In addition to changes in precipitation patterns, a number of other components of global climate change, e.g. elevated CO_2, N deposition and changes in land use, are also expected to affect soil organisms (Wardle *et al.*, 1998). These consequences of climate change are likely to induce changes within functional groups or shifts in the balance between different functional groups in the soil decomposer community, which could significantly affect soil processes (Swift *et al.*, 1998). The combined influence of changes in biodiversity of decomposer organisms and fluctuating moisture conditions could have profound effects upon ecosystem processes.

In the present paper, we investigated the potential influence of changing rainfall patterns, expressed as fluctuations in litter moisture, on the relationship between soil community diversity and selected ecosystem functions. Litterbags containing spruce litter were used to examine the response of decomposer communities with different degrees of taxonomic and functional diversity (with and without mesofauna) to changes in rainfall patterns.

The term 'mesofauna' refers to a functional concept, which separates soil invertebrates into three size classes: micro-, meso-, and macrofauna (Swift *et al.*, 1979; Verhoef & Brussaard, 1990). The microfauna (body width 2–100 μm) includes protozoans, Nematoda, rotifers and tardigrades (i.e. groups that are limited to the water film around surfaces). The mesofauna (100 μm to 2 mm) comprises Enchytraeidae, microarthropods (mainly Acari and Collembola but also Symphyla, Diplura, Protura) and dipterous larvae that live in the air-filled pore space of the soil and litter. The main components of the macrofauna (2–20 mm) are earthworms, Diptera larvae, millipedes, woodlice, insects, slugs and snails. Since 'size' reflects the adaptation of the fauna to spatial constraints of the soil habitat (Lavelle, 1997), it is assumed that invertebrates with comparable body width also have similar functions in litter decomposition (Swift *et al.*, 1979). Many authors suggest that changes in diversity at coarse levels of resolution, such as the lack of a functional group, are more likely to impact ecosystem function than changes at finer levels of resolution, e.g. the loss of a single species (e.g. Beare *et al.*, 1997; Bengtsson, 1998). We, therefore, hypothesized that the effect of stress, induced by extreme fluctuations in litter moisture, on a decomposer community will be altered when the functional/structural diversity of the community is depleted by excluding the mesofauna.

Each size class of the soil fauna comprises different trophic groups, such as saprophages, microphytophages and zoophages (Wallwork, 1976; Petersen & Luxton, 1982; Moore *et al.*, 1988; Schaefer, 1995). Thus, by excluding the mesofauna, we not only manipulated the size structure but also the trophic structure of the soil invertebrate community. Various experimental (Anderson, 1975; Berg *et al.*, 1980; Santos *et al.*, 1981; Seastedt, 1984; Huston, 1989; Scholle *et al.*, 1995; Takeda, 1995) and modelling approaches (Moore *et al.*, 1988; Schröter *et al.*, 2003) have shown that the mesofauna gains most of its functional importance via numerous direct and indirect interactions with the decomposer microflora. In the present study, the functional effects of mesofauna exclusion were therefore estimated through microbial parameters. Carbon (C) mineralization was used to assess microbial activity and mass loss was used as a measure of decomposition. In addition, net mineralization of N was estimated by extractable N and used as a measure of plant available N.

Materials and methods

Site description and experimental design

The study site was a spruce monoculture (*Picea abies* [L.] Karst.), situated between 695 and 730 m elevation (50°31′N 9°17′E) in the Vogelsberg area of Hessia, Germany. In 1996, when the experiment was carried out, the trees were ca. 46–54 years old. The climate of the region is subatlantic. In 1996, mean long-term annual temperature was 5.4 °C and mean long-term annual precipitation was 988 mm. During the studied period, monthly precipitation was 97 mm in August, 90 mm in September, 102 mm in October, 124 mm in November and 157 mm in December. The experiment was started in August 1996 when a total of 60 litterbags of two mesh sizes (45 and 1000 μm) were exposed to two irrigation treatments (regular and irregular irrigation). This experimental design, therefore, consisted of four irrigation/mesh size treatment combinations. Seven, 14 and 18 weeks after the start of the experiment, five replicate litterbags were sampled from each treatment combination. At each sampling date, five samples that had received ambient rainfall were also collected at random from the L-layer of undisturbed plots adjacent to the experimental site.

Irrigation treatment

The litterbags were distributed at random, beneath roofs, between the L and F organic horizons. A distance

of ca. 25 cm was kept between adjacent litterbags and the edge of the roof. Each roof consisted of a wooden frame (125 cm × 175 cm) on four wooden posts (height from ground 80 cm) that were covered with transparent plastic. A wooden frame around the roofs that had an opening in one corner prevented water percolation from the side of the roofs down onto the litterbags. At that corner the roof was slightly lower allowing the rainwater to be collected by pipes into a storage container. Horizontal percolation from the surrounding soil into the litterbags was unlikely, as the site was relatively flat.

