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Nutritional constraints in ombrotrophic *Sphagnum* plants under increasing atmospheric nitrogen deposition in Europe

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Summary

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- We studied the effects of increasing levels of atmospheric nitrogen (N) deposition on nutrient limitation of ombrotrophic *Sphagnum* plants.
- Fifteen mires in 11 European countries were selected across a natural gradient of bulk atmospheric N deposition from 0.1 to 2 g/m² year⁻¹. Nutritional constraints were assessed based on nutrient ratios of N, phosphorus (P), and potassium (K) in *Sphagnum* plants collected in hummocks (i.e. relatively drier microhabitats) and in lawns (i.e. relatively wetter microhabitats).
- Nutrient ratios in *Sphagnum* plants increased steeply at low atmospheric N input, but above a threshold of N deposition of c. 1 g/m² year⁻¹ the N : P and N : K ratios tended to saturation. Increasing atmospheric N deposition was also accompanied by a reduced retention of Ca and Mg in *Sphagnum* plants and a decreased stem volumetric density in hummock *Sphagnum* plants.
- We suggest a critical load of N deposition in Europe of 1 g/m² year⁻¹ above which *Sphagnum* plants change from being N-limited to be K + P colimited, at N : P > 30 and N : K > 3.

Key words: critical load, ecological stoichiometry, global change, nitrogen (N), nutrient limitation, phosphorus (P), potassium (K), *Sphagnum*.

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Introduction

Nutrient availability is a fundamental factor in controlling plant structure and processes from the individual level up to the ecosystem and landscape level. It is generally assumed that nitrogen (N) and phosphorus (P) are the most important nutrients in the light of their growth-limiting role in natural and seminatural environments (Vitousek & Howarth, 1991). Nutrient limitation takes place when one or more nutrients are insufficiently available for the maximum growth of either

a single plant species or a plant community (Van Duren & Pegtel, 2000).

Ecological stoichiometry (i.e. nutrient ratios in plant tissues) provides a helpful, integrative approach for the analysis of nutrient balance at the species, community and ecosystem levels (Elser *et al.*, 1996). The use of plant tissue nutrient ratios is based on the assumption that plant tissue chemistry reflects the long-term nutrient and/or water availability in soil, thus integrating the fluxes of nutrients over the growing period of the plants (Koerselman & Meuleman, 1996; