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Organic matter and nutrient dynamics of the litter layer on a forest Rendzina under beech

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Summary. The decomposition of beech (*Fagus sylvatica* L.) leaf litter was investigated in a calcareous beech forest using mesh cages containing two layers, fresh leaf litter (O layer), and partly decomposed leaf litter (F layer). C loss was monitored, together with the changes in the contents of total N, hexosamines, ash, Na, K, Mg, Ca, Fe, Mn, Al, Cl, Sulphate, and Phosphate.

In 1-mm mesh cages, which excluded access to the macrofauna, the mean annual loss rates for C were 28% in the O leaf litter and 17% in the F leaf litter, totalling approximately 23% for the two layers. The mean loss rates from the 12-mm mesh cages were 54% in the O leaf litter and 58% in the F leaf litter. Degradation processes and feeding activities caused increased contents of ash, total N, and hexosamines in the O layer of both treatments. This increase was greater for the ash and smaller for N, glucosamine, and galactosamine in the 12-mm mesh cages. The sum of ions ($Na+K+Mg+Ca+Fe+Mn+Al+Cl+SO_4+PO_4$) and also the contents of most single ions were not markedly affected, despite the much higher ash content in the O leaf litter of the 12-mm mesh cages. The ash content increased mainly as a consequence of contamination by soil, which increased the contents of Fe and Al in the ash.

Key words: Litter decomposition – Litter bag experiment – Macrofaunal effects – Organic matter turnover – Nutrient dynamics – Hexosamines

The processes of litter decomposition and mineralization of the constituent elements are important parts of the nutrient cycle. Dead leaves are first subjected to breakdown processes in the surface layer. In forests on limestone, comminuted litter is subsequently incorporated into the mineral soil by earthworms (Scheu and Wolters 1991). Nonetheless, 90% of the litter substrate is mineralized by bacteria and fungi (Schaefer 1990). Thus, faunal litter-feeding mainly results in mechanical disintegration, with a relatively small assimilation of substrate. However, there is increasing evidence that soil animals have a stronger influence on the nutrient flux (Anderson et al. 1985). These conclusions are supported by laboratory studies in microcosms, especially for N (Ineson et al. 1982; Anderson et al. 1983; Scheu 1987). However, it is often difficult to extrapolate results from the laboratory to the field situation. Litter bag experiments can be used as an alternative approach in obtaining information about interactions between soil animals and soil microflora (Seastedt 1984). These experiments have demonstrated significant mesofauna (Wolters 1991) and macrofauna (Staaf 1987) effects on decomposition in mull sites. However, litter bags, especially small ones, also introduce some artifacts, such as changes in the microclimate (Seastedt 1984). This paper presents the results of an experiment with large litter cages designed to provide information on (1) the C loss from beech litter of different ages, (2) the effect of organisms >1 mm on nutrient release from the litter, and (3) the influence of organisms >1 mm on the hexosamines produced by microbial metabolism.

Materials and methods

Study area

The experiment was carried out in the Göttingen Forest, Lower Saxony, Germany. The elevation above sea level ranges between 400 and 420 m, the mean annual air temperature is 7.9 °C, and the mean annual precipitation 720 mm. The bedrock is limestone (shell-lime). The forest is a mature beech, 100–130 years old, with a dense cover of understory herb species (*Melico fagetum hordelymetosum*). The soil is a Rendzina [Rendzic Leptosol (FAO) or Lithic Rendoll (USDA)]. The soil faunal biomass is 15 g m^{-2} dry weight, of which one-third can be attributed to *Lumbricus terrestris*, one-third to other earthworms such as *Aporrectodea caliginosa, Octolasion cyaneum*, and *O. lacteum*, and one-third to the remaining soil animal groups (Schaefer 1990).

Litter enclosures

The experiment was carried out in cages (1 m×1 m×0.2 m deep) made of plastic-coated, 12-mm wire mesh to minimize variability. In 1-mm mesh cages, macrofauna was excluded with an inlaid nylon bag (1 mm mesh). The 12-mm mesh cages were closed on top with a nylon gauze

(1 mm mesh) to keep out new litter falling during the year. Each cage consisted of two layers of leaf litter separated by a wire mesh (100×100, 12 mm mesh). The upper layer (O-layer) contained freshly fallen leaf litter collected in three 100-m^2 nets in the middle of November, which was air-dried, weighed, and reapportioned. The dry weight was 300 g m^{-2} of air-dried material, equivalent to 144 g C m^{-2} in 1983 and to 145 g C m^{-2} in 1984. The lower layer (F layer) consisted of wintered and partly deomposed leaf litter which was collected directly from the soil by sampling an area of 30 m^2. The leaf litter remaining on the surface of the mineral soil was collected after the current year's fresh litter had been removed with nets. All twigs, fruit bodies, etc., were removed from this F leaf litter before it was weighed and reapportioned (1983: 340 g C m^{-2}, 1984: 289 g C m^{-2}). The cages were replaced on the sampling plot, approximately 0.5 m apart, and the spaces were refilled with litter previously removed. Three cages were removed for analysis on each sampling day, and the spaces were refilled with other leaf litter.