One set of 30 litterbags was irrigated regularly (R: twice weekly, 6 L throughfall m^{-2} per watering event) to maintain a relatively constant level of substrate moisture. This 'regular irrigation' treatment delivered ca. 80% of average ambient precipitation between August and November 1996. The 'irregular irrigation' (IR) treatment, by contrast, created strongly fluctuating moisture conditions: periods of 5 weeks without irrigation (drying) followed by the application of 36 L throughfall m^{-2} over a period of two consecutive days (rewetting), 18, 32, and 20 days before the respective sampling date. The throughfall applied during the irregular irrigation rewetting events collectively represented ca. 40% of average ambient precipitation between August and November 1996.

Mesh size treatment

The mesh size treatment comprised 45 μm litterbags, which excluded both macro- and mesofauna, and 1000 μm bags, which excluded only macrofauna. Litterbags (nylon gauze, 25 cm × 25 cm) were filled with ca. 50 g of air-dried litter material collected from the L-layer at the experimental site. The litter was previously processed in a high-gradient extractor (at a maximum of 30 °C over a period of 15 days; see Wolters 1983) to carefully remove most of the macro- and mesofauna. According to preliminary tests, this procedure removes all of the macrofauna and ca. 90% of the mesofauna without significantly altering the physicochemical conditions of the litter. The successful and persistent reduction of the fauna was confirmed at each sampling date: mesofauna abundance in the 45 μm bags accounted for only ca. 8% of the abundance in the respective 1000 μm bags in the irregular irrigation treatment and ca. 5% in the regular irrigation treatment. One portion of the partly defaunated litter was filled directly into the 45 μm litterbags. A second portion was refaunated with microarthropods to field density before being filled into the 1000 μm litterbags. Refaunation was used to reduce the effects of inconsistent colonization by Collembola and Acari (microarthropods) in the field. Microarthropods for refaunation were obtained following the same extraction scheme as for macro- and mesofauna removal (see above) from an equal volume of litter collected from the experimental site. In the following text, the litterbag treatments are abbreviated to L45 for the 45 μm bags and L1000 for the 1000 μm bags.

Analytical procedures and extraction methods

Immediately after sampling, the content of each litterbag was weighed, carefully mixed and stored, in sealed plastic bags, at 4 °C. Subsamples of 5 g litter were dried at 105 °C for 24 h to determine the water content of the litter material (expressed as litter dry mass (% DM)). Mass loss in each litterbag was then calculated as percentage mass loss of initial mass. Extraction of soil fauna was initiated on the day of collection. Microarthropods (Collembola, Acari) were extracted from subsamples (ca. 3 g DM) into ethylene glycol in a high-gradient extractor (Wolters. 1983) over a period of 14 days. Adults and immatures, stored in 70% alcohol, were counted under a dissection microscope at × 160 magnification. Nematoda and enchytraeids were counted live after extraction with a modified O'CONNOR-wet-funnel-extraction (O'Connor 1955) followed by milk-filter cleaning (s'Jacobs & Van Bezooijen 1984).

Microbial carbon (C_{mic}) was measured following the fumigation-extraction method (Brookes *et al.*, 1985; Vance *et al.*, 1987) and finally calculated assuming a k_{EC} -value of 2.22 (Wu *et al.*, 1990). The amount of mineral N (NH_4^+, NO_3^-) that was extracted from a set of unfumigated samples (see fumigation-extraction method) was used as an estimate of extractable nitrogen. It is subsequently referred to as N_{extr}. Both carbon and nitrogen were extracted using 0.5 M K_2SO_4 and subsequently measured photometrically with a continuous-flow system (PERSTORP ANALYTICAL GmbH, Perstorp, Sweden).

The rate of CO_2 evolution was used to estimate microbial C mineralization. The methodology followed the alkali trap and titration method by Isermeyer (1952), incubating field moist litter material for 6 days in a dark room (10 °C temperature).

Statistical analysis

The experiment was a split-plot design (Mead *et al.*, 1993) with irrigation as the main plot factor and litterbag mesh size and time (sampling date) as split-plot factors. The effects of the main plot and the two subplot factors were examined by means of a three-way ANOVA. The factor time was considered to be an independent factor, as each sample consisted of a separate litterbag.

Mesofauna abundance in the L45 at the three sampling dates was very limited and the data set contained a high number of zero values. Consequently the effects of irrigation and time on the mesofauna in L1000 were evaluated by a two-way ANOVA (i.e. irrigation × time). As a second step in statistical analyses, parameter means of the treatment combinations from the split plot design were compared with the L-layer samples by computing *t*-tests ($P < 0.05$). Normality was tested using the Shapiro–Wilk's *W* test. When necessary, data were log (ln + 1) transformed prior to analysis to achieve normality. All data were analysed for statistical differences using SAS (SAS Institute Inc., 1996). Analyses were conducted using the mixed procedure.

