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Plant Litter Decomposition and Nutrient Release in Peatlands

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Decomposition of plant litter is a crucial process in controlling the carbon balance of peatlands. Indeed, as long as the rate of litter decomposition remains lower than the rate of above- and belowground litter production, a net accumulation of peat and, thus, carbon will take place. In addition, decomposition controls the release of important nutrients such as nitrogen, phosphorus, and potassium, the availability of which affects the structure and the functioning of plant communities. This chapter describes the role of the main drivers in affecting mass loss and nutrient release from recently deposited plant litter. In particular, the rate of mass loss of *Sphagnum* litter and vascular plant litter is reviewed in relation to regional climatic conditions, aerobic/anaerobic conditions, and litter chemistry. The rate of nutrient release is discussed in relation to the rate of mass loss and associated litter chemistry by means of a specific case study.

1. INTRODUCTION

Peatlands are characterized by a significantly large storage of soil organic matter per unit of surface compared to the other major ecosystems of the world [*Batjes*, 1996]. Although net primary production (NPP; i.e., the net amount of biomass accumulated by phototrophic biosynthesis per unit area and time) is relatively small in peatlands [*Ito and Oikawa*, 2004], the imbalance between NPP and decomposition is strong enough to cause significantly high rates of soil organic matter accumulation [*Schlesinger*, 1997; *Clymo et al.*, 1998].

At global scale, the largest fraction of NPP is delivered to the soil as dead organic matter through above- and belowground litter. If we estimate a global annual aboveground litter fall of 54.8×10^{15} g [*Meentemeyer et al.*, 1982] over a worldwide land area of about 121×10^6 km^2, and if we estimate a mean bulk density of litter fall of about 0.2 g cm^{-3}, then each year, a litter layer of about 2 mm would be deposited on the world's land so that this layer would theoretically reach a thickness of 2 m in 1,000 years. However, decomposition prevents such a rate of organic matter accumulation by breaking down the litter into carbon dioxide (CO_2), dissolved organic carbon (DOC), inorganic and organic nutrients, as well as stable humus.

The accumulation of soil organic matter in terrestrial ecosystems is universal, in the sense that higher rates of NPP compared to decomposition take place also in those ecosystems apparently characterized by very low soil organic matter content [*Batjes*, 1996]. Indeed, it is the "magnitude" of the long-term imbalance between NPP and decomposition that allowed peatlands to build up impressive stores of soil organic matter: the peat [*Wieder*, 2006].

In the light of the role played by decomposition in controlling the ability of peatlands to act as C sinks, in this chapter,

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we will review the main factors controlling decomposition of recently deposited plant litter, paying particular attention to mass loss and nutrient release from aboveground litter. For a discussion of peat decomposition and associated release of dissolved organic carbon (DOC), carbon dioxide (CO_2), and methane (CH_4), the reader is referred to the chapters by *Fenner et al*. [this volume], *Moore* [this volume], and *Nilsson and Öquist* [this volume] in the present monograph.

Although litter decomposition is a complex process simultaneously affected by multiple chemical, physical, and biological drivers, we will try to highlight some general trends. To this aim, we first discuss the roles of the main drivers affecting litter mass loss and, second, we describe the trends in C, nitrogen (N), phosphorus (P), and potassium (K) releases based on a 3-year-long field study of litter decomposition in a peatland of the Italian Alps.

2. MASS LOSS

Decomposition of plant litter "involves a complex set of processes including chemical, physical, and biological agents acting upon a variety of organic substrates that are themselves constantly changing" [*Berg and McClaugherty*, 2003]. It is clear from the above definition that decomposition can be highly variable in relation to the spatial and temporal diversity of interacting abiotic and biotic factors.

A simple way to estimate decomposition rate is by measuring litter mass loss, an estimate typically obtained by means of litter bags. The litter bag technique consists in confining fresh litter in mesh bags that are placed on the ground and periodically collected so as to measure the remaining litter mass and associated litter chemistry [*Singh and Gupta*, 1977]. This simple and cheap technique has been, however, criticized because (1) confined litter bags may create their own microenvironment different from surrounding bulk soil; (2) litter bags may exclude specific faunal groups in relation to the mesh size [*Nieminen and Setala*, 1997; *Bradford et al*., 2002]; and (3) litter bags are usually filled with litter from a single species [*Gartner and Cardon*, 2004]. Nevertheless, the litter bag technique is widely applied to monitor temporal mass loss in both terrestrial and aquatic environments.

Different mathematical models have been proposed to describe litter mass loss based on information obtained from litter bags [*Wieder and Lang*, 1982; *Berg and McClaugherty*, 2003]. The most commonly applied model, particularly for early stages of decomposition, is the single exponential model [*Olson*, 1963], which is supposed to work well for a variety of litter types until about 80% of initial litter is lost.

In the following, we will try to review how and to what extent mass loss of recently deposited litter is affected by regional and local drivers, an essential background to understand the potential response of peatlands to global change.