Analysis of leaf litter

All samples were air-dried before analysis and homogenized by grinding in a centrifugal mill with a 0.25 mm mesh. Each analysis was performed twice for day 0 and for the other sampling dates (three in 1983 and four in 1984).

Dry weight

An aliquot was dried at 105 °C for 20 h.

Ash

One g of the sample was heated at 700 °C to constant weight.

Cations and phosphate

A 1-g sample was heated at 550 °C for at least 12 h, then dissolved in 50% HNO_3, filtered (Schleicher & Schuell 595-1/2), and made up to 100 cm^3. Na, K, Mg, Ca, Fe, Mn, and Al were determined by atomic absorption spectrophotometric analysis. To measure PO_4, 7.5 cm^3 50% HNO_3, 10 cm^3 NH_4-molybdate, and 10 cm^3 NH_4-vanadate were added to an aliquot of the filtrate and made up to 100 cm^3. After 30 min, the absorption was read at 430 nm.

Chloride

Two grams of sample were mixed with 20 cm^3 of 0.1 *M* NaOH in a crucible and heated at 105 °C until all water had evaporated, and then heated at 480 °C for at least 10 h. After cooling, 15 cm^3 0.05 *M* H_2SO_4 was added to the residue, and this was allowed to stand for 3 h. After filtration (Schleicher & Schuell 595-1/2), the solution was made up to 100 cm^3 (Jungk 1968). Chloride was measured potentiometrically by the addition of 0.01 *M* $AgNO_3$ to an aliquot that had been acidified with HNO_2.

Sulfate

A 2-g sample was treated as for chloride except that after cooling, 15 cm^3 0.1 *M* HCl was added to the residue. Cations were eliminated from an aliquot using a strong acidic cation exchange resin, and then 7 cm^3 0.005 *M* $BaCl_2$ was added and mixed for 10 min on a magnetic stirrer to precipitate $BaSO_4$. The excess of $BaCl_2$ was measured potentiometrically by the addition of 0.005 *M* Na_2-ethylenediamine tetraacetic acid.

Total C and total N

After dry combustion, CO_2 and N_2 were determined by gas chromatography.

Amino sugars

A 0.5-g sample was hydrolysed by treating it with 15 cm^3 6 *M* HCl for 24 h followed by refluxing for 6 h. The amino sugars were separated by cation exchange chromatography and, after reaction with ninhydrin, detected colorimetrically at 560 nm (Joergensen and Meyer 1990a).

Statistics

All statistical analyses were performed using the SAS statistical package (SAS Institute Inc. 1982). Figures presented here are arithmetic means and significance tests are based upon appropriately transformed data. A logarithmic transformation was used in most cases.

Results

C

The C content in fresh leaf litter was approximately 550 mg g^{-1} ash-free dry weight and did not change significantly during decomposition (Table 1). In F leaf litter the C content as a percentage of the ash-free dry weight was only slightly lower, despite an increasing ash content, which was nine to ten times higher than in fresh leaf litter (Table 2).

In 1-mm mesh cages, the mean annual loss rates for C were 28% in the O leaf litter and 17% in the F leaf litter, totalling approximately 23% in the two layers. It was not possible to determine how much organic material was exchanged between the two layers. The mean loss rates from the 12-mm mesh cages were 54% in the O leaf litter and 58% in the F leaf litter. The loss rates in O leaf litter were lower during the cold winter months and increased in autumn (Fig. 1 a). The loss rates in F leaf litter were less depressed during the winter and tended to show an exponential decline (Fig. 1 b). A single exponential model provided a fairly correct approximation of the C loss from recalcitrant beech leaf litter over a 2-year period (Joergensen and Meyer 1990b). The function used is:

$$C_t = (Ct_0)e^{-k}$$

Table 1. Content of C, N, and hexosamines [glucosamine (GlcN) and galactosamine (GalN)] in fresh leaf litter, in O leaf litter after 1 year of decomposition, and in F leaf litter

