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ORIGINAL PAPER

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Microbial activity and leaching during initial oak leaf litter decomposition

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Abstract The decomposition of oak leaf litter was studied by means of a litterbag experiment in an oak forest in the Netherlands. The contribution of microbial activity and leaching to weight loss and element dynamics during the first 6 weeks of decomposition was investigated by means of frequent respiration measurements and extractions of the litter and by a qualitative comparison of throughfall and litter percolation water chemistry. The oak-leaf litter lost 9.3% of its initial dry weight during the first 6 weeks. In total, 90% of this observed weight loss was explained by the processes studied. About 5.9% (64% of the total) of this weight loss was attributed to microbial respiration and 0.5% (5%) to the loss of inorganic solutes. Leaching of dissolved organic compounds was estimated to account for 2.0% (21%). The results indicated a fast leaching of K and Cl out of the fresh litter during the first 2 weeks, while Mg, Fe, Mn, Si, *ortho* P, and dissolved organic N were released at a much lower rate. At the same time, small amounts of H^+ , NH_4^+ and NO_3^- were retained in the litter.

Key words Oak-leaf litter · Decomposition · Leaching · Microbial activity · Litterbag method · Immobilization

Introduction

The decomposition of organic matter in terrestrial ecosystems is an important process regulating the cycling and thus the availability and mobility of essential elements.

The initial phase of the decomposition of fresh organic matter is often characterized by a relatively fast weight loss (Hågvær and Kjendal 1981; Berg 1984; Tietema 1993), and loss of dissolved organic compounds (Berg et al. 1982; Yavitt and Fahey 1986) and inorganic solutes (Gosz et al. 1973; Berg and Staaf 1987; Van Wesemael 1993). The rapid rate of disappearance of soluble organic compounds may be a result of both assimilation or dissimilation by the decomposer microflora and leaching. Both processes may also interact when metabolic processes result in soluble components that are leached (Swift et al. 1979). Inorganic solutes are readily leached from the fresh litter depending on the mobility and on the microbial metabolic requirement for that element (Joergensen and Meyer 1990).

Though microbial activity and leaching are often acknowledged as important processes during initial decomposition, only a few studies have addressed the relative contribution of the two processes. Yavitt and Fahey (1986) combined litterbag results with percolation water chemistry underneath the whole ectorganic layer (LFH). This approach did not allow any conclusions on initial decomposition, as the net effect of the processes in fresh litter on water chemistry was completely clouded by the relatively large pool of old organic matter. Joergensen and Meyer (1990) sampled percolates from fresh beech litter in a field situation. However, they integrated their results on an annual basis, which also clouded the initial phase. Processes like leaching and immobilization are only expected to be of importance during a few weeks or months after litter production.

A litterbag experiment was started in an oak forest in the Netherlands in December 1988 in order to study long-term decomposition of oak-leaf litter. The results on weight loss and N dynamics for the first 2 years have been presented by Tietema (1993). Parallel to this experiment the relative contribution of leaching and microbial activity to the first 6 weeks of decomposition was studied by combining litterbag data, respiration measurements, litter extractions, and analysis of percolates. The results of this latter experiment are presented in this paper.

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Material and methods

Study area

The study was conducted in an oak forest (*Quercus robur* L.) called De Buunderkamp, near Wolfheze in the central part of the Netherlands. The oak trees (mean diameter at breast height 55 cm) are about 50 years old and are planted at a density of about 600 ha⁻¹. No undergrowth is present in the forest. The ectorganic layer has a thickness of 6 cm and consists of recognizable L and F horizons. Some chemical characteristics of the ectorganic layer and the top of the mineral soil are summarized in Table 1. The sandy soil is acid, with pH_(CaCl₂) values increasing from 3.0 in the AEh horizon to 4.6 in the C horizon. The soil has been classified as a Fimic Anthrosol (FAO 1988). The parent material is coversand. The climate in the Netherlands is temperate humid, with a mean annual precipitation of about 800 mm.

Litterbag experiment

In the beginning of November 1988, freshly fallen oak leaves were collected from the forest in a period with almost no precipitation. The leaves were air-dried, and an amount corresponding to 6.4 g at 70 °C was put in litterbags measuring 20 by 20 cm with a mesh size of 2 mm. A large number of litterbags were placed on the forest floor on December 6, 1988. They were divided over six subplots. The weight at the time of placing of the bags (T_0) and after 6 weeks (T_6) was determined by collecting one replicate bag from each subplot, giving a total of six replications.

