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Mass loss and nutrient release during litter decay in peatland: The role of microbial adaptability to litter chemistry

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Abstract

In peatlands the reduced decomposition rate of plant litter is the fundamental mechanism making these peat-accumulating ecosystems effective carbon sinks. A better knowledge of litter decomposition and nutrient cycling is thus crucial to improve our predictions of the effects of anthropogenic perturbation on the capacity of peatlands to continue to behave as carbon sinks. We investigated patterns of plant litter decomposition and nutrient release along a minerotrophic–ombrotrophic gradient in a bog on the south-eastern Alps of Italy. We determined mass loss as well as P, N, K, and C release of seven vascular plant species and four moss species after 1 year in both native and transplanted habitats. Hence, differences in litter decay were supposed to reflect the degree of adaptability of microbial communities to litter quality. Polyphenols/nutrient and C/nutrient quotients appeared as the main parameters accounting for decomposition rates of *Sphagnum* litter. In particular, litter of minerotrophic *Sphagnum* species decomposed always faster than litter of ombrotrophic *Sphagnum* species, both in native and transplanted habitats. Decomposition rates of vascular plant litter in native habitats were always higher than the corresponding mass loss rates of *Sphagnum* litter. Minerotrophic forbs showed the fastest decomposition both in native and transplanted habitats in accordance with low C/P and C/N litter quotients. On the other hand, C/P quotient seems to play a primary role also in controlling decomposition of graminoids. Decomposition of deciduous and evergreen shrubs was negatively related to their high lignin content. Nitrogen release from *Sphagnum* litter was primarily controlled by C/N quotient, so that minerotrophic *Sphagnum* litter released more N than ombrotrophic *Sphagnum* litter. Overall, we observed slower N release from litter of ombrotrophic vascular plant species compared to minerotrophic vascular plant species. No single chemical parameter could predict the variability associated with different functional groups. The release of K was very high compared to all the other nutrients and rather similar between ombrotrophic and minerotrophic litter types. In *Sphagnum* litter, a higher C/P quotient was associated with a slower P mineralisation, whereas a faster P release from vascular plant litter seems primarily associated with lower C/P and polyphenols/P quotients.

Keywords: Carbon; Lignin; Litter bags; Mineralisation; Nitrogen; Phosphorus; Polyphenols; Potassium; *Sphagnum*; Vascular plants

1. Introduction

Litter decomposition, i.e., the physical, chemical and biological process converting plant residues into their elemental chemical constituents, controls nutrient availability in natural ecosystems and, ultimately, the amount of carbon (C) released to the atmosphere (Schlesinger and Andrews, 2000; Swift, 2001). On the whole, litter decomposition involves two simultaneous processes: (a) the degradation of litter chemical compounds by a pool of soil micro- and macro-organisms; (b) the leaching of water-soluble compounds into the soil (Couteaux et al., 1995). These two fundamental processes are controlled both by abiotic factors, such as climate and litter chemistry, and by biotic factors, such as soil organism activity (Aerts, 1997).

Peatlands are peculiar ecosystems accumulating organic matter as a consequence of an imbalance between net primary production and decomposition, with decomposition being slower than net primary production (Clymo, 1984). Such imbalance makes peatlands effective sinks for atmospheric C, so that these ecosystems are estimated to

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store about one-third of global soil C pool (Gorham, 1991; Clymo et al., 1998). Reduced litter decomposition in peatlands is supposed to be primarily a consequence of the harsh nature of peatland habitats (e.g., low soil pH and temperature, frequent lack of oxygen) and the low nutrient quality of plant litter (Johnson and Damman, 1993; Belyea, 1996; Bridgham and Richardson, 2003).

Peatlands are typically divided into ombrotrophic bogs and minerotrophic fens (Bridgham et al., 1996). Bogs are exclusively fed by atmospheric precipitation and for this reason plant species of ombrotrophic bogs have adopted a set of biological mechanisms to cope with low nutrient availability (Aerts et al., 1999). In contrast, fens receive water and nutrients from precipitation as well as from local groundwater so that fen plant species rely upon higher nutrient availability resulting in a greater biomass productivity compared to bog plants (Aerts et al., 1999). Different tissue chemistry of bog and fen plant species affects differently the rates of litter decomposition and nutrient mineralisation (Bridgham et al., 1996).

In peatlands, fungi and bacteria are mostly responsible for litter decomposition, whereas animals play a minor role, particularly in ombrotrophic bogs (Dickinson and Maggs, 1974; Coulson and Butterfield, 1978). Most of the decomposition activity is restricted to the upper peat layers (i.e., the acrotelm) that is only temporally water saturated (Bridgham and Richardson, 2003). Fungi, being aerobic micro-organisms, are primarily found in the acrotelm (Nilsson et al., 1992), whereas bacteria, being represented by both aerobic and anaerobic species, show more complex distributional patterns along the peat profile (Sundh et al., 1997). Although micro-organism biomass is relatively low in peatlands (Fisk et al., 2003), significant differences have been found in both microbial diversity and microbial functional activity among peatland habitats (Williams and Crawford, 1983; Fisk et al., 2003), especially in relation to the chemical composition of plant remnants (Borga et al., 1994; Thormann et al., 2004).

Assessing to what extent micro-organism activity is affected by litter chemistry and, particularly, to what extent micro-organism communities are adapted to cope with changes in litter chemistry is an important topic in the light of the ongoing global change. Indeed, increasing atmospheric CO_2 concentration and nitrogen (N) deposition alter the chemical composition of living peatland plants (van der Heijden et al., 2000; Bragazza et al., 2004; Freeman et al., 2004a; Aerts et al., 2006), so that cascade consequences are expected on litter decay. In this sense, a better knowledge of the mechanisms regulating litter decomposition and nutrient cycling can improve our predictions of the effects of anthropogenic perturbation on the capacity of peatlands to continue to behave as C sinks.