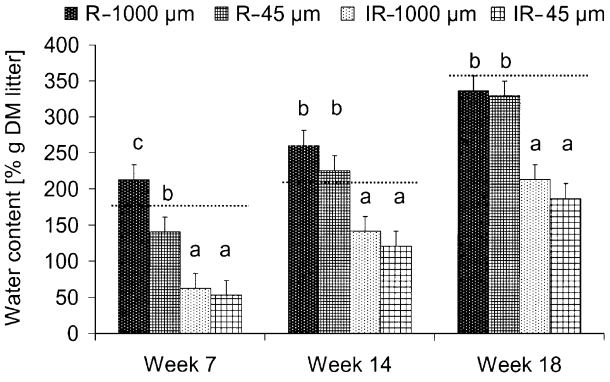

Fig. 1. Mean water content (% DM litter) in 1000 and 45 µm litterbags subjected to regular (R) and irregular (IR) irrigation. The broken line indicates the mean water content of L-layer samples that received ambient irrigation. At each sampling date, columns sharing the same letters are not significantly different, *t*-test, $P < 0.05$, error bars indicate SE, $n = 5$.

Results

Treatment evaluation

The irregular irrigation was very effective at creating fluctuating moisture conditions within the litter. Moisture content in the L-layer underneath the irregularly irrigated roofs increased from 30% to 144%, 69% to 270%, and 131% to 370%, when measured immediately prior to irrigation and immediately after at the three, 2-day irregular irrigation events. Moisture levels declined rapidly after irrigation such that within 1 week, values had, on average, already decreased to ca. 40% of the value measured immediately after irrigation.

In general, irregular irrigation decreased average water content by ca. 48% compared to regular irrigation. However, due to a steady increase in the background litter moisture, the average water content in the litterbags of both irrigation treatments gradually increased during the experimental period (Fig. 1). This development is likely to have reduced the effectiveness of the irregular irrigation treatment in creating a dry phase between the irrigation events.

In general, within each irrigation treatment, the average water content in the litterbags of both mesh sizes was similar (Fig. 1). Only at the first sampling date were there differences between the two mesh sizes within the regular irrigation treatment (Fig. 1). However, no significant interaction between the irrigation and the mesh size treatment was found (Table 1), indicating that the effects of experimental treatments on substrate moisture did not influence each other.

Effects of experimental treatments on functional parameters

The effect of the irrigation treatment on N_{extr} was related to community structure (Table 1): significant differences in N_{extr} content between the irrigation treatments were only apparent in L1000 (Fig. 2). The significant mesh size effect on N_{extr} (Table 1) was evident in lower average N_{extr} values in L45 (Fig. 2, *t*-test, $P < 0.01$). The strength of the mesh size effect on N_{extr} changed significantly over time (Table 1), mainly because differences in average N_{extr} content between the two mesh sizes increased over the course of the experiment (Fig. 2). By week 18, ca. 50% of the N_{extr} measured in L45 at week 7 had either been immobilized or lost, presumably via leaching (Fig. 2). The values of N_{extr} in L1000 showed little change over the same period (Fig. 2).

The significant effect of irrigation on carbon mineralization changed over time (Table 1). Strong differences between treatments due to lower values in the irregularly irrigated bags at week 7 (Fig. 2) weakened over the course of the experiment and were not evident at week 18 (Fig. 2). Community structure did not affect the irrigation effect (Table 1). In general, C mineralization was higher in L45 (Fig. 2, *t*-test, $P < 0.001$). Significant differences between means were, however, restricted to the regularly irrigated litterbags at weeks 14 and 18 (Fig. 2).

Significant differences in mass loss were confined to the mesh size treatment (Table 1), with greater mass loss occurring from L1000 (week 18: 9.7% of initial mass) than from L45 (week 18: 0.7% of initial mass).

Effects of experimental treatments on biological parameters

No significant interactions were observed for the effects of the mesh size and the irrigation treatment on

Table 1 Summary of a three-way ANOVA on parameters derived from litterbags buried in the L-layer of a 46–54year-old spruce forest in Central Germany

Dependent variable	Irrigation (I)	Mesh size (MS)	Time (T)	I × MS	I × T	MS × T	*N*
Substrate humidity							
Water content (% DM litter)	21.5***	47.9**	33.3***	4.2 NS	7.0**	10.3***	60
Functional parameters							
N_{extr} ($\mu g\,g^{-1}$ DM litter)	6.3*	94.1***	16.5***	3.3 NS	1.1 NS	11.7***	58
C mineralization ($\mu g\,C\,g^{-1}$ DM litter h^{-1})	26.2***	20.6***	8.1**	2.4 NS	10.6***	2.6 NS	60
Mass loss (% initial mass)	0.3 NS	5.0*	0.5 NS	0.3 NS	0.4 NS	0.4 NS	58
Biological parameters							
C_{mic} ($mg\,g^{-1}$ DM litter)	30.3***	6.5*	37.4***	0.3 NS	24.9***	7.2**	58
Nematoda (ind g^{-1} DM litter)	11.3**	35.1***	47.1***	3.8 NS	5.8**	5.0*	60
Collembola (ind g^{-1} DM litter)†	1.4 NS	–	5.3*	–	2.5 NS	–	30
Acari (ind g^{-1} DM litter)†	0.0 NS	–	14.1**	–	2.2 NS	–	30