Twelve extra bags were placed in two of the six subplots to study decomposition during the first 6 weeks. Under these bags in a buried polyvinyl chloride tube, 500-ml collection bottles with a 48-cm² funnel were placed (Fig. 1). Litter percolates were obtained only after the first 2 weeks; after 4 and 6 weeks the volumes of the percolates were too small (< 10 ml) for analyses. After the first 2 weeks, 8 out of 12 bottles contained percolate but only 3 bottles contained sufficient percolate (> 100 ml) for analyses of all elements.

After each 2 weeks, 4 of these 12 litterbags were collected and taken to the laboratory. The fresh litter was weighed and divided into four equal parts. The parts were used to determine (1) the CO₂ production rate, (2) the concentrations of dissolved elements using an aqueous extraction, (3) the concentration of exchangeable elements using a KCl extraction, and (4) the moisture content. CO₂ production rates were measured by gas chromatograph analysis of the headspace CO₂ accumulation in air-tight bottles (350 ml). The bottles contained approximately 1.5 g litter and were incubated for 3 days at 5 °C. This temperature approximated the mean temperature in the litter layer during the 6 weeks of the experiment (Table 2). The second and the third parts of the litter were extracted in 80 ml demineralized water and 80 ml 1 M KCl, respectively. For the T_0 determination the air-dried initial material was prewetted in a plastic bag with demineralized water (300% dry weight) for 2 h and respiration measurements and extractions were carried out likewise.

The heterogenous moisture distribution in the subsamples of the litter made it impossible to calculate total dry weight at T_2 and T_4 from the total fresh weight of each litterbag and the calculated moisture content of the subsample. As a result, no weight loss data

Fig. 1 Schematic illustration of the experimental set up (PVC polyvinyl chloride)

Table 2 Throughfall and mean soil temperature in three fortnightly periods. The soil temperature was measured every 30 min on the interface of the organic and mineral layers

	6. 12. 1988 – 20. 12. 1988	20. 12. 1988 – 3. 1. 1989	3. 1. 1989 – 17. 1. 1989
Throughfall (mm)	45	9	22
Mean soil temperature (°C)	6.5	7.3	6.4

were available for T_2 . At T_4 , two extra litterbags were sampled to determine the weight loss after 4 weeks. The concentrations of N, P, K, Na, Ca, Mg, Mn, Fe, and Al were determined in all six replicate litterbags at T_0 and T_6 , in the four subsamples used for moisture content determinations at T_2 , and in the four subsamples used for moisture content determinations plus the two extra litterbags at T_4 .

Throughfall

The chemical composition and the total amount of throughfall were measured by means of three and seven collectors, respectively. The collectors consisted of a funnel ($A = 491$ cm²) and a 5-l dark-coloured bottle. Coarse filters (meshsize 2 mm) were used in the funnels to prevent contamination by fallen leaves and insects. Funnels, filters, and collection bottles were made of polyethylene.

Calculations

Weight loss as a result of respiration during each of the three intervals was calculated by averaging the values for CO₂ respired at the start and at the end of each interval. It was assumed that the CO₂ produced came from the complete dissimilation of $C_nH_{2n}O_n$ organic material.

Table 1 Soil chemical characteristics of the relevant soil horizons sampled in April 1990 (Tietema et al. 1992); M top 5 cm of the mineral soil

Layer	Thickness (cm)	pH (KCl)	Total N (mg g ⁻¹)	Organic matter (%)	NH ₄ ⁺ (mg N kg ⁻¹)	NO ₃ ⁻ (mg N kg ⁻¹)
L	0–1	3.66	21.9	97	405	26
F	4–8	2.94	22.7	84	97	20
M	5 (Ah)	3.06	3.6	13	3	2

The differences in mean solute concentrations between the litter percolate and the throughfall were used to investigate the effect of the litter on water chemistry. This calculation assumed that evaporation losses were negligible and that differences in the amount of percolate between the litterbags were caused by differences in the amount of litter draining to the collection bottles between these bags.

Chemical analyses

All water samples were filtered and analyzed colorimetrically for NH_4 , $\text{NO}_2 + \text{NO}_3$, NO_3 , SO_4 , Cl , *ortho* P, and dissolved organic C using a continuous flow autoanalyzer and for K, Na, Ca, Mg, Fe, Mn, and Al using an atomic absorption/emission spectrophotometer. The dissolved organic N and P concentrations in the water samples were determined as NH_4^+ and *ortho*- PO_4 after reduction of the organic N and P compounds in the samples in a $\text{K}_2\text{SO}_4/\text{H}_2\text{SO}_4$ environment. The pH and alkalinity of the throughfall and litter percolate water samples were determined in the field immediately after collection. The KCl extracts were analyzed for NH_4^+ , $\text{NO}_2^- + \text{NO}_3^-$ and NO_3^- according to the methods described above.

All litter samples were dried (70°C) and ground. The total N concentration in the litter was determined by means of salicylic acid–thiosulfate modification of the regular Kjeldahl procedure (Brenner and Mulvaney 1982). The other elements were determined after HNO_3 – H_2O_2 destruction; the total concentration of P was determined colorimetrically with a continuous flow autoanalyzer, and total K, Na, Ca, Mg, Mn, Fe, and Al were determined by atomic absorption/emission spectrometry.

Results

The weight loss after 6 weeks of decay amounted to 9.3% in the oak leaves (Table 3). About a third of this weight loss occurred during the last 2 weeks of this period. The initial litter (T_0) had the lowest respiration rate ($16 \text{ mg C kg}^{-1} \text{ h}^{-1}$, Table 4). The highest respiration rates of 26 – $27 \text{ mg C kg}^{-1} \text{ h}^{-1}$ were measured after 2 and 4 weeks of field incubation. The calculation of total weight loss through respiration showed that in each interval the loss of about 2% of the initial weight of that interval could be attributed to respiration (Table 4).

The concentration of K and Na in the litter decreased significantly during the 6 weeks of decomposition (Fig. 2). A relatively large part of this decrease was measured during the first 2 weeks. The N concentration increased during the experiment. All other element concentrations remained during the experiment (Fig. 2).

Only 24 and 30% of the initial Na and K, respectively, remained in the litter after 6 weeks (Table 5). For P, Mg, and Mn this percentage was about 80%, while the total N,

Ca, Fe, and Al in the litter after 6 weeks was about the same as at the start.

A large variation in percolate volume was found in the collection bottles, indicating that the water flux followed preferential pathways through the litter. Only the three

Fig. 2 Total element concentrations in decomposing oak-leaf litter during the first 6 weeks of decomposition. Values are the means of six (T_0 , T_4 , and T_6) and four replicates (T_2). The closed triangular symbols indicate the mean plus (▼) and minus (▲) SD

Table 3 Remaining weight as percentage of initial

	Initial (T_0)	4 weeks (T_4)	6 weeks (T_6)
Mean	100.0	94.0	90.7
SD	0.2	2.0	1.8
Number of replicates	6	2	6

Table 4 Respiration rates in fresh litter sampled at different time intervals

	Initial (T ₀)	2 weeks (T ₂)	4 weeks (T ₄)	6 weeks (T ₆)
Respiration rate (mg C kg ⁻¹ h ⁻¹)				
Mean	16.0	26.3	27.2	22.9
SD	1.7	0.7	3.1	3.2
		T ₀ - T ₂	T ₂ - T ₄	T ₄ - T ₆
Respiration rate (mg C kg ⁻¹ h ⁻¹)		21.2	26.8	25.0
Carbohydrate loss (g CH ₂ O kg ⁻¹ 2 weeks ⁻¹)		17.8	22.5	21.0
Estimated weight loss (% of initial)		1.8	2.2	2.0

samples with the largest volumes were large enough to allow analyses for all elements. The higher calculated water flux in these three percolates compared to the throughfall (Table 6) affirmed these preferential pathways.

The comparison of element concentrations in throughfall and litter percolates during the first 2 weeks of decomposition showed that the concentration of most elements had increased in the water during the passage

through the fresh oak-leaf litter (Table 6). A large increase in concentration was measured for K (63 and 754 µmol l⁻¹ in throughfall and litter percolate, respectively), Cl (304 and 627 µmol l⁻¹), *ortho* P (0.2 and 46 µmol l⁻¹), and dissolved organic C (360 and 6170 µmol l⁻¹). A small decrease in solute concentration was found for H⁺, NH₄⁺ and NO₃⁻.

The water extracts showed that dissolved K, Na, NH₄, Cl, *ortho* P, SO₄, and dissolved organic C were generally higher in the initial litter than after 2, 4, or 6 weeks of field incubation (Table 7). The KCl extracts showed a similar pattern for exchangeable NH₄⁺ and NO₃⁻. Concentrations of the other elements in the water extracts remained constant.

Table 5 Amounts of elements remaining in decomposing oak-leaf litter after 6 weeks of field incubation, calculated as a percentage of the initial amount. Values are means and SD of six replicates

Element (% of initial)									
	N	P	Ca	Mg	K	Na	Mn	Fe	Al
Mean	101	84	93	82	30	24	78	105	103
SD	5	6	8	2	4	5	13	6	12

Discussion

Microbial activity accounted for the dominant part of the weight loss during the first 6 weeks of decomposition; res-

Table 6 Element concentrations in throughfall and litter percolate and the change in concentration due to litter percolation during the first 2 weeks of incubation. Values are the means and SD of three replicates (*DOC* dissolved organic C, *DON* dissolved organic N, *DOP* dissolved organic P)

Element	Throughfall		Litter percolate		Percolate - throughfall	
	Mean	SD	Mean	SD	Mean	SD
Free H (µmol l ⁻¹)	20.8	4.3	7.9	6.7	-13	8
K (µmol l ⁻¹)	63	17	754	239	692	240
Na (µmol l ⁻¹)	238	1	321	56	83	56
NH ₄ (µmol l ⁻¹)	173	12	70	20	-103	24
Ca (µmol l ⁻¹)	32	3	63	34	31	34
Mg (µmol l ⁻¹)	35	4	88	28	53	29
Fe (µmol l ⁻¹)	0.3	0.1	2.0	0.6	1.7	0.6
Mn (µmol l ⁻¹)	1.7	0.7	8.5	3.4	6.9	3.4
Al (µmol l ⁻¹)	tr	tr	5.4	1.0	5.4	1.2
Si (µmol l ⁻¹)	1.9	0.3	46	26	44	26
Cl (µmol l ⁻¹)	304	4	627	167	323	167
NO ₃ (µmol l ⁻¹)	66	4	51	28	-15	28
<i>ortho</i> P (µmol l ⁻¹)	0.2	0.1	46	29	46	29
SO ₄ (µmol l ⁻¹)	125	12	231	37	106	39
Alkalinity (µmol l ⁻¹)	0	0	27	46	27	46
DOC (mg l ⁻¹)	4.3	0.6	74	33	70	33
DON (mg l ⁻¹)	34	12	129	30	95	32
DOP (mg l ⁻¹)	0.1	0.1	1.0	1.7	0.9	1.7
H ₂ O (mm)	45	7	55	27		
Σ cations (µmol _c l ⁻¹)	633	29	1477	405		
Σ inorganic anions (µmol _c l ⁻¹)	621	32	1304	327		
Apparent anion deficit (µmol _c l ⁻¹)	12	7	173	80		

Table 7 Element concentrations in water and KCl extracts of decomposing oak leaf litter. Values are means and SD of four replicates; all values are in mg kg^{-1} (ND not determined)

	T ₀		T ₂		T ₄		T ₆	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Water extraction								
K	1803	143	ND	ND	365	82	171	53
Na	184	16	ND	ND	156	5	81	28
N/NH ₄	36	7	1	1	3	2	6	2
Ca	43	15	27	5	55	4	6	2
Mg	43	13	12	3	39	7	12	3
Fe	2.8	0.2	2.8	0.1	3.4	0.7	9.2	15.0
Mn	7.7	3.4	2.5	0.3	8.4	2.0	2.6	0.4
Al	5.6	0.8	ND	ND	2.7	0.2	ND	ND
Si	ND	ND	13	1	ND	ND	11	2
Cl	785	156	284	45	251	90	132	69
N/NO ₃	7.4	2.9	6.7	2.3	0.4	0.5	3.8	1.6
<i>ortho</i> P	204	45	8	3	1	0	0	0
S/SO ₄	199	49	31	26	53	29	106	51
DOC	5981	1310	1527	182	2254	113	781	159
DON	158	26	50	12	107	15	0	0
DOP	3.8	5.8	3.9	5.4	0.8	0.2	1.1	0.8
KCl extraction								
N/NH ₄	48	11	2	2	4	1	2	1
N/NO ₃	5.9	2.5	1.1	0.8	1.2	0.5	0.1	0.1

piration explained 5.9% (64%) of the observed 9.3% weight loss. This estimate might even be considered as a minimum due to the higher actual mean soil temperatures (Table 2) compared to the incubation temperature of 5 °C. Total weight loss as a result of loss of inorganic solutes was estimated from the initial concentrations (Fig. 2) and the remaining amounts (Table 5) of the elements. Assuming a Cl loss equal to the difference in H₂O-extractable Cl concentration between T₀ and T₆ (Table 6) and negligible loss of S and Si, a total weight loss of 0.5% (5%) of initial weight was calculated. The leaching of dissolved organic C could only be estimated by using the comparison between throughfall and percolation water chemistry (Table 6), which makes this estimate the most uncertain. Assuming that the ratio between leaching of K and dissolved organic C during the first 2 weeks (Table 6) remained constant for the whole 6-week period and that the loss of K (Table 5) was completely due to this leaching, the weight loss as a result of leaching of dissolved organic compounds (as CH₂O) was estimated to be 2.0% (21%) of the initial weight. The total weight loss thus explained by these independently measured, calculated, and/or estimated processes amounted to 90% of the observed weight loss during the first 6 weeks.