In this study we want to assess the role of litter chemistry in affecting the decomposing activity of micro-organism communities in different peatland habitats. To this aim, we performed a reciprocal transplanting of litter bags of different plant species between minerotrophic and ombrotrophic habitats looking at mass loss (i.e., decomposition rate) and N, P, K and C release (i.e., mineralisation or immobilisation) after 1 year of burial in the acrotelm. As we transplanted only plant litter and not microbial communities, we can assume that differences in mass loss and nutrient release from the same litter type between the native and the new habitat reflect a different level of adaptability of habitat-specific microbial communities to decompose native and transplanted plant litter.

2. Materials and methods

2.1. Study site

The study was carried out in an bog (Wölf Moor) located on the south-eastern Alps of Italy (46°26′N, 11°24′E), province of Bolzano (Bozen), at an altitude of 1300 m a.s.l. A detailed description of floristic, morphological and geochemical aspects of the bog can be found in Bragazza et al. (2005). Very briefly, the bog is characterised by ombrotrophic (i.e., rain-fed) conditions in the inner portion, whereas inflows of groundwater take place along the bog margins where minerotrophic conditions are found.

The climate of the area is cool-temperate continental with a mean annual temperature of ca. 6 °C and a total annual precipitation of ca. 800 mm peaking in summer months (Bragazza et al., 2005).

2.2. Plant species and litter collection

We decided to sample plant litter of the most common species in the ombrotrophic inner sector of the bog (hereafter called ''ombrotrophic habitat'') and along the minerotrophic margins (hereafter called ''minerotrophic habitat''). Species representative of the minerotrophic habitat were: *Trichophorum caespitosum* (L.) Hartman, *Carex lasiocarpa* Ehrh., *Molinia coerulea* (L.) Moench, *Potentilla erecta* (L.) Räuschel, *Sphagnum flexuosum* Dozy & Molk., and *Sphagnum subsecundum* Nees s. str. Species representative of the ombrotrophic habitat were: *Calluna vulgaris* (L.) Hull, *Vaccinium uliginosum* L., *Eriophorum vaginatum* L., *Sphagnum fuscum* (Schimp.) Klinggr., and *Sphagnum capillifolium* (Ehrh.) Hedw. On the whole, seven vascular plant species and four moss species were selected.

At the end of September 2001, freshly senesced, undecomposed leaves were collected from vascular plants. When leaves were not shed, we collected leaves that had already lost their green colour. Leaves of *V. uliginosum* were harvested after gently shaking the plants. Leaves of *C. vulgaris* were harvested along with brown shoots to which they were still loosely attached.

Decomposition of *Sphagnum*-dominated litter is a continuum process which makes virtually impossible to determine when *Sphagnum* litter begins to decompose (Hogg, 1993). So, in accordance with previous studies

(Aerts et al., 2001), we used the stem section located 2–4 cm below the growing tip (i.e., the capitulum) as representative of freshly deposited *Sphagnum* litter which is still stored in the acrotelm, i.e., in the upper layer periodically aerated where most of the decomposition activity takes place (Chanton et al., 1995; Belyea and Malmer, 2004).

The litter material was sorted and cleaned, then air dried and stored in paper bags at room temperature. Litter bags were prepared using about 1.0 g of air-dry leaves for vascular plants and about 0.5 g of *Sphagnum* litter. Litter bags were made of polyethylene fabric with 0.5 mm × 0.5 mm openings. For each plant species, three sub-samples of litter were oven-dried for 48 h at 40 °C in order to calculate oven-dry weight of each litter bag before burial.

At the beginning of October 2001, five litter bags of each species were placed horizontally just beneath the bog surface after remoistening in both ombrotrophic and minerotrophic habitat. To reduce the effect of habitat variability, all litter bags where buried close to each other within an area of about 5 m^2.

At each habitat a 50-cm long perforated pipe was inserted into the peat for monthly measurements of water-table depth and pore-water samplings during summer 2002.

After 1 year, all litter bags were retrieved and cleaned from coarse and fine debris before drying at 40 °C for 48 h. Each bag was then weighed to the nearest 0.001 g to determine the remaining litter mass.

At the centre of each habitat, after litter bag harvesting, a 10-cm long peat core was collected for chemical analyses.

2.3. Chemical analyses

In the initial litter, C and N concentrations were determined with an elemental analyser (EA 1110, Carlo Erba, Milan, Italy). After litter digestion with nitric acid, K and P concentrations were determined by atomic absorption spectrometry (Solaar 969, ThermoOptek) and by the colorimetric method of molybdenum blue using a continuous-flow autoanalyser (FlowSys, Systea, Rome, Italy), respectively. Standard reference material (NIST Citrus leaves 1572, National Bureau of Standards, Washington, DC, USA) was analysed along with litter samples to ensure accuracy of nutrient determination. The same analytical procedures were followed to determine C, N, P and K concentration in the residual mass of each litter bag after retrieval.

Concentrations of total non-structural carbohydrates (TNC) in initial litter were calculated after determination of starch, glucose, fructose and sucrose. Starch was determined colorimetrically, at 680 nm, according to Allen (1989). Glucose, fructose and sucrose were determined enzymatically (Enzytec™ procedure) according to Bergmeyr and Bernt (1974). Briefly, 250 mg of air-dried plant litter was extracted in 25 ml of boiling distilled water for 30 min, then filtered, transferred to 50 ml volumetric flask and diluted to volume with distilled water; an aliquot of 100 µl of extract was added with specific enzymes (Enzytec™ procedure) and its absorbance was measured at 340 nm.

Total soluble phenols in initial litter were determined by the Folin–Ciocalteu method using ethanol 40% for extraction and tannic acid as standard (Allen, 1989). Initial lignin (only for vascular plant litter) and holocellulose contents were determined according to van Soest's assay as described in Allen (1989).

All chemical analyses were performed after having milled each litter sample. Five replicates were used to characterise initial litter chemistry of each plant species. All concentrations were converted to standard oven-dry weight (40 °C for 48 h).

Pore-water samples were analysed for Ca^{2+} and Mg^{2+} by atomic absorption spectrophotometry after filtration of water samples through a 0.45 µm glass filter. Peat samples were analysed for total N and total P according to the procedures used for litter bags.

2.4. Decomposition and nutrient release measurements

Decomposition rate was expressed as percentage of mass loss after 1 year of field burial as follows:

$$\text{decomposition rate } (\%) = ((W_0 - W_1)/W_0) \times 100,$$

where W_0 is the weight of plant litter in the bag before burial and W_1 refers to the weight of the same content after 1 year.

For each litter bag we also calculated the release of N, P, K and C as percentage (%) of initial total content:

$$\text{nutrient release } (\%) = ((X_0 W_0 - X_1 W_1)/(X_0 W_0)) \times 100,$$

where X_0 is the mean nutrient concentration ($\mu g\, g^{-1}$) of plant litter before burial and X_1 is the nutrient concentration in the litter bag after one year of burial. Positive values indicate net mineralisation, negative values indicate net immobilisation.

2.5. Statistical analyses

Based on initial litter chemistry, we used principal component analysis (PCA) both to separate plant species into functional groups, and to assess correlations between decomposition rate and nutrient release. One- and two-way analysis of variance (ANOVA) was applied to assess significant differences of chemical parameters between litter types and between habitats. All statistical analyses were performed using Statistica for Windows v. 6.0 (StatSoft Italia, 2002).

3. Results

3.1. Habitat conditions

Minerotrophic and ombrotrophic habitats differed sharply from each other on the basis of pore-water

chemistry and peat chemistry (Table 1). Indeed, minerotrophic habitats were characterised by higher values of all chemical variables in both pore-water and in surface peat. Water-table depth was similar in the habitats so that we can assume that the degree of peat aeration during litter burial did not differ (Table 1).

3.2. Plant functional groups and litter chemistry

Multivariate ordination of plant species on the basis of their initial litter chemistry permitted to separate seven different functional groups (Fig. 1).

Sphagnum species were splitted into two different groups including the ombrotrophic *Sphagnum* species (i.e., *S. fuscum* and *S. capillifolium*) and the minerotrophic *Sphagnum* species (i.e., *S. subsecundum* and *S. flexuosum*), respectively. Stoichiometric quotients between N, P, and K did not differ between the minerotrophic and ombrotrophic *Sphagnum* litter (Table 2). On the other hand, ombrotrophic *Sphagnum* litter had higher C/nutrient, polyphenols/nutrient, and TNC/nutrient quotients compared to minerotrophic *Sphagnum* litter (Table 2).

Vascular plant species were separated into five functional groups (Fig. 1). The first group was represented by minerotrophic graminoids and included three species: *Trichophorum caespitosum* (Tri cae), *Carex lasiocarpa* (Car las) and *Molinia coerulea* (Mol coe). All the other functional groups were represented by just a single species. Indeed, forbs were represented by *Potentilla erecta* (Pot ere), ombrotrophic graminoids included *Eriophorum vaginatum* (Eri vag), deciduous shrubs included *Vaccinium uliginosum* (Vac uli), whereas evergreen shrubs were represented by *Calluna vulgaris* (Cal vul) (Fig. 1).

High lignin concentration characterised the woody species *C. vulgaris* and *V. uliginosum* compared to all the other herbaceous species (Fig. 1). Minerotrophic graminoids were differentiated by higher N/P, C/P, and holocellulose/lignin quotients, as well as by a lower polyphenols/N quotient compared to the other functional groups (Table 2). Minerotrophic forbs were characterised by lower C/N, C/P, TNC/K, lignin/P, and lignin/K quotients (Table 2). Ombrotrophic graminoids were primarily characterised by relatively low lignin/P and lignin/K quotients as well as by a relatively higher TNC/N quotient compared to the other herbaceous functional groups (Table 2). Deciduous and evergreen shrubs presented significantly higher polyphenols/nutrient and lignin/nutrient quotients, but a lower holocellulose/lignin quotient (Table 2).

Table 1
Mean values (±1 SEM when available) of representative environmental variables measured in the minerotrophic and the ombrotrophic habitat at Wölfl Moor

Environmental variable	Minerotrophic habitat	Ombrotrophic habitat
Water-table depth (cm)	−10.6 (1.8)	−9.2 (1.4)
Water Ca^{2+} ($mg\,l^{-1}$)	3.2 (0.3)	2.0 (0.1)
Water Mg^{2+} ($mg\,l^{-1}$)	0.71 (0.03)	0.49 (0.03)
Water pH	5.67 (0.09)	4.43 (0.10)
Water $NO_3^- + NH_4^+$ ($mg\,l^{-1}$)	0.14	0.08
Electrical conductivity ($\mu S\,cm^{-1}$)	25.5 (1.2)	14.3 (4.3)
Total Ca in surface peat ($mg\,kg^{-1}$)	4776	2343
Total N in surface peat (%)	1.7	0.4
Total P in surface peat ($mg\,kg^{-1}$)	442	86

Water-table depth and water chemistry values are based on monthly samplings from May to September 2002 with the only exception of water N concentration taken from Bragazza et al. (2003). Peat values are based on a single 10-cm long peat core collected in autumn 2002.

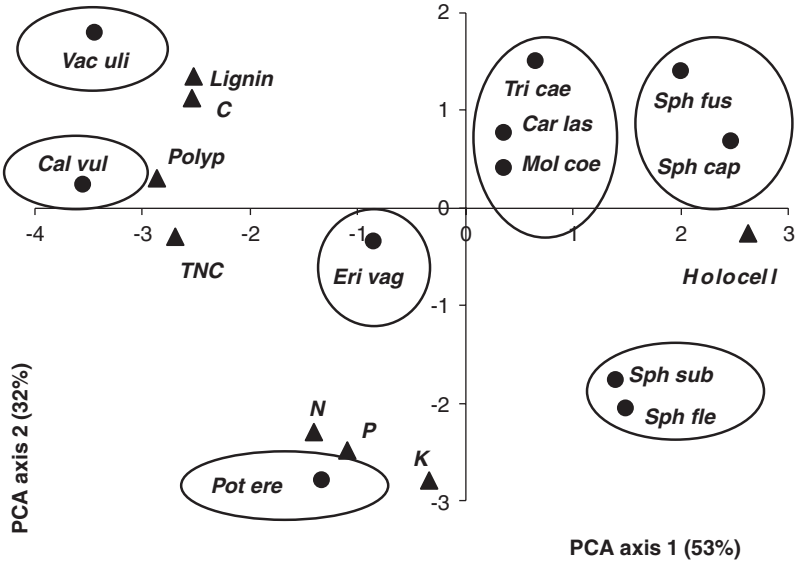

Fig. 1. Ordination diagram (principal component analysis, PCA) of selected plant species based on initial nitrogen (N), phosphorus (P), potassium (K), carbon (C), polyphenols (Polyp), total non-structural carbohydrates (TNC), holocellulose (Holocell) and, in the case of vascular plant species, lignin concentration in litter. (Plant names were abbreviated using the first three letters of the corresponding genus and species name).

Table 2
Mean values (±1 SEM) of litter chemical parameters of seven plant functional groups from minerotrophic (Min.) and ombrotrophic (Omb.) habitats

	Min. *Sphagnum* litter ($n = 10$)	Omb. *Sphagnum* litter ($n = 10$)	Min. graminoids ($n = 15$)	Min. forbs ($n = 5$)	Omb. graminoids ($n = 5$)	Omb. evergreen shrubs ($n = 5$)	Omb. deciduous shrubs ($n = 5$)
N/P	23.2 (1.7)^{bc}	26.1 (2.1)^{b}	54.8 (4.4)^{a}	15.3 (0.7)^{c}	21.3 (0.2)^{bc}	18.5 (0.3)^{bc}	28.5 (0.9)^{b}
N/K	2.1 (0.4)^{bc}	2.6 (0.3)^{c}	3.8 (0.4)^{a}	1.4 (0.1)^{b}	1.6 (0.1)^{b}	2.8 (0.1)^{ac}	3.4 (0.1)^{a}
K/P	12.0 (2.4)^{b}	10.2 (0.8)^{bc}	15.5 (1.5)^{a}	11.0 (0.5)^{bc}	13.5 (0.8)^{ab}	6.5 (0.3)^{c}	8.3 (0.3)^{bc}
C/N	42.2 (3.0)^{b}	75.2 (3.7)^{c}	68.3 (6.8)^{ac}	42.1 (2.9)^{b}	62.0 (1.4)^{a}	55.8 (1.1)^{ab}	63.3 (1.9)^{a}
C/P	903 (79)^{b}	1975 (210)^{c}	3692 (387)^{a}	641 (20)^{d}	1322 (17)^{c}	1029 (18)^{bc}	1802 (19)^{c}
C/K	90.2 (20.8)^{b}	197 (24)^{ac}	269 (49)^{a}	58.3 (1.2)^{b}	98.2 (5.8)^{bc}	159 (4)^{bc}	218 (10)^{ac}
Polyphenols/N	0.07 (0.01)^{f}	0.2 (0.02)^{d}	0.7 (0.1)^{e}	2.7 (0.1)^{b}	1.9 (0.1)^{c}	7.0 (0.5)^{a}	7.2 (0.2)^{a}
Polyphenols/P	1.6 (0.2)^{e}	6.1 (0.9)^{d}	41.6 (8.8)^{c}	40.6 (1.5)^{c}	40.9 (0.6)^{c}	129 (11)^{b}	206 (3)^{a}
Polyphenols/K	0.14 (0.02)^{e}	0.60 (0.08)^{d}	2.8 (0.5)^{c}	3.7 (0.1)^{c}	3.0 (0.3)^{c}	19.9 (1.0)^{b}	24.9 (1.0)^{a}
TNC/N	1.4 (0.1)^{d}	1.7 (0.1)^{d}	3.4 (0.3)^{c}	3.8 (0.3)^{c}	7.1 (0.1)^{a}	5.0 (0.1)^{b}	5.1 (0.1)^{b}
TNC/P	29.1 (2.7)^{c}	44.6 (6.1)^{b}	191 (30)^{a}	58.6 (2.3)^{b}	152 (9)^{ab}	92 (3)^{b}	145 (3)^{ab}
TNC/K	2.9 (0.6)^{d}	4.5 (0.6)^{c}	12.4 (1.5)^{b}	5.3 (0.1)^{c}	11.3 (0.2)^{b}	14.2 (0.3)^{ab}	17.5 (0.5)^{a}
Lignin/N	n.a.	n.a.	6.5 (0.6)^{d}	6.7 (0.6)^{d}	10.6 (0.2)^{c}	14.6 (1.0)^{b}	20.4 (0.6)^{a}
Lignin/P	n.a.	n.a.	362 (44)^{b}	102 (4)^{c}	226 (8)^{c}	279 (10)^{bc}	581 (14)^{a}
Lignin/K	n.a.	n.a.	26 (5)^{c}	9.4 (0.8)^{d}	16.7 (0.7)^{cd}	44 (1.5)^{b}	70 (4.0)^{a}
Holocell/Lignin	n.a.	n.a.	7.4 (0.3)^{a}	2.7 (0.2)^{c}	4.3 (0.1)^{b}	0.8 (0.1)^{d}	0.9 (0.1)^{d}

Different superscript letters indicate significant differences of the same chemical parameter between functional groups ($P<0.05$; ANOVA post-hoc comparisons using LSD Fisher test). n is the number of replicates; TNC is non-structural carbohydrates; Holocell is holocellulose.