2.1. Climate

The role of climatic factors in affecting litter mass loss has received much attention in ecological studies so that, at a global scale, mean annual temperature and actual evapotranspiration were shown to have the strongest influence [*Meentemeyer*, 1978; *Aerts*, 1997; *Gholz et al*., 2000; *Liski et al*., 2003].

For assessing the role of climate on litter mass loss in peatlands, we related the annual k decomposition constant [*Olson*, 1963] from seven major terrestrial ecosystem types to corresponding mean annual temperature and mean total annual precipitation. To this aim, we selected data where (1) the litter bag technique was applied to estimate litter mass loss; (2) the k values were calculated on the basis of the single exponential model; (3) the decomposition was monitored at least for 2 years or longer, so as to include changes associated both with physical leaching and with microbial activity [*Siegenthaler et al*., 2001].

We were able to select a total of 179 k values from 40 published and unpublished papers fulfilling the above criteria (data are available on request). Particularly for peatlands, most of the selected papers monitored litter mass loss during a burial period varying from 2 to 5 years, except for the paper by *Latter et al*. [1998] where mass loss was monitored for 22 years.

Across the seven ecosystem types, k values were positively correlated with the mean annual temperature (Pearson's $r = 0.37$; $p < 0.001$; $n = 179$) but not with mean total annual precipitation (Figure 1). In the specific case of peatlands, the mean k value of vascular plant litter ($0.225\ \mathrm{yr}^{-1}$) did not differ significantly from the mean k values of marshlands, Mediterranean shrublands, and deserts (Figure 2), whereas the mean k value of *Sphagnum* litter ($0.081\ \mathrm{yr}^{-1}$) was significantly lower compared to the k values of all the other ecosystem types including the mean k value of vascular plant litter (Figure 2). In addition, k values of vascular plant litter in peatlands were positively related with both the mean annual temperature (Pearson's $r = 0.37$; $p < 0.001$; $n = 69$) and the mean total annual precipitation (Pearson's $r = 0.39$; $p < 0.001$; $n = 69$), whereas the k values of *Sphagnum* litter were not correlated to either of these climatic factors. Increased decomposition rates of vascular plant litter in peatlands with increasing temperature were also reported by other authors [*Hobbie*, 1996; *Thormann et al*., 2004; *Moore et al*., 2005; *Breeuwer et al*., 2008]. Furthermore, many laboratory and field experiments have shown that higher temperature resulted in increasing decomposition of vascular plant and

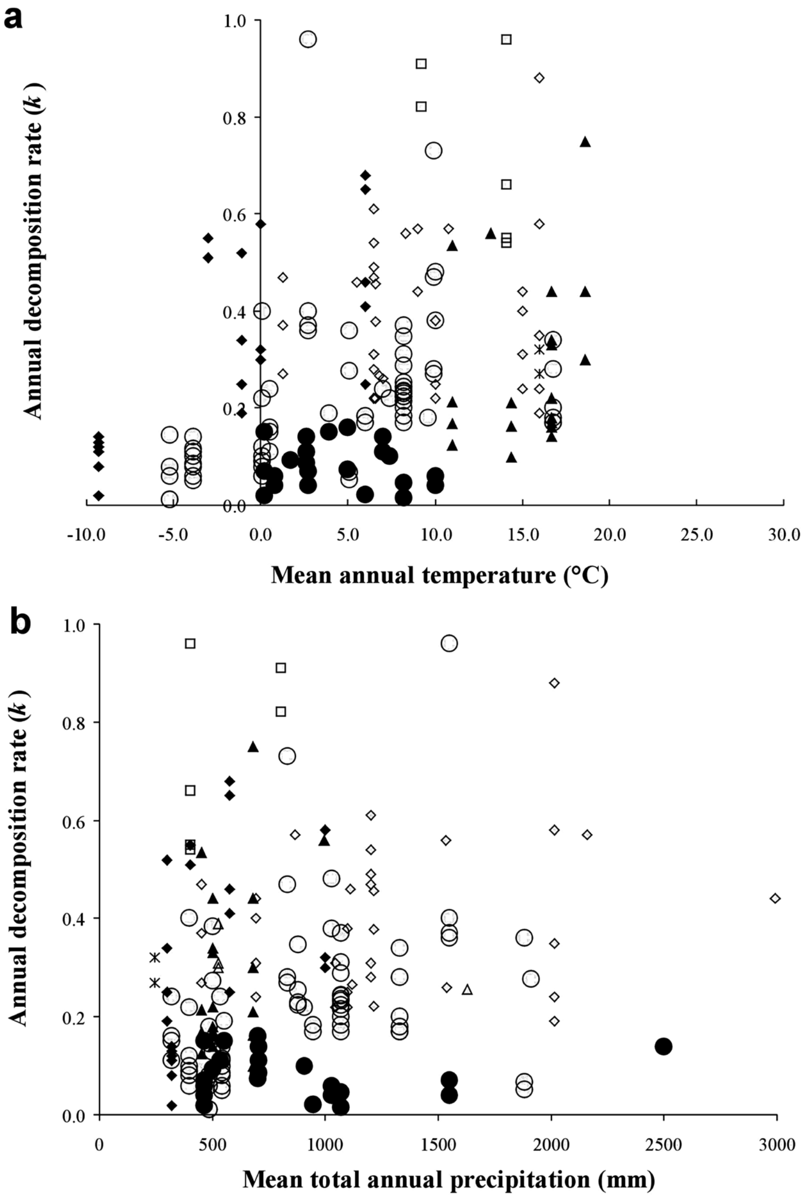

Figure 1. Relationship between annual decomposition *k* value and (a) mean annual temperature and (b) mean total annual precipitation for different plant species in seven major ecosystem types. Decomposition *k* values were obtained from studies lasting more than 1 year. For peatlands, *k* values of *Sphagnum* species (solid circles) and vascular plant species (open circles) were reported separately. Other symbols are as follows: open diamonds, forests; solid triangles, Mediterranean shrublands; open squares, grasslands; asterisks, deserts; open triangles, marshlands; solid diamonds, tundra. Sources are *Latter and Cragg* [1967], *Rochefort et al.* [1990], *Johnson and Damman* [1991], *Gallardo and Merino* [1993], *Aerts and De Caluwe* [1997], *Foote and Reynolds* [1997], *Wrubleski et al.* [1997], *Latter et al.* [1998], *Gholz et al.* [2000], *Moro and Domingo* [2000], *Scheffer et al.* [2001], *Seastedt and Adams* [2001], *Thormann et al.* [2001], *Aerts et al.* [2003], *Bridgham and Richardson* [2003], *Kemp et al.* [2003], *Koukoura et al.* [2003], *Quested et al.* [2003], *Albers et al.* [2004], *Heim and Frey* [2004], *Hobbie and Gough* [2004], *Palviainen et al.* [2004], *Asada and Warner* [2005], *Fioretto et al.* [2005], *Moore et al.* [2005], *Quideau et al.* [2005], *Sariyildiz et al.* [2005], *Aerts et al.* [2006], *Weerakkody and Parkinson* [2006], *Bokhorst et al.* [2007], *Bubier et al.* [2007], *Cortez et al.* [2007], *Lindo and Winchester* [2007], *Moore et al.* [2007], *Breeuwer et al.* [2008], *Buttler* [1987], *Miyamoto and Hiura* [2008], *Sariyildiz* [2008], *Turetsky et al.* [2008], Bragazza, unpublished data [2008].

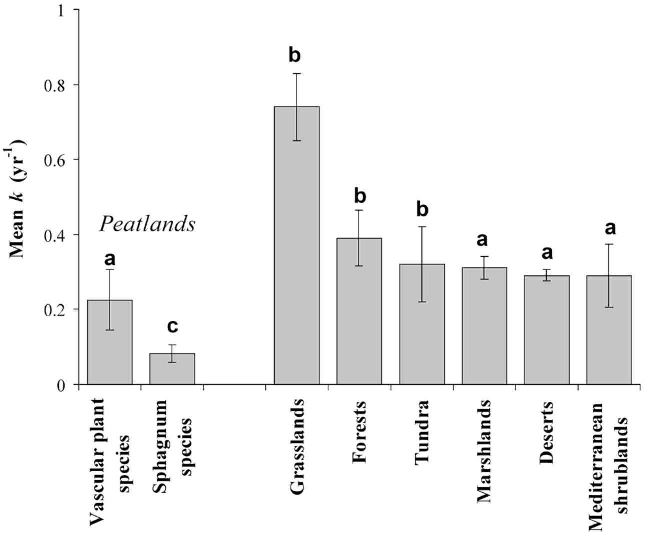

Figure 2. Mean annual k values (plus/minus SD) of plant litter in seven major ecosystem types. The analysis of variance was applied to compare mean k values of *Sphagnum* litter and vascular plant litter in peatlands with other ecosystems. The different superscripts indicate significant differences based on LSD Fisher post hoc test ($p < 0.05$). For sources, see Figure 1.

Sphagnum litter under nonlimiting moisture conditions [*Dioumaeva et al.*, 2003; *Domisch et al.*, 2006; *Glatzel et al.*, 2006] and that under excess drought the decomposition of organic matter is hampered [*Laiho et al.*, 2004; *Aerts*, 2006; *Gerdol et al.*, 2008]. On the other hand, considering the sole *Sphagnum* litter, the absence of relationship between its decay and climatic factors seems to highlight the prevailing role of litter quality in controlling *Sphagnum* decomposition in peatlands (see below).

2.2. Litter Decomposition in Aerobic Versus Anaerobic Conditions

The intensity of water flow and the degree of hydric saturation of the peat substrate are supposed to affect the rate of plant litter decomposition in peatlands. Indeed, laboratory and field experiments have demonstrated that mass loss is higher under aerobic conditions than under anaerobic conditions [*Belyea*, 1996; *Scanlon and Moore*, 2000; *Yavitt et al.*, 2000; *Blodau et al.*, 2004; *Laiho*, 2006; *Moore and Basiliko*, 2006; *Jaatinen et al.*, 2008; *Wickland and Neff*, 2008]. In Figure 3, mass losses from vascular plant litter and *Sphagnum* litter decomposing in parallel under aerobic and anaerobic conditions are compared. The percentage of mass loss was on average about 2.3 times higher in the aerobic layer both for vascular plant and *Sphagnum* litter. It follows that the faster the decomposing plant litter enters the anaerobic zone to become saturated by water, the higher the rate of peat accumulation will be as a consequence of reduced mass loss. It is then clear that any disturbance lowering the water table can enhance, at least temporarily, the decomposition of previously water-saturated peat which becomes exposed to aerobic conditions [*Laine et al.*, this volume].

If aerobic conditions enhance litter decomposition, this raises the question of why decomposition rates of *Sphagnum* litter is generally lower in hummocks, i.e., in habitats well aerated for most of the year, compared to the litter produced by *Sphagnum* species inhabiting moister habitats such as hollows [*Johnson and Damman*, 1991; *Belyea*, 1996; *Asada and Warner*, 2005; *Dorrepaal et al.*, 2005; *Bragazza et al.*, 2007; *Moore et al.*, 2007; *Breeuwer et al.*, 2008]. This can be explained taking into account the role of litter chemistry, in particular the relatively higher content of structural carbohydrates in *Sphagnum* species forming high hummocks [*Turetsky et al.*, 2008]. Thus, the complex interactions between physical conditions at habitat scale and *Sphagnum* litter chemistry play an important role in controlling the topographical variability of peatland surface and associated rates on peat accumulation [*Ohlson and Dahlberg*, 1991; *Belyea and Malmer*, 2004].

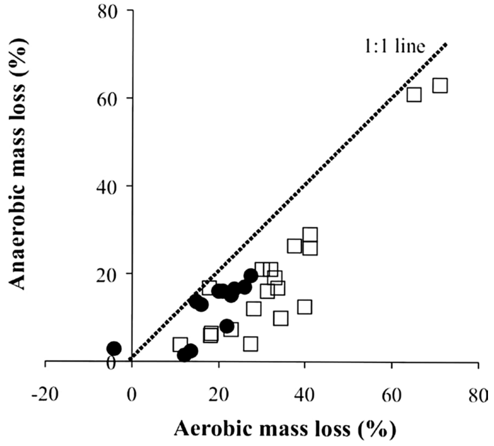

Figure 3. Comparison of mass loss (percent of initial dry weight) of vascular plant litter (open squares) and *Sphagnum* litter (solid circles) buried simultaneously both in aerobic and anaerobic conditions. Data were obtained using litter bags with different burial time intervals and different mesh size. The dotted line shows the 1:1 ratio. Sources are *Clymo* [1965], *Johnson and Damman* [1991], *Asada and Warner* [2005], *Moore et al.* [2007], *Trinder et al.* [2008], Bragazza, unpublished data [2008].

2.3. Litter Chemistry

The role of initial litter chemistry in affecting decomposition in peatlands will be separately reviewed for vascular plant litter and *Sphagnum* litter in the light of their significantly different *k* values (Figure 2).

Considering the most common stoichiometric parameters [*Hessen et al*., 2004], it appears that mass loss of vascular plant litter is negatively correlated with the initial value of the lignin/N quotient (Pearson's $r = -0.46$; $p < 0.05$; $n = 27$), but positively correlated with the initial value of the holocellulose/lignin quotient (Pearson's $r = 0.59$; $p < 0.05$; $n = 13$; Figure 4). It is here necessary to underline that the sources selected in Figure 4 did not apply the same protocol for lignin quantification in initial litter. Indeed, more often the term "lignin" is operationally defined as the acid unhydrolyzable residue (AUR) of a sequential fractionation analysis so that AUR incorporates both true lignin as well as compounds such as cutins and tannins. Nevertheless, on the basis of our results, it seems that higher initial values of the AUR/N quotient hamper litter decomposition as a consequence of the lower chemical quality of plant litter [*Melillo et al*., 1982; *Aerts and De Caluwe*, 1997; *Thorman et al*., 2001; *Siegenthaler et al*., 2001; *Cornelissen et al*., 2004]. On the other hand, a higher initial holocellulose/AUR quotient in vascular plant litter seems to enhance decomposition because microbes have access to more easily decomposable C compounds [*Melillo et al*., 1989; *Bridgham and Richardson*, 2003; *Comont et al*., 2006; see also *Artz*, this volume].

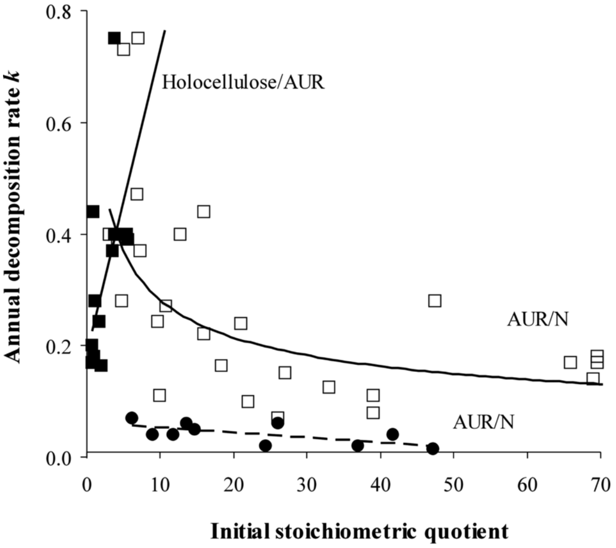

Figure 4. Relationship between initial values of selected stoichiometric quotients and annual *k* values of vascular plant litter (open and solid squares) and *Sphagnum* litter (solid circles) based on studies in which mass loss was monitored for more than 1 year. AUR is acid unhydrolyzable residue. Sources are *Aerts and De Caluwe* [1997], *Scheffer et al*. [2001], *Thormann et al*. [2001], *Bridgham and Richardson* [2003], *Aerts et al*. [2006], *Bubier et al*. [2007], *Breeuwer et al*. [2008], *Turetsky et al*. [2008], Bragazza, unpublished data [2008].

Decomposition of *Sphagnum* litter has been demonstrated to be enhanced, at least after 1 year of field burial, by low initial values of phenolics/nutrient and C/nutrient quotients [*Szumigalski and Bayley*, 1996; *Limpens and Berendse*, 2003; *Dorrepaal et al*., 2005; *Bragazza et al*., 2007]. On the basis of selected data, we observed that *k* values of *Sphagnum* litter were negatively correlated with initial AUR/N quotients (Pearson's $r = -0.66$; $p < 0.05$; $n = 11$; Figure 4). Anyway, we must underline that (1) Sphagna do not contain true lignin as do vascular plants, so that the AUR in *Sphagnum* litter mainly refers to lignin-like polymeric phenolics [*Bland et al*., 1968; *van der Heijden*, 1994], and (2) as mentioned above, the methods used to quantify lignin-like compounds, and therefore the results, vary among authors. The role of the phenolics/N quotient in affecting *Sphagnum* litter decomposition is confirmed by higher decomposability of litter deposited by minerotrophic *Sphagnum* species compared to ombrotrophic *Sphagnum* litter [*Bragazza et al*., 2007], the latter being characterized by a higher phenolic content [*Rudolph and Samland*, 1985]. It has also been suggested that a better predictor of moss decomposition rate in peatlands is represented by the quotient between fructose/pentose carbohydrates in initial litter [*Turetsky et al*., 2008], so that moss species investing relatively more in structural carbohydrates (i.e., pentosans) such as hummock-forming Sphagna are more resistant than moss species investing relatively more in metabolic carbohydrates (i.e., fructosans), such as hollow inhabiting Sphagna. In this review, the limited data did not reveal a significant role for C/nutrient quotients on *Sphagnum* litter decomposition, although the C/P and C/N quotient have been reported to significantly explain mass loss of *Sphagnum* litter after 1 year of field burial [*Hogg et al*., 1994; *Aerts et al*., 2001; *Limpens and Berendse*, 2003; *Bragazza et al*., 2007].

From a global change perspective, increasing atmospheric N deposition and global climate change can have contrasting effects on litter decomposition in peatlands. Indeed, increasing N availability can be expected to enhance short-term *Sphagnum* litter decomposition through an increase of N content [*Williams et al*., 1999; *Bragazza et al*., 2006; *Gerdol et al*., 2007] and a decrease of (soluble) phenolics [*Bragazza and Freeman*, 2007], thereafter reducing the phenolics/N and the C/nutrient quotients. On the other hand, *Sphagnum* litter decomposition is strongly affected by its water content, so that below a certain level of litter moisture, decomposition initially slows down and then stops completely [*Crow and Wieder*, 2005; *Aerts*, 2006; *Gerdol et al.*, 2007]. For vascular plants, increasing N availability had variable species-specific effects on mass loss depending on the chemistry of initial litter [*Aerts et al.*, 2006; *Breeuwer et al.*, 2008]. At ecosystem level, increased N deposition can provoke a shift in species composition, with vascular plants or brown mosses displacing *Sphagnum* species as a result of efficient use of nitrogen [*Berendse et al.*, 2001; *Mitchell et al.*, 2002; *Bubier et al.*, 2007], and this ultimately will change the litter quality of both individual species and the plant community.