	C	N	Hexosamines	GlcN	GalN
	(mg g^{-1} ash-free dry weight)				
Fresh leaf litter	552	12.5	2.2	2.2	0.0
±SD	1	2.2	1.7	1.7	
O leaf litter	548	18.3*	11.7*	5.6*	6.1*
(1 mm) ±SD	3	2.1	1.1	0.5	0.6
O leaf litter	552	16.6*	7.8*†	4.3*	3.5*†
(12 mm) ±SD	8	1.8	0.4	0.3	0.3
F leaf litter	543	23.0*†‡	17.8*†‡	9.7*†‡	8.1*†‡
±SD	8	1.2	1.6	0.8	1.1
	(g m^{-2})				
Fresh leaf litter	145	3.3	0.6	0.6	0.0
O leaf litter (1 mm)	105*	3.5	2.2*	1.1*	1.2*
O leaf litter (12 mm)	66*†	2.0*†	0.9†	0.5†	0.5*†

Fresh leaf litter, $n = 6$ (2 years × three replicates) ; O leaf litter, $n = 6$ (2 years × three replicates of November samples); F leaf litter, $n = 18$ (2 years × three replicates in December + 2 years × two treatments × three replicates in November samples a year later); significantly different from fresh leaf litter, $^*P<0.01$; from O leaf litter (1 mm), $^\dagger P<0.01$; from O leaf litter (12 mm), $^\ddagger P<0.01$

Table 2. Contents of ash and sum of ions, ratios of silicate material, and Fe, Al and Mn contents in fresh leaf litter, in O leaf litter after 1 year of decomposition, and in F leaf litter

	Ash (mg g^{-1} dry weight)	Σ ions (mg g^{-1} dry weight)	Silicates[b]/ Fe	Silicates[b]/ Al	Silicates[b]/ Mn
Fresh leaf litter	46.3	27.7	44	45	80
±SD	0.9	0.9	4	7	5
O leaf litter (1 mm)	74.7*	30.8*	24*	44	149*
±SD	5.0	0.9	5	4	21
O leaf litter (12 mm)	135.9*†	32.5*	30*	38	339*†
±SD	33.6	1.7	8	11	111
F leaf litter	391.4*†≠	65.9*†≠	27*	19*†≠	656*†≠
±SD	38.3	3.6	2	2	112

[a] Σ ions = Na + K + Mg + Ca + Fe + Mn + Al + Cl + SO_4 + PO_4
[b] Silicates = ash − Σ ions
For explanation of significance, see Table 1

as proposed by Jenny et al. (1949), where C_t is the amount of C at time t, Ct_0 the amount of C at time t = O (end of the autumnal litter fall, start of the experiment), and k is the decomposition constant. A single, and even more, a double exponential model strongly contradicts the observed loss rates in the O layer (Fig. 1 a). However, the single exponential model gives a fairly correct estimate of the measured loss rates in the F leaf litter (Fig. 1 b). After recalculation of the measured data by the simple model of Jenny et al. (1949), the mean annual loss rates for C were estimated as 49.3% of the initial C content the O leaf litter and 58.9% of that in the F leaf litter

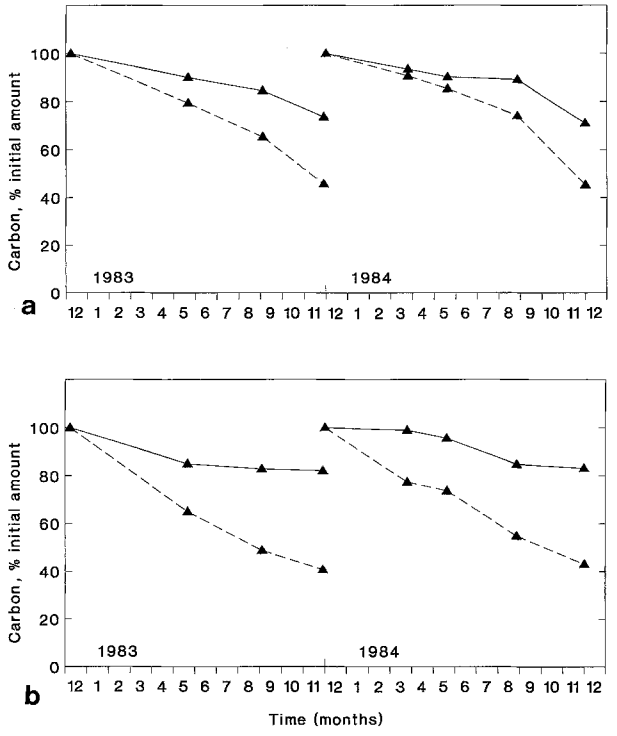

Fig. 1a. C (▲) in the O layer shown as a percentage of the initial value in 1-mm mesh cages (——) and in 12-mm mesh cages (– –); pooled coefficients of variation are ± 2.4% for 1-mm mesh cages and ±5.8% for 12-mm mesh cages. **b** C (▲) in the F layer shown as a percentage of the initial value in 1-mm mesh cages (——) and in 12-mm mesh cages (– –); pooled coefficients of variation are ±4.6% for 1-mm mesh cages and ± 13.5% for 12-mm mesh cages