Table 3
Mean (±1 SEM) litter decomposition rate, calculated as percentage of initial litter mass, of different functional groups after 1 year of burial in minerotrophic and ombrotrophic habitats

Functional groups	Mass loss (%) in minerotrophic habitat	Mass loss (%) in ombrotrophic habitat
Minerotrophic Sphagna ($n = 10$)	21.5±0.9^{a}	26.1±1.5^{b}
Ombrotrophic Sphagna ($n = 10$)	15.3±0.8^{a}	18.2±1.1^{b}
Minerotrophic graminoids ($n = 15$)	37.2±1.8^{a}	22.8±1.9^{b}
Minerotrophic forbs ($n = 5$)	71.3±1.0^{a}	64.6±1.7^{b}
Ombrotrophic graminoids ($n = 5$)	36.6±2.0^{a}	32.5±0.6^{b}
Ombrotrophic evergreen shrubs ($n = 5$)	36.8±0.6^{a}	38.2±0.6^{a}
Ombrotrophic deciduous shrubs ($n = 5$)	15.4±1.1^{a}	23.9±1.8^{b}

Different superscript letters between habitats indicate significant differences for the same functional group ($P<0.05$; Student t-test). n is the number of litter bags in each habitat.

3.3. Decomposition rates

Minerotrophic *Sphagnum* litter showed significantly faster mass losses when transplanted in the ombrotrophic habitat compared to the native habitat (Table 3), whereas ombrotrophic *Sphagnum* litter decomposed more rapidly in the native habitat than in the minerotrophic habitat (Table 3).

Both minerotrophic and ombrotrophic graminoids had higher decomposition rates in the minerotrophic habitat, whereas not significant differences between habitats were found for the litter of ombrotrophic evergreen shrub *C. vulgaris* (Table 3). Minerotrophic forbs showed the highest decomposition rate compared to all the other functional groups with significantly faster mass loss in the minerotrophic than in the ombrotrophic habitat (Table 3). Litter of the ombrotrophic deciduous shrub *V. uliginosum* decomposed more rapidly in the ombrotrophic habitat compared to the minerotrophic habitat (Table 3).

3.4. P, N, K and C release

Minerotrophic *Sphagnum* litter released significantly more P, N and C than ombrotrophic *Sphagnum* litter in both the minerotrophic and the ombrotrophic habitat (Fig. 2). Total release of P was significantly lower in the minerotrophic habitat than in the ombrotrophic habitat for both the *Sphagnum* litter types (Fig. 2). Total release of N from minerotrophic *Sphagnum* litter did not differ between minerotrophic and ombrotrophic habitats, whereas N release from ombrotrophic *Sphagnum* litter was significantly slower in the ombrotrophic habitat than in the minerotrophic habitat (Fig. 2). The release of both K and C did not differ between native and transplanted habitat for the same *Sphagnum* litter types (Fig. 2). On the whole, K and C showed, respectively, the greatest and the lowest release compared to P and N (Fig. 2).

Release of P from vascular plant litter differed significantly in relation to habitat and plant functional group (Table 4). Indeed, P release in the minerotrophic habitat was significantly slower than in ombrotrophic habitat for all functional groups with the exception of minerotrophic forbs (Fig. 2). The release of N and K differed significantly between functional groups with interaction between functional group and habitat (Table 4). In particular, N release from minerotrophic graminoids and minerotrophic forbs was significantly faster in both habitats compared to all the

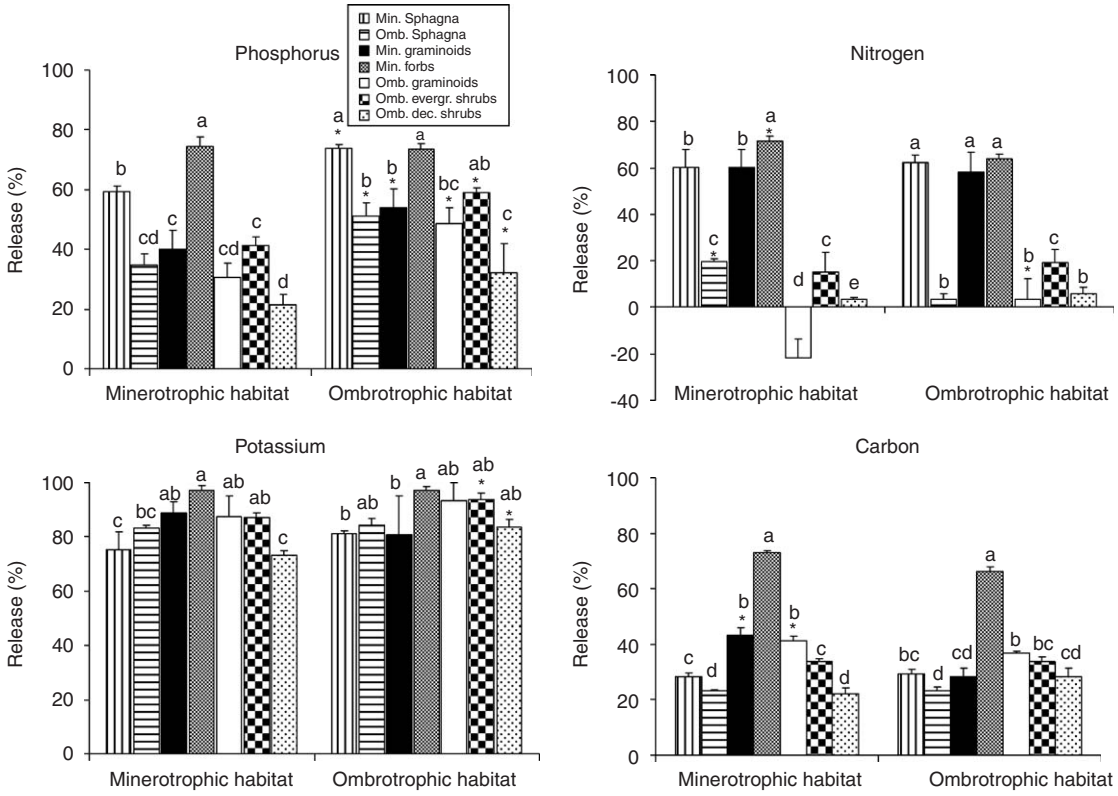

Fig. 2. Mean percentage release (±1 SEM) of P, N, K, and C from the litter of the seven plant functional groups after 1 year of burial in minerotrophic and ombrotrophic habitat. Positive values indicate net mineralisation and negative values net immobilisation. Significant differences (based on ANOVA and LSD Fisher post-hoc comparisons; $P<0.05$) between different functional groups in the same habitat are indicated by different letters, whereas significant differences of the same functional group between different habitats are indicated by an asterisk (* = $P<0.05$).

Table 4
Two-way ANOVA results for P, N, K, and C release from vascular plant litter after 1 year of burial

Nutrient	Source	*F*	df	*P* value
P	Habitat	4.6	1	0.038
	Functional group	8.9	4	$p<0.001$
	Habitat × functional group	0.8	4	0.55
N	Habitat	1.9	1	0.17
	Functional group	172	4	$p<0.001$
	Habitat × functional group	5.8	4	$p<0.001$
K	Habitat	1.0	1	0.32
	Functional group	5.2	4	$p<0.001$
	Habitat × functional group	2.2	4	0.08
C	Habitat	3.5	1	0.07
	Functional group	45.0	4	$p<0.001$
	Habitat × functional group	3.8	4	0.01

other functional groups (Fig. 2). Net N immobilisation was observed only for ombrotrophic graminoids transplanted into the minerotrophic habitat (Fig. 2). The release of C was different between functional groups with significant interaction between functional groups and habitats (Table 4). A significantly greater C release was found in minerotrophic forbs (Fig. 2).

3.5. Litter chemistry, decomposition rates and nutrient release

Litter decomposition rates (i.e., mass loss) of all plant species in their native habitats were positively correlated with corresponding C, N and P release (Fig. 3). Potassium release was negatively correlated with mass loss in *Sphagnum* litter (Fig. 3a), but positively correlated with mass loss in vascular plant litter (Fig. 3b). Decomposition rate of *Sphagnum* litter was negatively affected by high C/nutrient and polyphenols/nutrient quotient, whereas decomposition of vascular plant litter was negatively affected by lignin/nutrient, polyphenols/nutrient and C/N quotient (Fig. 3).

When differences of mass loss and nutrient release between transplanted and native habitats are calculated, we found a negative correlation between mass loss and correspondent N release for *Sphagnum* litter as well as for vascular plant litter, indicating an inverse relationship between decomposition and N mineralisation (Table 5). A similar inverse relationship was found for P in vascular plant litter, but a positive correlation between mass loss and P release was found in *Sphagnum* litter (Table 5). Positive correlations between mass loss and C release were found for both vascular plant and *Sphagnum* litter (Table 5).

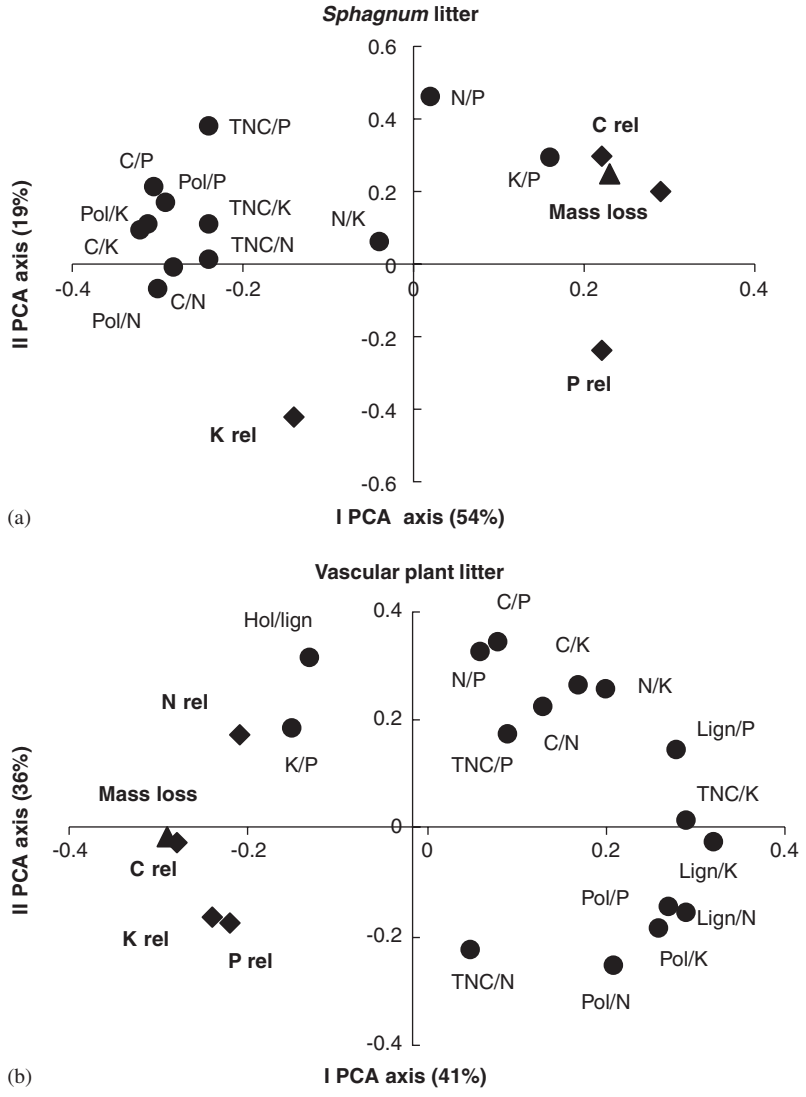

Fig. 3. Ordination of mass loss and nutrient release (rel) from *Sphagnum* litter (a) and vascular plant litter (b) in native habitat in relation to chemical parameter of initial litter. Ordination is based on principal component analysis (PCA).

Table 5
Pearson's correlation coefficients between mass loss differences and correspondent nutrient release differences between transplanted and native habitat for *Sphagnum* litter and vascular plant litter

Mass loss differences vs.				
	P release differences	N release differences	K release differences	C release differences
Sphagnum litter ($n = 20$)	0.50*	−0.51*	0.11	0.81**
Vascular plant litter ($n = 35$)	−0.43*	−0.46*	0.37	0.92**

*$P<0.05$; **$P<0.01$. (n is the number of samples).

4. Discussion

4.1. Litter decomposition rate

A slower mass loss of ombrotrophic *Sphagnum* litter in the minerotrophic habitat compared to the native habitat and, at the same time, a higher decomposition rate of minerotrophic *Sphagnum* litter in the ombrotrophic habitat suggest that microbial communities of ombrotrophic and minerotrophic habitats are differently affected by *Sphagnum* litter chemistry in relation to their metabolic requirements (Scheffer et al., 2001). In particular, polyphenols/nutrient and C/nutrient quotients appear as the primary litter chemistry parameters controlling decomposition of

Sphagnum litter (Szumigalski and Bayley, 1996a; Bridgham and Richardson, 2003; Limpens and Berendse, 2003; Dorrepaal et al., 2005).

All *Sphagnum* species are characterised by peculiar polyphenols with antibiotic activity and decay resistant properties (Verhoeven and Toth, 1995; Verhoeven and Liefveld, 1997; Freeman et al., 2004b), but ombrotrophic *Sphagnum* species generally contain a higher amount of polyphenols compared to minerotrophic *Sphagnum* species (Rudolph and Samland, 1985). When ombrotrophic *Sphagnum* litter was transplanted into the minerotrophic habitat, minerotrophic microbial communities had to face with a new litter type which was more decay-resistant. The result was a slower mass loss of ombrotrophic *Sphagnum* litter in the transplanted habitat compared to native *Sphagnum* litter suggesting a microbial adaptability to habitat-specific *Sphagnum* litter chemistry. On the whole, our data support the conclusion that intrinsic *Sphagnum* litter chemistry plays a major role in controlling aerobic *Sphagnum* litter decay compared to abiotic habitat conditions (Johnson and Damman, 1993).

Because C/N quotient in *Sphagnum* litter was significantly correlated with polyphenol concentration (Pearson's $r = 0.71$; $P < 0.01$; $n = 20$) and positive correlations were found between C/N, C/P and C/K quotients ($P < 0.01$), the C/N quotient can be reliably used as a single predictor of *Sphagnum* litter decomposability (Limpens and Berendse, 2003). In this sense, our results support the concern that increasing atmospheric N inputs on peatlands can indirectly stimulate the decomposing activity of ombrotrophic microbial communities through a reduction of the C/N quotient of *Sphagnum* litter (Aerts et al., 2001; Limpens and Berendse, 2003).

Higher TNC/nutrient quotients in ombrotrophic *Sphagnum* litter are in accordance with previous studies reporting a decrease in non-structural carbohydrates with increasing N availability (van der Heijden et al., 2000). Anyway, the relatively faster mass loss of minerotrophic *Sphagnum* litter in the ombrotrophic habitat suggests that microbial communities of ombrotrophic habitat are much more limited by nutrient availability than by the amount of easily available carbon (Damman, 1988).

Decomposition rates of vascular plant litter in native habitats were always higher than corresponding mass losses of *Sphagnum* litter (Table 3), according to the general findings that vascular plant litter decays faster than *Sphagnum* litter (Hobbie, 1996; Aerts et al., 1999; Scheffer et al., 2001; Dorrepaal et al., 2005). The higher decomposition rate of minerotrophic forbs compared to all the other functional groups seems to be primarily explained by low C/P and C/N quotients (Szumigalski and Bayley, 1996a; Aerts and De Caluwe, 1997; Cornelissen et al., 2004; Dorrepaal et al., 2005). Anyway, a prominent role of C/P quotient in affecting microbial metabolism seems to explain the reduced decomposition rate of minerotrophic graminoids and the correspondent increased decomposition of ombrotrophic graminoids in transplanted habitats (Tables 2 and 3). Indeed, if decomposition differences between transplanted and native habitat are calculated, a negative correlation is found between decomposition differences and initial C/P quotient of graminoids (Pearson's $r = -0.93$; $P < 0.001$).

The very slow mass loss of deciduous ombrotrophic shrubs in the native habitat can be explained by high polyphenol and lignin content (Melillo et al., 1982; Aerts and De Caluwe, 1997; Bridgham and Richardson, 2003). The significantly lower decomposition rate of ombrotrophic deciduous shrubs when transplanted in the minerotrophic habitat is in accordance with their high lignin content which hampers litter decomposition through N condensation with phenolic compounds under high exogenous N availability (Dijkstra et al., 2004; Knorr et al., 2005). Because ombrotrophic evergreen shrubs did not show a significantly slower decomposition in the minerotrophic habitat compared to the ombrotrophic habitat (Table 3) and because polyphenols/nutrient quotient did not differ between deciduous and evergreen shrubs (Table 2), the main chemical parameter in controlling decomposition of highly lignified litter seems to be the lignin/nutrient quotient (Bridgham and Richardson, 2003; Waldrop et al., 2004). This conclusion underlines that the type of polyphenols rather than total content of polyphenols plays a crucial role in affecting litter decay (Aerts et al., 2006). It is noteworthy that a greater exogenous nutrient availability is not necessarily accompanied by higher litter decomposition rates, confirming as litter quality (i.e., endogenous factors) plays a primary role in controlling mass loss under aerobic conditions (Szumigalski and Bayley, 1996a).