As previously underlined, this chapter centers on aboveground litter decomposition because most of the studies on litter decomposition in peatlands deal with leaf decay. Nevertheless, belowground litter derived from roots and rhizomes can play an important role in C sequestration and nutrient cycling, particularly in fens, i.e., peatlands receiving mineral inputs from surrounding mineral soil, where belowground production represents the greatest part of total NPP [*Buttler*, 1992; *Wieder*, 2006]. At the global scale, it has been suggested that leaf litter decomposition is more controlled by (micro)climate factors, whereas belowground litter decomposition is more affected by root and rhizome chemical quality [*Whendee and Miya*, 2001]. Particularly in peatlands, the very few studies on belowground litter decomposition [e.g., *Hartmann*, 1999; *Scheffer and Aerts*, 2000; *Thormann et al.*, 2001; *Moore et al.*, 2007] seem to indicate that mass loss of roots and/or rhizomes is lower than the corresponding leaf mass loss, particularly for vascular plant species adapted to waterlogged soils. In addition, *Scheffer and Aerts* [2000] reported a greater net loss of N and P from decomposition of roots and rhizomes compared to leaves. Although more studies are necessary on belowground litter decomposition, the few available results highlight the important role of belowground litter for C accumulation and nutrient cycling, particularly in fens.

3. NUTRIENT RELEASE

The supply of nutrients in peatlands is provided by external and internal sources. External sources are represented by atmospheric wet and dry deposition as well as by groundwater influxes from the surrounding mineral soil. In bogs (i.e., ombrotrophic peatlands), atmospheric deposition is the primary external source of nutrients, whereas atmospheric deposition and groundwater inputs represent the external sources supplying fens (i.e., minerotrophic peatlands) with nutrients. Internal sources are, instead, associated with nutrient release during organic matter decomposition. The rate of nutrient release is not necessarily equal to the rate of mass loss because some nutrients can be immobilized by microbes and incorporated in humic compounds rather than being mineralized during mass loss [*Jonasson and Shaver*, 1999]. The degree of nutrient release during litter decomposition can then affect nutrient availability for plant growth and, ultimately, the structure and the functioning of plant communities [*Aerts et al.*, 1999; *Parton et al.*, 2007].

In this section, we will assess the rates of release of C, N, P, and K during (aboveground) litter decomposition in peatlands. To this aim, we will use data from a 3-year long litter decomposition experiment carried out in a peatland of the Italian Alps.

3.1. Study Area, Material, and Methods

The Marcesina peatland (45°57′N; 11°37′E) is located at 1300 m above sea level under climatic conditions characterized by a mean annual temperature of 3°C and total annual precipitation of 1550 mm. On the basis of the floristic composition, the study site can be classified as an ombrotrophic peatland or bog.

For the aims of this study, two *Sphagnum* species (i.e., *S. magellanicum* and *S. fuscum*) and four vascular plant species (i.e., *Potentilla erecta*, *Eriophorum vaginatum*, *Calluna vulgaris*, and *Carex rostrata*) were selected. Litter samples from each plant species were collected in mid-September 2004 so as to prepare litter bags (mesh size = 0.5 mm), which were then buried at the beginning of October 2004 just below the bog surface in the typical habitat of each plant species. The total number of litter bags was 48 for *Sphagnum* litter and 96 for vascular plant litter.

At the beginning of October 2005, 2006, and 2007, eight litter bags for each species were retrieved, and mass losses as well as N, P, K, and C concentrations were determined. For technical details concerning litter bag preparation, cleaning, and chemical analyses, see *Bragazza et al.* [2007].

For each litter bag, nutrient release was calculated as: $[(M_0C_0 - M_tC_t) / M_0C_0] \times 100$ where M_0 and M_t are, respectively, the oven-dry mass of litter in the bag at the beginning of the experiment and at time t (i.e., years 1, 2, and 3), whereas C_0 and C_t are the corresponding nutrient concentrations in the litter. Positive values of release indicate net loss of the nutrient, whereas negative values indicate immobilization of the nutrient.

3.2. Results and Discussion

During 3 years of field decomposition, the cumulative release, i.e., at time t, of C, N, P, and K was always positive, therefore indicating a net loss of these nutrients from decomposing litter (Figure 5). However, at the end of the third year