(Table 3). In the 1-mm mesh cages, the mean annual loss rates were 24.4 and 20.1%, respectively. The loss rates predicted by the model did not differ significantly between the 2 years, despite different climatic conditions and a varying ash content in the F leaf litter. The average turnover time increased from approximately 1.2 years in the 12-mm mesh cages to 4.5 in the 1-mm mesh cages (Table 3).

N

The N content in O leaf litter increased independently of the initial N content by 6 mg g^{-1} ash-free dry weight in the 1-mm mesh cages and by only 4 mg g^{-1} in the 12-mm mesh cages in both years (Table 1); 80% of the increase occurred between March and August (Fig. 2). The initial N content was very different in the 2 years, being high in 1983 (1.45 mg g^{-1} ash-free dry weight) and low in 1984 (1.01 mg g^{-1} ash-free dry weight). Thus, the 2-year average N content did not differ significantly between the two treatments (Table 1 and Fig. 3). In each single year, however, the N content was significantly higher

Table 3. Calculated intercept and constant k of the exponential decomposition model (Jenny et al. 1949) $Ct = (Ct_0)e^{-k}$, where t is time and t_0 is the start of the experiment

Year	Layer	Mesh size	Intercept	k	C loss year^{-1} (% Ct_0)	Turnover time (years)
1983	O	1 mm	4.6215	0.2852	24.8	3.5
		12 mm	4.6605	0.7265	51.6	1.4
1984	O	1 mm	4.6336	0.2760	24.1	3.6
		12 mm	4.7102	0.6359	47.1	1.6
1983–1984	O	1 mm	4.6285	0.2804	24.4	3.6
		12 mm	4.6904	0.6787	49.3	1.5
1983	F	1 mm	4.5783	0.2349	20.9	4.3
		12 mm	4.6009	0.9982	63.1	1.0
1984	F	1 mm	4.6325	0.1896	17.0	5.3
		12 mm	4.6182	0.7896	54.6	1.3
1983–1984	F	1 mm	4.6098	0.2096	18.9	4.8
		12 mm	4.6148	0.8890	58.9	1.1
1983–1984	O+F	1 mm	4.6126	0.2240	20.1	4.5
		12 mm	4.6451	0.8196	55.9	1.2

C loss is given as % of the initial measure level

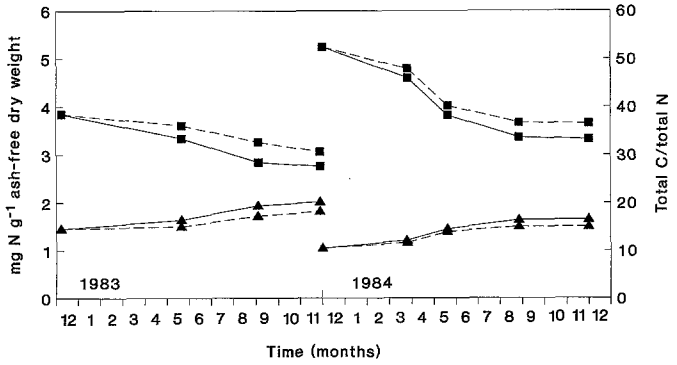

Fig. 2. Change in N content (▲) in O leaf litter in 1-mm mesh cages (——) and in 12-mm mesh cages (– –), and ratio of total C to total N (■) in 1-mm mesh cages (——) and in 12-mm mesh cages (– –)

in the 1-mm mesh cages. As the N content increased, the C : N ratio fell to 33 in the 12-mesh cages and to 30 in the 1-mm mesh cages (Fig. 2). In the 1-mm cages, N increased above the initial level in both experimental years (0.5 g m^{-2} in 1983 and 1.1 g m^{-2} in 1984). The maximum N concentration was reached in August in both years.

In the F leaf litter, the N content did not change during the year, remaining constant at about 2.3 mg g^{-1} ash-free dry weight (Table 1). Neither the total N content nor any other of the organic and inorganic components analyzed showed significant differences between treatments at the beginning and the end of the experiment. The loss rates for each component followed the rates of C loss. All results for the quality of F leaf litter were therefore averaged (Tables 1, 2, 4).