The method used did not allow a complete calculation of the contribution of leaching to initial decomposition on a weight basis as it was not known how much litter contributed to the leaching. The experimental design of the leaching part was based on a compromise between collecting litter percolates from freshly fallen oak leaves and allowing physical contact between these leaves and the organic layer. The latter is necessary for the colonization of the new substrate by decomposing organisms. This colonization was actually observed as hyphen-like structures connecting the content of the litterbags with the organic layer when the bags were sampled.

The changed solute chemistry as a result of the passage of the throughfall water through the oak-leaf litter during the first 2 weeks indicated a profound leaching of many elements. The solutes were leached in the following order: K > Na > Mg > Ca > Mn ≈ Al > Fe (cations) and Cl > SO₄ > *ortho* P ≈ HCO₃ (anions). The fast initial leaching of K and Na was confirmed by a decrease in the total concentration of these elements in the same period (Fig. 2). This indicated that the water-soluble fraction of these elements in the litter forms a substantial part of the total amount in the litter (Wessel and Tietema 1994). Profound initial leaching of K has been found in many litterbag studies (Gosz et al. 1973; Yavitt and Fahey 1986). A large part of K is present as soluble salts in the cell protoplasm (Epstein 1972) which is leached from the dead leaves when the cell membranes are damaged. This process starts when the dead leaves are still attached to the trees in autumn and continues when the leaves are on the forest floor (Swift et al. 1979). This study indicated that leaching of K⁺ is dominantly accompanied by Cl⁻. It may be argued that part of the leached Cl⁻ originated from marine (NaCl) aerosols deposited on the leaves (Joergensen and Meyer 1990). A comparison of precipitation and throughfall fluxes, however, indicated that there was no increase in Na and Cl flux in throughfall taking evaporation into account (A. Tietema, unpublished results). This indicates that dry deposition of marine aerosols in this forest located 120 kilometers from the coast is of minor importance. The relative importance of the leaching of Cl seems to contradict the use of Cl as a conservative parameter to estimate water fluxes (Tietema and Verstraten 1991). By combining the water-extractable concentration of Cl at T₀ of 785 mg kg^{-1} (Table 7) and the annual leaf-litter production of 3.5 $\text{t ha}^{-1} \text{year}^{-1}$ (Table 1), an annual Cl flux originating from leaching of fresh litter of 0.08 $\text{kmol ha}^{-1} \text{year}^{-1}$ was calculated. This

value is very small compared to the measured annual Cl flux in precipitation ($1.1 \text{ kmol ha}^{-1} \text{ year}^{-1}$) and throughfall ($1.3 \text{ kmol ha}^{-1} \text{ year}^{-1}$) in the same forest (A. Tietema, unpublished results). From this we concluded that the initial Cl leaching from fresh litter does not interfere with the method that assumes Cl as conservative.

The net retention of inorganic N from the percolating water during the first 2 weeks indicated a net immobilization of throughfall inorganic N (Van Vuuren and Van der Eerden 1992). The total N concentration increased during the first 6 weeks from 15.2 to 16.8 mg N g^{-1} . The total amount of N, however, remained at about the same level during that same period. This indicates that the net retention of inorganic N was balanced by leaching of dissolved organic N. The net retention of H^+ was probably the result of H^+ exchange with cations adsorbed on the exchange complex. This acid-neutralizing capacity of litter is illustrated by the higher pH in litter percolate (5.10) than in throughfall (4.68). However, the microbial uptake of NH_4^+ and NO_3^- may also have contributed to this change in pH as a proton-producing and -consuming process, respectively (Van Breemen et al. 1982).

The charge deficit between cations and inorganic anions increased as a result of the passage through the fresh litter. This was probably caused by a change in the importance of organic anionic sites (Oliver et al. 1983) as a result of an increase in organic anions (Table 6) and/or an increased dissociation of dissolved organic acids into organic anions (Van Wesemael and Verstraten 1993).

Although litter percolates could be sampled only during the first 2 weeks, the decreasing concentrations of nearly all elements in the extractions indicated that the potential amount of "leachable" solutes had decreased rapidly after the first 2 weeks. In combination with the lower throughfall fluxes during the T_2 – T_4 and T_4 – T_6 periods (Table 2) it may be concluded that weight loss by leaching in this experiment might have been of quantitative importance during the first 2 weeks only.

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