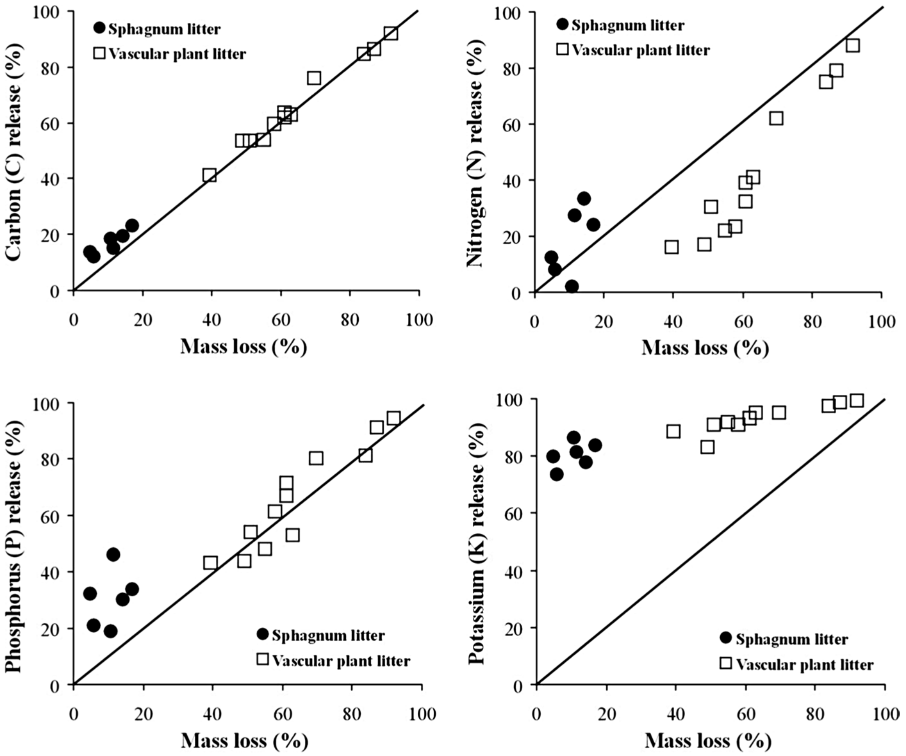

Figure 5. Relationship between mass loss after 1, 2, and 3 years of decomposition and corresponding release of C, N, P, and K from two *Sphagnum* species (i.e., *S. fuscum* and *S. magellanicum* litter) and four vascular plant species (i.e., *Potentilla erecta*, *Carex rostrata*, *Eriophorum vaginatum*, and *Calluna vulgaris* litter). Data represent, for each plant species, mean values calculated on eight annually retrieved litter bags. The line corresponds to the 1:1 ratio.

of burial, the release of C, N, P, and K was significantly lower in *Sphagnum* litter than in vascular plant litter, suggesting a relatively lower rate of nutrient loss from *Sphagnum* litter (Figure 5). Similarly, the mean annual mass loss of *Sphagnum* litter (11.2%, standard deviation (SD) = 4.7; $n = 48$) was significantly lower ($p < 0.001$) than the mean annual mass loss of vascular plant litter (64.5%, SD = 16.3; $n = 96$).

Independently from litter type, the mean annual release of K (89% ± 7%) was significantly greater ($p < 0.01$) compared to all other nutrients (C = 49.5% ± 27%; N = 35% ± 24%; P = 54% ± 22%). The high leaching of K from decomposing litter was already reported [*Brock and Bregman*, 1989; *Sundstrom et al.*, 2000; *Bragazza et al.*, 2007], and it seems to explain the peaks of K concentration in peatland waters typically found outside the growing season, when plant growth has not yet started, but K is released by decomposing litter [*Buttler*, 1992; *Proctor*, 1992; *Vitt et al.*, 1995; *Bragazza et al.*, 1998].

In the case of vascular plant litter, the cumulative release of C and P paralleled the mass loss (i.e., the nutrient release/mass loss quotient was always around 1 during the decomposition period), whereas the cumulative release of N and K was, respectively, lower and higher than the corresponding mass loss (Fig. 5). Instead, in the case of *Sphagnum* litter, the cumulative release of N, P, and K was greater than the corresponding mass loss (i.e., the nutrient release/mass loss quotient was always > 1), whereas the cumulative C release tended to parallel the mass loss (Figure 5). Different trends in nutrient release between *Sphagnum* litter and vascular plant litter can initially be explained by the absence of protective tissues and waxes on *Sphagnum* leaves allowing a rapid physical leaching of N and P [*Scheffer et al.*, 2001].

Vascular plant litter had initial C/N quotients ranging from 38 to 48, and the absence of N immobilization is in accordance with findings of *Parton et al.* [2007], who reported net N loss with leaf litter C/N quotient < 40. For *Sphagnum* litter, during the first year of decomposition, immobilization is absent as already reported by *Brock and Bregman* [1989] and *Vehoeven et al.* [1990], but N release tended to decrease over time (Figure 6). More precisely, with increasing mass loss, the AUR/N quotient increased significantly for both *Sphagnum* litter and vascular plant litter, but the corresponding