Amino sugars

The amino sugar content in O leaf litter increased to an average of 11.7 mg g^{-1} ash-free dry weight in the 1-mm mesh cages, roughly five times above the initial level, and to only 7.8 mg g^{-1} ash-free dry weight in the 12-mm mesh cages (Table 1). This was mainly caused by a lower galactosamine content, which increased continuously from 0 to an average of 6.1 mg g^{-1} ash-free dry weight in the 1-mm mesh cages and to only 3.5 mg in the 12-mm mesh cages (Table 1; Figs. 3, 4). The accumulation of glucosamine was markedly different in the 2 years (Fig. 4). The N-rich fresh leaf litter had an initial glucosamine content of 3.7 mg g^{-1} ash-free dry weight in 1983, which remained relatively constant with some variations in the 12-mm mesh cages and increased to 5.8 mg g^{-1} in the 1-mm mesh cages. The N-poor fresh leaf litter had a very low glucosamine content of 0.7 mg g^{-1} ash-free dry weight in 1984, but this increased to the level of the year before in both the 1- and 12-mm mesh cages.

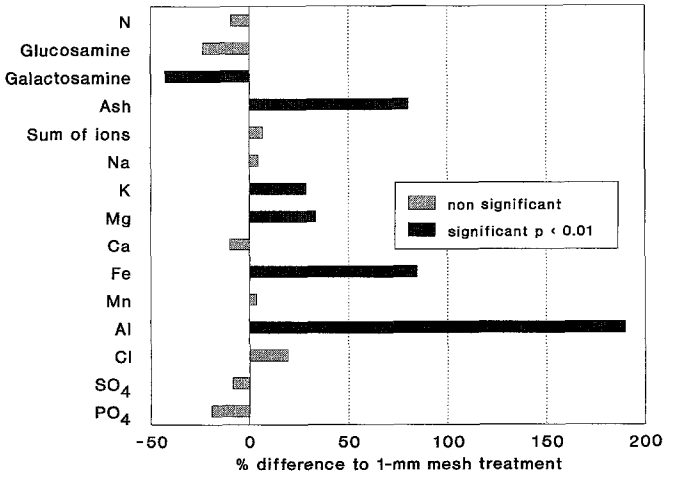

Fig. 3. Influence of macrofauna on nutrient contents, expressed as a percentage of the difference between 12-mm mesh and 1-mm mesh cages

Ash

On average, the ash content in O leaf litter increased from 46 to 75 mg g^{-1} dry weight in the 1-mm mesh cages and to 136 mg g^{-1} in the 12-mm mesh cages (Table 2; Fig. 5a). This increase in the ash content was mainly due to the input of silicate material, because the sum of ions ($Ca^{2+} + K^{+} + Mg^{2+} + Na^{+} + Al^{3+} + Fe^{2+} + Mn^{2+} + Cl^{-} + SO_4^{2-} + PO_4^{3-}$) increased less markedly. In contrast to the ash content, the sum of ions did not differ significantly after 1 year with either cage mesh size (Fig. 3).

Ca, Na, K, and Mg

Ca comprised approximately two-thirds of the sum of ions. The Ca content remained relatively constant without marked variation between years, seasons, treatments (Fig. 5a) and layers. Thus, the Ca loss rates roughly followed the C loss rates. However, some differences were significant (Table 4). The time-course of the Na content was similar to that of Ca, but with less distinct variations (Fig. 5b). The small amounts held in the leaf litter layer varied only slightly over the 2 years of the experiment (Table 4).

K is only electrostatically bonded to cell membranes and is readily leached when these membranes are destroyed. After the autumnal leaf fall at the end of November, the beech leaf litter contained only 2.5 mg K g^{-1} (Table 4). The content decreased markedly at the beginning of the year to 1 mg K g^{-1}, remained constant for a few months, and then increased again (Fig. 5b). After 1 year, the K content was so much higher in the 12-mm mesh cages that the loss (g m^{-2}) in the 1-mm mesh cages was no longer significantly lower. In F leaf litter, the K content was constant at 4.9 mg g^{-1} (Table 4), indicating a greater degree of K fixation by silicate soil material. The time-course of the Mg content was similar to that of K but at half the value, for both cage mesh sizes, despite a somewhat flatter decline during the early months (Fig. 5b).