The three main effects used in the model were irrigation treatment (regular, irregular), mesh size of litterbag (45, 1000 μm) and sampling time (week 7, 14 and 18). *F*-values of main effects and first-order interactions on each of the dependent variables are presented. *$P<0.05$. **$P<0.01$. ***$P<0.001$. $P \geq 0.05$ = NS (not significant).

†For the Collembola and Acari, a two-way ANOVA on the data from the 1000 μm litterbags was performed, as microarthropod densities in the 45 μm mesh size were very low.

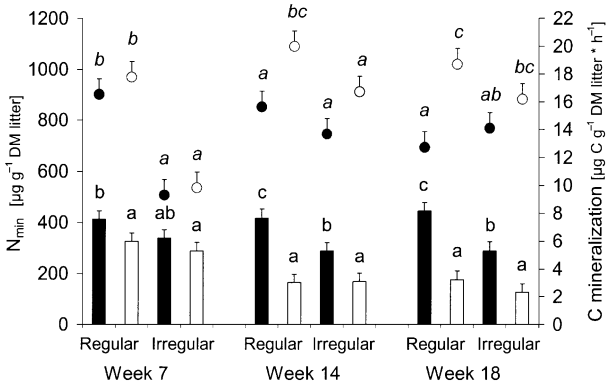

Fig. 2. Mean extractable nitrogen (N_{extr}) values (columns) and C mineralization (circles) in 1000 μm (black background) and 45 μm (white background) litterbags subjected to regular and irregular irrigations. At each sampling date, columns (standard letters) or circles (italic letters) sharing the same letters are not significantly different, *t*-test, $P<0.05$, error bars indicate SE, $n=5$.

microbial carbon and Nematoda abundance (Table 1), indicating that community structure, characterized by either a high or a low abundance of mesofauna did not influence the response of microorganisms and microfauna to the irrigation treatments.

The significant main effects found for both irrigation and mesh size on microbial biomass (Table 1) are most likely a consequence of the C_{mic} values recorded at week 7 (Fig. 3). At this sampling date, both treatment effects were evident in a comparison of mean values (Fig. 3). C_{mic} values were, on average, 62% lower in the irregularly irrigated bags compared to the regularly irrigated ones (Fig. 3) and significantly diminished by, on average, ca. 38% in L45 (Fig. 3). The low number of significantly different means at the later two sampling dates (Fig. 3) indicates that overall, there was no persistent effect of mesh size upon C_{mic} values (Table 1). From week 7 to week 14, values decreased in the regularly irrigated bags by, on average, 61% (Fig. 3, *t*-test, $P<0.001$) which may explain the significant interaction of both irrigation and mesh size with sampling time for this parameter (Table 1). A general pattern, apparent in both the treated litterbags (Fig. 3) and the undisturbed litter (Table 2), was that microbial biomass declined over the course of the experiment.

Nematoda abundance was, on average, ca. 26% lower under irregular compared with regular irrigation (Fig. 4, *t*-test, $P=0.0001$). This irrigation effect (Table 1) was apparent for the comparison of means (Fig. 4) at week seven (for L45) and at week 14 (for L1000), but was not evident at week 18. At the latter sampling date, Nematoda abundance was low in all treatment combinations. This was most probably a seasonal effect since Nematoda abundance in the undisturbed litter samples had also decreased to similarly low numbers (Table 2).

Nematoda abundance was also affected by mesh size (Table 1). This was apparent between treatment means at week 7 (in the regular irrigation treatment) and 14 (in both irrigation treatments) (Fig. 4). There were no significant differences at week 18. In general, average Nematoda abundance was increased in L45 (Fig. 4,

t–test, $P = 0.0001$). The strength of the mesh size effect varied over time as indicated by the significant interaction of these two factors (Table 1).

Microarthropod abundance was unaffected by the irrigation treatment (Table 1), with neither Collembola nor Acari showing any difference between the treatments. The abundance of the microarthropods changed significantly over time (Table 1), mainly as a result of low abundances in all treatment combinations at the last sampling date (Table 2). At that sampling date, microarthropod abundance did not differ between the litterbags and the undisturbed litter samples (Table 2).