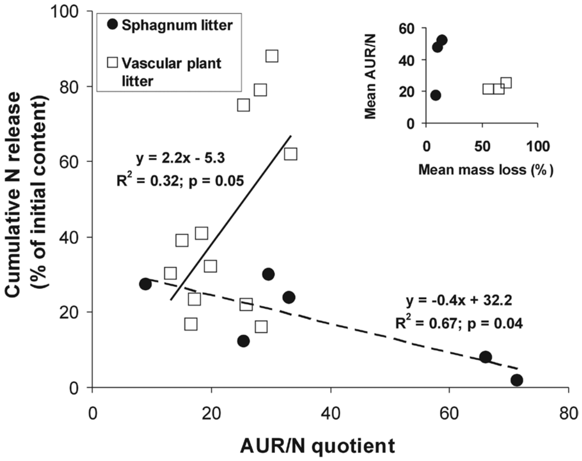

Figure 6. Relationship between AUR/N quotient after 1, 2, and 3 years of decomposition and corresponding N release for *Sphagnum* litter and vascular plant litter. Each value for each species is the mean based on eight litter bags annually retrieved. The inner graph represents the relationship between cumulative mean mass loss and corresponding AUR/N quotient for *Sphagnum* litter and vascular plant litter (in this case the individual species have been merged for *Sphagnum* litter and vascular plant litter).

cumulative N release tended to decrease for *Sphagnum* litter and to increase for vascular plant litter, therefore indicating that, over time, *Sphagnum* litter tends to retain more N (Figure 6).

Carbon released from both *Sphagnum* and vascular plant litter was much more linearly related to mass loss than for P, K, and N (Figure 5). Accordingly, the rate of C release effectively indicates the rate of mass loss [*Bragazza et al.*, 2007].

Phosphorus release was enhanced by low initial C/P quotient (Figure 7), suggesting that litter with greater initial C/P quotient tends to lose P at lower rates [*Aerts and De Caluwe*, 1997; *Bragazza et al.*, 2007]. It is generally assumed that P release in bogs is higher than in fens because of a geochemical P immobilization in fen habitats through the formation of complexes with Fe, Ca, or Al, which allows a faster turnover of P in ombrotrophic habitats compared to minerotrophic habitats [*Verhoeven et al.*, 1990; *Bridgham et al.*, 1998; *Scheffer et al.*, 2001; *Bragazza et al.*, 2007].

4. CONCLUSIONS

The low rate of plant litter decomposition in actively growing peatlands is not only a peculiarity of this type of ecosystem, but it is also the key process to ensure peat accumulation and, consequently, to guarantee that active peatlands act as C sinks. Litter quality and anoxic soil conditions appear as the major factors affecting decomposition rates in peatlands. It has been shown that the peculiar chemistry of *Sphagnum* litter is fundamental for enhancing long-term peat accumulation. Accordingly, any environmental change favoring vascular plants at the expense of *Sphagnum* plants can potentially reduce peat accumulation by increasing the rates of litter decomposition. This is particularly true in bogs where *Sphagnum* litter form the bulk of dead biomass. At the same time, changes in litter chemistry can also affect nutrient release and therefore nutrient availability in peatlands, thus potentially altering the competitive balance between different plant species.

Our review has also identified three important current limitations in studies of litter decomposition and associated nutrient release in peatlands: (1) There are relatively few studies monitoring decomposition in peatlands for periods longer than 1 year, so that the patterns and mechanisms of longer-term litter decomposition are poorly known. (2) There are few data on belowground litter decomposition in peatlands, so that we currently miss the functioning of an important component for peatland biogeochemistry, especially for fens where belowground litter production is highest. (3) For some chemical analyses, such as for lignin (AUR) and polyphenols, the methodologies are not standardized. Hence, we suggest that future studies should extend the burial time of litter bags and pay more attention to belowground

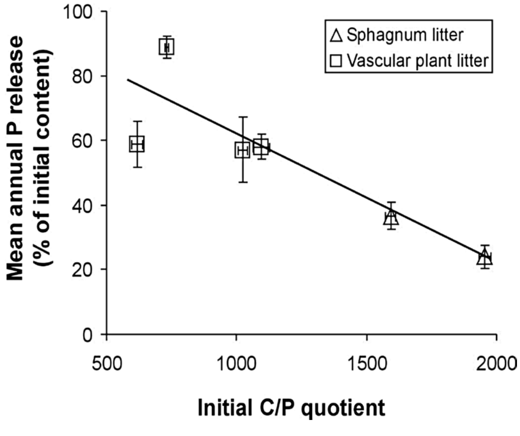

Figure 7. Relationship between mean (plus/minus SD) annual release of phosphorus (P) during 3 years of decomposition and corresponding mean (plus/minus SD) initial C/P quotient in four vascular plant litter types and two *Sphagnum* litter types ($Y = -0.04X + 97.8$; $r^2 = 0.76$; $p = 0.02$). The values of annual P release were calculated on 24 litter bags for each plant species, whereas the mean initial C/P quotient was calculated on three initial litter samples for each plant species.

litter decomposition. In addition, we call for the definition of a standard protocol for the chemical characterization and quantification of plant litter components, particularly for lignin (AUR) and polyphenols, so as to make comparisons among studies more reliable.

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