Fe, Al, and Mn

The litter contents of Fe and Al were closely correlated with the ash content ($n = 66$; $r = 0.994$, $r = 0.987$, respectively). Consequently, the increase in these two elements was much higher in the 12-mm than the 1-mm mesh cages (Fig. 5c). The ratio of silicates to Fe was 44 in fresh leaf

Table 4. Content of nutrients in fresh leaf litter, in O leaf litter after 1 year of decomposition, and in F leaf litter

	Na	K	Mg	Ca	Fe	Mn	Al	Cl	SO_4	PO_4
	($mg\ g^{-1}$ dry weight)									
Fresh leaf litter	0.44	2.4	1.1	17.7	0.4	0.23	0.4	0.36	2.9	1.6
±SD	0.16	0.1	0.1	0.2	0.0	0.00	0.0	0.09	0.4	0.1
O leaf litter (1 mm)	0.44	1.4*	0.9*	18.6	1.9*	0.30*	1.0*	0.26	3.6	2.4*
±SD	0.02	0.1	0.0	0.9	0.4	0.03	0.1	0.03	0.2	0.6
O leaf litter (12 mm)	0.46	1.8*†	1.2*	16.8	3.5*†	0.31*	2.9*†	0.31	3.3	2.0
±SD	0.05	0.3	0.2	1.7	1.2	0.02	1.1	0.07	0.6	0.3
F leaf litter	0.57*†	4.9*†‡	2.6*†‡	21.4*‡	12.2*†‡	0.50*†‡	17.8*†‡	0.32	2.9†	2.8*‡
±SD	0.05	0.5	0.1	3.5	1.8	0.05	3.0	0.21	0.3	0.2
	($g\ m^{-2}$)									
Fresh leaf litter	0.12	0.65	0.31	4.9	0.12	0.06	0.12	0.10	0.81	0.45
O leaf litter (1 mm)	0.09	0.29*	0.18*	3.8*	0.39*	0.06	0.21*	0.05*	0.74	0.50
O leaf litter (12 mm)	0.06*	0.25*	0.16*	2.3*†	0.50*	0.04*†	0.40*†	0.04*	0.46*†	0.27*†

For explanation of significance, see Table 1

litter and 24–30 in the other litter samples. The ratio of silicates to Al was 45 in fresh leaf litter, remained relatively constant in O leaf litter, and was reduced to 19 in F leaf litter. Despite a C loss of roughly 50% in the 12-mm mesh cages, the contents of Fe and Al in the mesh cages were equal to or more than four times higher than the original fresh litter contents after 1 year (Table 4). In contrast to Fe and Al, the Mn content increased only slightly during the 1st year of decomposition (Fig. 5c) and was only doubled in the F leaf litter, although the ash content was eight times higher. Thus, the ratio of silicates to Mn increased from 80 to 660 (Table 2). Since there was no difference in Mn content between the two cage mesh sizes, less Mn ($g\ m^{-2}$) was held in the 12-mm mesh cages (Table 4).

Sulfate, phosphate and chloride

The SO_4 and PO_4 contents in O leaf litter went up slightly during the year, without significant differences between the cage mesh sizes. However, there was a tendency for a higher content in the 1-mm mesh cages. This was more evident for PO_4 (Table 4), as the Cl content was relatively constant throughout both years. The molar Cl:Na ratio was 0.5 in the O and F leaf litter (Table 4), but 1.5 in the canopy throughfall, indicating that more Na was retained than Cl (Joergensen and Meyer 1990b).

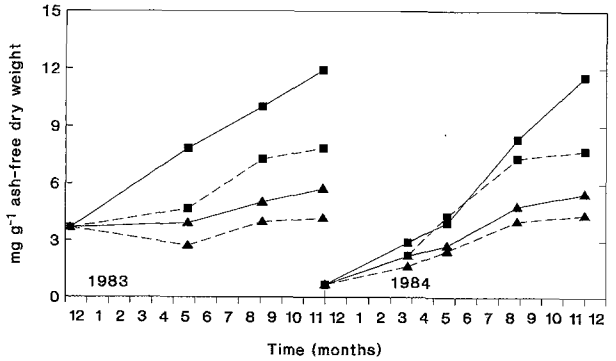

Fig. 4. Change in content of hexosamines (■) and glucosamine (▲) in O leaf litter in 1-mm mesh cages (——) and in 12-mm mesh cages (– –)