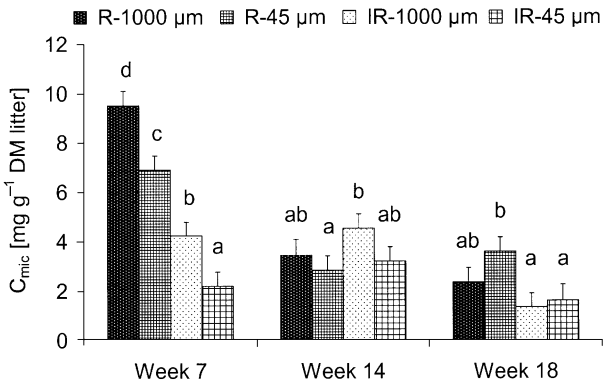

Fig. 3. Mean microbial carbon (C_{mic}) values (mg g^{-1} DM litter] in 1000 and 45 µm litterbags subjected to regular (R) and irregular (IR) irrigations. At each sampling date, columns sharing the same letters are not significantly different, *t*-test, $P < 0.05$, error bars indicate SE, $n = 5$.

Methodological evaluation of the litterbag approach

Removal of mesofauna. The defaunation of the litter had effectively expelled both enchytraeids and microarthropods. However, a small number of animals were found in the L45 when these were checked for mesofauna at each sampling date. Averaged over the course of the experiment as well as irrigation treatment, the L45 contained 0.15 ± 0.28 ind g^{-1} DM litter Enchytraeidae, 1 ± 3.6 ind g^{-1} DM litter Collembola and 4 ± 8 ind g^{-1} DM litter Acari. All microarthropod individuals were immature or belonged to species of small body size. Even if the initial litter material had been 100% animal free, the L45 would most probably have contained mites or Collembola in low abundances as microarthropods can hatch from eggs that were not affected by the defaunation process or from eggs placed into the bags by oviposition (for the microarthropods).

Data on Enchytraeidae were not evaluated since their abundance in the L1000 was not sufficient for statistical analysis (average abundance: 1.3 ± 0.3 ind g^{-1} DM litter). Due to their low abundances, these animals are assumed to be of only minor importance for the effect of the mesofauna treatment. Didden & de Fluiter (1998) found that Enchytraeidae might need between 10 and 12 months to colonize litterbags containing

Table 2 Mean values of parameters derived from 1000 µm litterbags subjected to regular (R) and irregular (IR) irrigation and from L-layer samples

Parameter	Sample type	Week 7	Week 14	Week 18
N_{extr} (µg g^{-1} DM litter)	Litterbag (R)	414 b	417 c	446 c
	Litterbag (IR)	340 b	290 b	290 b
	L-layer	105 a	58 a	61 a
C mineralization (µg C g^{-1} DM litter h^{-1})	Litterbag (R)	17 b	16 a	13 a
	Litterbag (IR)	9 a	14 a	14 a
	L-layer	27 c	29 b	19 b
C_{mic} (mg g^{-1} DM litter)	litterbag (R)	9.5 b	3.5 a	2.4 a
	Litterbag (IR)	4.2 a	4.5 a	1.3 a
	L-layer	11.5 b	7.3 b	4.3 b
Nematoda (ind g^{-1} DM litter)	Litterbag (R)	316 a	460 b	34 a
	Litterbag (IR)	202 a	108 a	69 a
	L-layer	198 a	272 ab	92 a
Collembola (ind g^{-1} DM litter)	litterbag (R + IR)*	13 b	9 a	5 a
	L-layer	4 a	3 a	4 a
Acari (ind g^{-1} DM litter)	Litterbag (R + IR)	63 b	94 b	44 a
	L-layer	29a	45 a	39 a

For each parameter, values measured at one particular sampling date sharing the same letters are not significantly different, *t*-test, $P < 0.05$, $n = 5$.

*As no significant effect of irrigation on microarthropods was found in the ANOVA for Collembola and Acari, values represent the mean of both irrigation treatments.

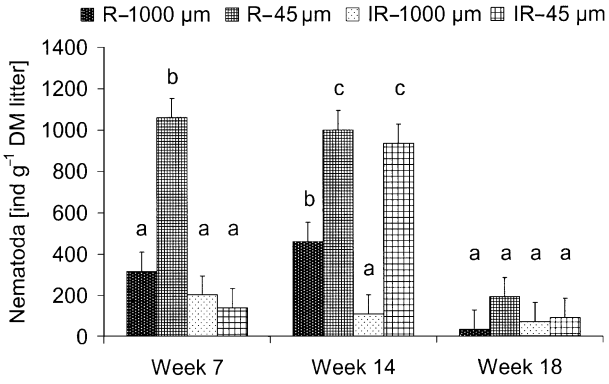

Fig. 4. Mean abundance of Nematoda (ind g^{-1} DM litter) in 1000 and 45 µm litterbags subjected to regular (R) and irregular (IR) irrigations. At each sampling date, columns sharing the same letters are not significantly different, *t*-test, $P < 0.05$, error bars indicate SE, $n = 5$.