4.2. Nutrient mineralisation and immobilisation

On the whole, we found that higher endogenous P and, particularly, N concentrations in plant litter were positively related with the correspondent degree of mineralisation (Aerts and De Caluwe, 1997; Bridgham and Richardson, 2003).

Nitrogen release from *Sphagnum* litter was primarily controlled by C/N quotient, so that minerotrophic *Sphagnum* litter characterised by a lower C/N quotient released more N than ombrotrophic *Sphagnum* litter (Bayley et al., 2005). A greater availability of exogenous N in the minerotrophic habitat (Table 1) determined a faster N release from ombrotrophic *Sphagnum* litter as a consequence of a reduced N immobilisation by microorganisms, but a higher N mineralisation was not accompanied by faster litter decomposition (Aerts and De Caluwe, 1997). If a higher exogenous nutrient availability results in higher N release from *Sphagnum* litter, the increasing availability of dissolved N in bog waters observed under increasing atmospheric N inputs (Bragazza and Limpens, 2004) will have the potential to reduce N immobilisation in ombrotrophic habitats so to increase N availability to vascular plants at detrimental of *Sphagnum*

plant cover (Berendse et al., 2001; Heijmans et al., 2001; Limpens et al., 2003).

We observed lower N release from the litter of ombrotrophic vascular plant species compared to minerotrophic vascular plant species. Anyway, no single chemical parameters were predictive of the variability associated with different functional groups. Indeed, a low C/N quotient explains N mineralisation of minerotrophic forbs, but a low polyphenols/N quotient seems to be the primary factor to enhance N release from minerotrophic graminoids which have a C/N quotient not significantly different from ombrotrophic vascular plant litter (Aerts and De Caluwe, 1997). In addition, net N immobilisation in the litter of ombrotrophic graminoids when transplanted in the minerotrophic habitat can be explained by a high TNC/N quotient which has been shown to stimulate microbial growth and mass loss, but also to enhance N immobilisation (Schmidt et al., 1997).

On the whole, lower N release from litter of ombrotrophic plant species compared to the litter of minerotrophic species is consistent with the decreasing plant productivity reported along the minerotrophic–ombrotrophic gradient (Szumigalski and Bayley, 1996b; Chapin et al., 2004) and highlights the potential role of competition for N between plants and micro-organisms in ombrotrophic habitats (Schmidt et al., 1997).

In *Sphagnum* litter, a higher C/P quotient was associated with lower P mineralisation, whereas a faster P release from vascular plant litter seems primarily related to lower C/P and polyphenols/P quotients (Aerts and De Caluwe, 1997). Lower P release in the minerotrophic habitat compared to the ombrotrophic habitat could be primarily explained by a geochemical control through the formation of complexes between phosphate and Fe, Ca or Al (Koerselman et al., 1993; Verhoeven et al., 1996; Aerts et al., 1999; Kellogg and Bridgham, 2003). Unfortunately, our data cannot unravel the relative role of biotic and abiotic factors in controlling P release from decaying litter in minerotrophic habitat. Anyway, our data confirm a faster P turnover in ombrotrophic habitats compared to minerotrophic habitats (Verhoeven et al., 1990; Bridgham et al., 1998; Scheffer et al., 2001).

The release of K was very high compared to all the other nutrients and the amount was rather similar between ombrotrophic and minerotrophic plant species. This pattern is consistent with a rapid K leaching from senescing and decaying litter as previously reported (Brock and Bregman, 1989; Sundström et al., 2000; Bridgham and Richardson, 2003).

Carbon release from *Sphagnum* and vascular plant litter was significantly correlated with mass loss, much more than the release of P, N, and K. Accordingly, the rate of C release effectively indicates the amount of litter used by micro-organisms in relation to the initial litter quality.

5. Conclusions

Our study has shown as litter decomposition and nutrient release under aerobic conditions are highly species-specific involving complex and multiple interactions between several litter chemical parameters. Litter bag transplanting has demonstrated that micro-organisms of minerotrophic and ombrotrophic habitats are highly adapted to litter chemistry of habitat-specific plant species in relation to their metabolic requirements. On the whole, the following patterns emerged:

(1) decomposition rate of *Sphagnum* litter was inversely related to initial C/nutrient quotient, so that ombrotrophic *Sphagnum* litter decays slowerly than minerotrophic *Sphagnum* litter;
(2) independently from growth form, litter produced by vascular plant species decays always faster than *Sphagnum* litter;
(3) decomposition rates of vascular plant litter were highly variable in relation to functional groups; accordingly, litter decomposition of herbaceous plants was inversely related to C/P quotient, whereas decomposition of lignolitic litter of shrubs was primarily affected by lignin/N quotient;
(4) the rate of nutrient release and mass loss were not necessarily correlated, primarily depending on the microbial metabolic requirements; in particular, N release was related to the total N content in initial litter so that N turnover in ombrotrophic habitats, where plant litter has a low N content, was lower than in minerotrophic habitats; P release was lower in minerotrophic habitats very probably as consequence of chemical immobilisation of phosphate under a greater exogenous availability of mineral ions; leaching played a primary role in affecting K release, whereas the amount of C release was always significantly correlated with the degree of mass loss.

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