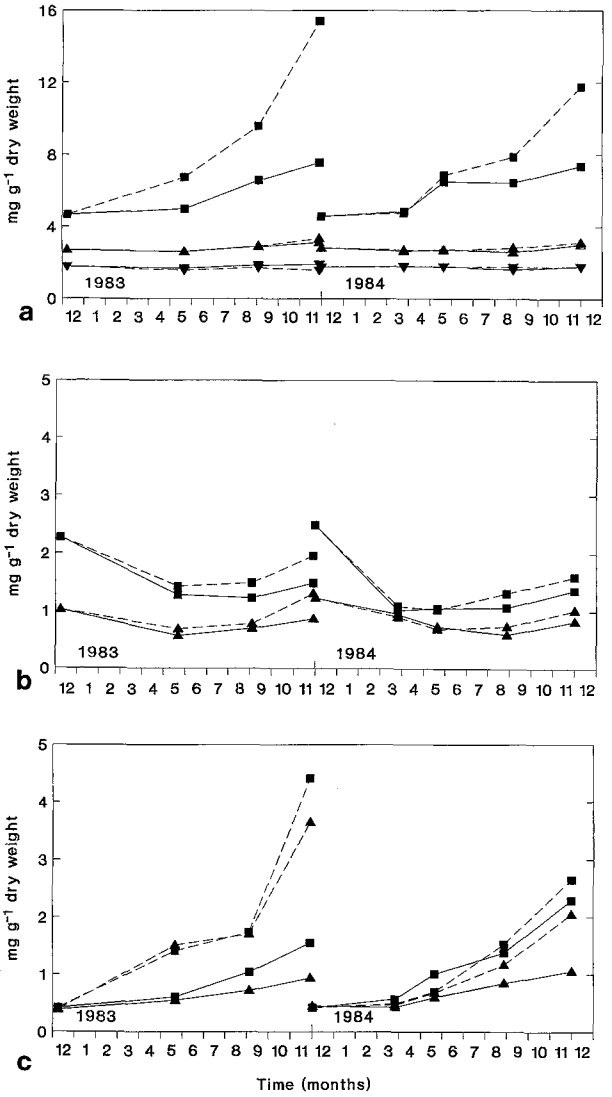

Fig. 5a. Change in ash content (■), sum of ions (▲), and Ca content (▼) in O leaf litter in 1-mm mesh cages (——) and in 12-mm mesh cages (– –); **b** change in the content of K (■) and Mg (▲) in O leaf litter in 1-mm mesh cages (——) and in 12-mm mesh cages (– –); **c** change in the content of Al (▲) and Fe (■) in O leaf litter in 1-mm mesh cages (——) and in 12-mm mesh cages (– –)

Discussion

Nutrient dynamics

Under the natural environmental conditions of the calcareous Göttingen Forest, roughly half the litter fall disappears from the surface layer after 1 year, mainly as a result of earthworms (Schaefer 1990). Earthworms accelerate the process of mineralization by incorporation into the subsurface soil (Staaf 1987; Scheu and Wolters 1991).

The time-course of the changing nutrient contents in decomposing fresh leaf litter in the present study generally conformed with observations by others. A slow increase in the N content over a period of 2 years to a maximum of roughly 20 mg g^{-1} dry weight has often been reported in different ecosystems for beech leaf litter (Staaf 1980; Joergensen and Meyer 1990b). A similar increase in PO_4 content has been measured less frequently (Gosz et al. 1973). A rapid decline in the K content during the early months and a renewed increase has been regularly observed in fresh leaf litter (Gosz et al. 1973; Staaf 1980). This new increase was presumably caused by an enlarged cation exchange capacity after the accumulation of soil particles. The Mg content had increased by the end of each year, obviously for the same reason, and was, thus, more than doubled in the F leaf litter. The change in Ca content in O leaf litter was less distinct, and no marked increase was measured at the end of each year. The release of plant-bonded Ca balanced or exceeded the input of adsorbed Ca transferred by soil particles in the 1st year of decomposition. However, the Ca content was also increased to a significantly greater extent in F leaf litter as a result of an enlarged cation exchange capacity. Fluctuations in the Na content have been observed, which were not caused by processes associated with decomposition but by a wide variability in deposition (Gosz et al. 1973; Staaf 1980). A slight increase in Mn and Fe contents is known from several studies (Gosz et al. 1973; Joergensen and Meyer 1990b).

The present litter cage experiment demonstrates that the soil fauna is effective in reducing nutrient immobilization by accelerating decomposition rates, as shown by others in temperate forests on mull sites (Anderson 1973; Staaf 1987). The soil fauna amplifies, rather than alters, the existing pattern of nutrient release (Anderson et al. 1983). However, the macrofauna had some characteristic effects on the chemical composition of the leaf litter remaining on the surface in the present experiment.