L-material. The short duration of the present study may, therefore, be the reason for the low Enchytraeidae abundance in the litterbags. Additionally, as Enchytraeidae abundances in the undisturbed L-layer samples were low (4.5 ± 0.6 ind g^{-1} DM at week 7, 4.1 ± 1.2 ind g^{-1} DM at week 14, 3.9 ± 0.8 ind g^{-1} DM at week 18), it seems likely L-material surrounding the litterbags also contained few Enchytraeidae.

Comparison between the community structure and functional parameters in the litterbags and the L-layer samples. The relative abundance (community composition) of the meso- and microfauna communities in the L1000 was, in general, similar to that recorded from the L-layer samples. Among the groups investigated, Nematoda were numerically the most abundant (Table 2). Acari were the dominant microarthropod group; their abundance was ca. one order of magnitude higher than the abundance of Collembola (Table 2). The litterbags in both irrigation treatments contained approximately twice as many microarthropods as the L-layer samples (Table 2, week seven and 14), whereas no differences in Nematoda abundance were observed. Microbial biomass (C_{mic}) and C mineralization were greater in the L-layer samples than in the L1000 (Table 2). In contrast, values of extractable nitrogen (N_{extr}) in the litterbags were, depending on the irrigation treatment, three to seven times higher than in the L-layer samples (Table 2).

Discussion

The role of soil organisms, in particular invertebrates, in mediating the influence of global change on soil processes has been given close attention in recent years. One point of contention is whether soil organisms that have an impact on small-scale processes are equally important for ecosystem responses at a larger scale (Anderson 1995). Support for the wider influence of soil organisms comes from the observation that incorporating the activities of soil invertebrates into predictive models of the effects of global change on ecosystem processes enhances their accuracy, particularly within C and N cycles (Groffman & Jones 2000). The results of the present study also show a potential influence of soil organisms upon soil processes, namely the influence of mesofauna on N dynamics.

In systems with faunal-microbial communities similar to those found in the current experiment in the L1000, a positive relationship between the inorganic N pool and soil moisture conditions has been reported (Clarholm *et al.*, 1981; Persson, 1989; Verhoef & Brussaard, 1990; Sulkava *et al.*, 1996; Huhta *et al.*, 1998b). This relationship was also valid for N dynamics in the present study, with higher N_{extr} in the moister litter of the regular irrigation treatment. However, an effect of the irrigation treatments on N_{extr} was coupled to the presence of mesofauna. This supports our hypothesis that the exclusion of mesofauna in decomposer communities alters the impact of strongly fluctuating moisture conditions on soil processes.

Mesofauna exclusion from the communities in the L45 not only eliminated the irrigation effect upon N_{extr} but also decreased N_{extr} content. Field and laboratory experiments that involved manipulations of biodiversity by adding trophic groups within a trophic level also observed altered rates of N mineralization (e.g. Persson, 1989; Setälä *et al.*, 1990, 1997). Generally, the exclusion of a whole trophic group has been found to negatively affect N mineralization (Huhta *et al.*, 1998a). It has been commonly suggested that a significant proportion of the NH_4^+ content in litter material containing communities with mesofauna has its origin in the faecal matter and urine of the mesofauna (Vedder *et al.*, 1996). In addition, leaching from damaged fungal hyphae due to mesofauna grazing may also increase NH_4^+ content. N mineralization rates were not directly measured in the present study. However, the lower mass loss in the L45 may indicate both a direct influence of mesofauna on N_{extr} through excretion and an indirect effect through enhanced decomposition rates.

For the functionally complex communities in the L1000, the significant difference between the N_{extr} values in the two irrigation treatments demonstrated the sensitivity of the processes regulating N_{extr} to strongly fluctuating litter moisture. However, the similar mesofauna density in both irrigation treatments indicated that factors other than simply lower amounts of faecal matter and urine or different intensities of

mesofauna grazing were responsible for lower NH_4^+ values under irregular irrigation.

Nitrogen is, in many systems (but with exceptions principally in humid tropical ecosystems: see Tanner *et al.*, 1998; Vitousek & Stanford, 1986), the most important mineral nutrient for plants and N supply generally limits plant productivity (Kaye & Hart, 1997). In terms of the classical understanding of the N cycle, mineral N (here N_{extr}) is a measure of plant available N (Melillo, 1981). A general conclusion from the present study would be that changes in decomposer community structure might decrease plant available N. Additionally, decomposer structure seemed to affect the sensitivity of the mechanisms of the N cycle towards fluctuating moisture conditions. It is tempting to speculate that, with respect to plant available N, the respective mechanisms are more sensitive to variable rainfall as a result of the more complex community structure in the L1000 compared to the L45. However, it is unclear to what extent the low levels of N_{extr} in the L45 could mask an effect of variable rainfall. The lack of an irrigation effect in the L45 would therefore reflect the low N_{extr} rather than suggest that the involved mechanisms are more resilient to fluctuating moisture.