Earthworms increased the ash content markedly by transferring soil material into the 12-mm mesh cages, mainly by the deposition of casts, although the sum of ions was not significantly affected by this transport. Nevertheless, some significant changes in element composition were measured in the 12-mm mesh cages. The Fe and Al contents rose markedly, K and Mg rose slightly, and Ca fell slightly compared with 1-mm mesh cages. The soil material that was transferred increased the Fe and Al contents as measured after the sample was ashed. However, the changes in nutrient contents were quite small in relation to the amount of soil material transferred by the earthworms.

The N content, which is the key component in terrestrial ecosystems (Anderson et al. 1985), was considerably influenced by macrofaunal activity. In both years, the N content of the leaf litter remaining in the O layer was significantly lower in the 12-mm mesh cages. A similar, but not significant, effect was observed for PO_4. Soil animals may incorporate leaf litter with a higher N content into the soil, but they may also counteract microbial N immobilization in the litter layer, both directly, by grazing the microbial biomass, and indirectly, by modifying the microbial environment (Anderson et al. 1985).

Hexosamine accumulation

Amino sugars are components of microbial cell walls and extracellular polysaccharides. They are only present in trace amounts in higher plants. The major source of glucosamine in decomposing plant material such as leaf litter is chitin from fungal cell walls, with exoskeletons of invertebrates and bacterial cell walls making a smaller contribution (Parsons 1981). The chitin content has therefore been used to estimate the fungal biomass in a wide range of solid substrates, including decomposing leaf litter (Frankland et al. 1978).

According to fungal species, ages, and growth conditions, the reported glucosamine content has varied from 8.5 to 92.8 mg g^{-1} dry weight (Hicks and Newell 1984). *Mycena* mycelium stripped from leaf litter have contained 42.83 mg g^{-1} dry weight (Frankland et al. 1978). This figure is used as an average to convert the glucosamine content to the weight of fungal mycelium. The fungal biomass in O leaf litter was thus calculated as 130 mg g^{-1} ash-free dry weight in the 1-mm mesh cages after 1 year of decomposition. Assuming that 70% of microorganisms are fungi (Parkinson et al. 1978; Domsch and Anderson 1986), the total microbial biomass was calculated as 190 mg g^{-1} or 19% in the 1-mm mesh cages. Obviously, not all the glucosamine occurred in living organisms. Microbial biomass usually accounts for 1–3% of organic matter in mineral soils (Jenkinson and Ladd 1981). Less, i.e., between 0.5 and 1% living biomass, has been found in the organic layers of moder soils (Parkinson et al. 1978; Wolters 1989). Thus, the content of living microbial biomass is likely to be 10–20 times smaller than that estimated by the glucosamine assay. This rough figure conforms with estimates by Söderström (1977), who found 1–5% live mycelium in a coniferous forest, and by Kjoeller and Struwe (1982), who used 10% as average for their calculations of live mycelium. However, living fungal biomass and dead residues cannot be accurately differentiated by this method, so it cannot be used to measure microbial biomass in materials in which dead tissue is accumulated. In organic matter, glucosamine is useful as an indicator of the degree of microbial transformation and of the pathways of decomposition.

Not only was the N content in the present study considerably influenced by macrofaunal activity, but the N fraction of amino sugars was also particularly affected. The content of the cell-wall component glucosamine was 23% lower in the 12-mm mesh cages (Table 1), indicating a higher grazing pressure by microorganisms or greater

consumption of microbial remains by earthworms. The content of galactosamine, a component of mucous substances mainly of bacterial origin (Parsons 1981), was reduced by 43% in the 12-mm mesh cages, much more than glucosamine (Fig. 4). Consequently, in the 1st year of decomposition, the glucosamine: galactosamine ratio declined to 0.9 in the 1-mm mesh cages and to 1.2 in the 12-mm mesh cages. In contrast to the total N content, it is inconceivable that the galactosamine content was reduced by incorporation of a leaf litter fraction with a higher galactosamine content, because a glucosamine: galactosamine ratio lower than 0.9 has never been measured (Joergensen 1987).

The lower galactosamine content in the 12-mm mesh cages may have reflected a change in the microbial population towards organisms that produce less mucous substances containing galactosamine. Earthworms prefer to feed on bacteria-rich microsites (Scheu 1987), so the galactosamine content might have been reduced by animal grazing of mucous substances. However, in laboratory experiments, grazing diminished two-thirds of the fungal standing crop (Ineson et al. 1982) and shifted microbial activity towards the bacteria (Hanlon and Anderson 1980). The reduction in total N and the galactosamine content apparently caused by earthworms indicates that there was a substantial change in the microbial decomposition pattern which was not fully understood.

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