There was an obvious contradiction between the measured levels of microbial activity and the mass loss data: respiration rates were significantly higher from the L45 litter, but mass loss was greater from the L1000. It could be speculated that the different respiration rates in the L45 and L1000 were a consequence of the development of two structurally different microbial communities. Alterations of the bacterial:fungal ratio, which could affect respiration rates have been observed as a result of selective grazing of the bacteriophagous microfauna (Griffith *et al.*, 1999). However, microbial PLFA profiles, determined in the litter material from week 14 and 18 of the present experiment, revealed similar bacterial:fungal ratios in the litter of all treatment combinations as well as in the undisturbed L-layer samples with a larger bacterial than fungal biomass (Wilkinson *et al.*, 2002). The most likely explanation for the discrepancy between the levels of microbial activity and actual mass loss is that the greater C mineralization measured from the L45 communities is an artifact. The lack of grazing by mesofauna is likely to have led to a larger pool of dead microbial biomass in the L45 compared to the L1000. This could have acted as a labile substrate during the 6 day period when microbial activity was determined resulting in higher C mineralization.

The experiment demonstrated that litter mass loss, used as an indicator of decomposition, was significantly affected by the strong structural changes in the decomposer community (i.e. the radical reduction of microarthropods due to the mesh size treatment). However, this parameter was not a sensitive indicator of potential effects induced by fluctuating moisture conditions.

Our study revealed that the response of the Nematoda and the microbial biomass to the irrigation treatments was independent of the abundance of mesofauna. Microorganisms, Nematoda and microarthropods each followed a different response pattern to manipulations of water availability and/or community structure.

The higher microbial biomass recorded at the first sampling in the regularly compared to the irregularly irrigated bags may be the result of rapid microbial growth under favourable conditions on nutrients liberated during the establishment of the litterbags: analogous to increased microbial activity after drying/rewetting or freezing/thawing cycles (Marumoto *et al.*, 1982; Orchard & Cook 1983; DeLuca *et al.*, 1992). Biomass then decreased between week seven and week 14 in the regular treatment, perhaps as resources became limiting. In the irregularly irrigated bags, the lower moisture availability seemed to have restricted the initial flush of microbial growth, particularly in the absence of mesofauna. With respect to this flush effect, the first sampling may be unrepresentative of a microbial response to the treatments. At the two remaining sampling dates, no consistent effect of irrigation or mesofauna exclusion on the microbial community was apparent.

Nematoda abundance has been positively linked with increasing substrate moisture content (Griffith *et al.*, 1995; Görres *et al.*, 1998; Schouten *et al.*, 1998) and to decreasing mesofauna abundance (Brussaard *et al.*, 1995). In the present experiment, highest average Nematoda abundance was also reached in the treatment with the most favourable combination of both factors mentioned above: constant moisture conditions and mesofauna reduction. However, at week 14, Nematoda abundance in the irregularly irrigated L45 was equally high as in the regular irrigation treatment (Fig. 4) due to a strong increase in Nematoda numbers between week seven and 14 under irregular irrigation. It seems likely that this increase was partly due to the rising background moisture which was most pronounced in the irregular irrigation treatment during the same time span (Fig. 1). At week 7, high Nematoda numbers, due to low mesofauna abundance, were only apparent in the regular irrigation treatment. We believe that at that date, Nematoda numbers in the L45 under irregular irrigation could not benefit from mesofauna reduction due to unfavourable moisture conditions. By week 14, however, a combination of relatively moist conditions in the irregularly irrigated litterbags (Fig. 1)

and mesofauna reduction resulted in increased Nematoda abundance. This result might suggest that for mesofauna reduction to affect Nematoda numbers, a threshold moisture level had to be reached before an increase in Nematoda numbers became measurable. A negative effect of mesofauna on Nematoda abundance can be the result of both predation, e.g. by mesostigmatic mites or Collembola (Karg 1983; Walter 1987; Brussaard *et al.*, 1995), and changes in resource availability due to competition for food (Hyvönen & Persson, 1996). The low abundance of predatory mesofauna in the L1000 (on average $<1\,\mathrm{ind\,g^{-1}}$ DM, data not shown) suggests that in the present experiment, resource competition rather than predation was the primary influence on Nematoda abundance.

In the present experiment, microarthropods were largely unaffected by the irrigation treatments, supporting previous results that found them to be tolerant of a wide range of moisture conditions, including temporary flooding and drought (Walter & Proctor, 1999).

Our results showed a strong impact of fluctuating moisture conditions on several of the measured ecological parameters. It could be argued that these findings are partly influenced by methodological problems associated with the litterbag approach. This aspect will be addressed in the following discussion:

(a) The higher mass loss in the L1000 could potentially be an artefact resulting from loss of material from the larger mesh size during placement and collection. However, bags were treated with great care. During transport to and from the plots each bag was placed in an individual plastic bag preventing the loss of any material that had fallen through the nets. The potential loss of material from the litterbags would have been most likely at the later decomposition stages. However, even at the last sampling date, needle structure was still largely intact. Loss on handling could only really have occurred where needles were actively pushed through the mesh; this was avoided by careful handling of the bags. We believe that loss of material during handling was not a significant factor in the measured mesh size effect on mass loss.

(b) It could be argued that the lower N_{extr} measured in the irregularly irrigated compared with regularly irrigated L1000 was a result of increased leaching associated with the addition of six times the volume of water being added to the irregularly irrigated L1000 in one irrigation event compared to the regularly irrigated L1000. Leaching impacts will depend on the amount of water-soluble material in the litter and the amount of water passing over it (Aber & Melillo, 1991). During the course of the study, irregular irrigation was only performed on three occasions. On each occasion the plots were watered three times a day (morning, noon, evening), over two consecutive days, with 6 L throughfall m^{-2} per watering event (i.e. each single watering event was comparable to one irrigation event within the regular irrigation treatment). This amounted to a total of 36 l throughfall m^{-2} per irregular irrigation event. It seems unlikely that these three irrigation events (morning, noon, evening) had a greater leaching impact than the continual regular irrigation, especially since the regularly irrigated L1000 received twice the amount of irrigation over the whole course of the experiment. In addition, it would be expected that the same leaching effect should have been observed in the L45. This disparity may be a consequence of differences in biology between the two mesh sizes affecting the comparability of the two systems in terms of impacts on mineral N available for leaching. However, in lysimeters equipped with entrances for only microfauna (45 μm mesh) or microfauna and mesofauna (1000 μm mesh), cumulative leaching of NH_4^+–N was not different between the two structurally different communities (Liiri *et al.*, 2002).

(c) Differences in microbial parameters between the L-layer samples and the L1000 could most likely be attributed to disturbance during the defaunation of the litter, as it has been demonstrated previously that this process can reduce C mineralization (Huhta *et al.*, 1989) and greatly increase extractable NH_4^+ levels (Sulkava *et al.*, 1996). However, comparative studies of defaunation procedures have shown that the effects of drying soil at the ambient temperatures applied in the present study (20-30 °C) are much less severe than the effects of drying at elevated temperatures (60-100 °C) (Sørensen, 1983) or more drastic methods, like microwaving, deep freezing or biocide application (Huhta *et al.*, 1989).

Extraction techniques extract soil fauna species and life stages within species with different efficiencies with more mobile forms more easily recovered (Takeda, 1979; André *et al.*, 2002; Søvik & Leinaas, 2002). This potential selection process may be particularly important when defaunation/refaunation of litter is required. In order to minimize the effects of the varying extraction efficiency in the present study, the same extraction scheme was used for the defaunation of litter and the acquisition of soil fauna for refaunation. It is therefore very likely that the faunal component added

during refaunation was rather similar to that removed by defaunation so that the final community was representative of the normal site. We cannot, however, exclude a shift in the composition of the mesofauna in the L1000 due to the experimental treatment.

With respect to the faunal community, animal abundances found in the litterbags lie well within the natural ranges reported in the literature from spruce forests (*e.g.* Wallwork 1983; Ellenberg *et al.*, 1986) and followed the same seasonal changes that were found for the adjacent undisturbed L-layer samples. We therefore believe that the data obtained from the litterbags are representative of undisturbed conditions and reflect trends that are also characteristic for a natural faunal and microbial community.

Conclusions

- Components of the N cycle and mass loss were sensitive indicators of changes in the structural and functional complexity of decomposer communities.
- The sensitivity of processes in the N cycle (indicated by extractable N) to strong fluctuations in litter moisture was coupled to the structural and functional complexity of the decomposer community.
- Major structural and functional impoverishment of the decomposer community, resulting from mesofauna exclusion, may reduce readily available soil nitrogen.
- Mesofauna abundance was not affected by strongly fluctuating litter moisture conditions.
- Irrespective of the presence of mesofauna, the control mechanisms regulating C mineralization and mass loss appeared unaffected by fluctuations in litter moisture availability.
- Major structural and functional impoverishment of decomposer communities strongly increased Nematoda abundance but did not alter the relative impact of strongly fluctuating moisture conditions on both Nematoda abundance and microbial biomass.

In the short-term perspective of the present study mesofauna abundance and microbial biomass showed little response to imposed fluctuating moisture conditions. However, a decrease of extractable N under fluctuating moisture conditions in the structurally and functionally more complex communities demonstrated a certain sensitivity of the decomposer community on a functional level. Extremes in rainfall patterns, generated by climate change, may have a negative impact on the availability of nutrients, particularly N, for plants. This effect could be amplified by an additional impoverishment in the structural and functional complexity of the respective decomposer communities.

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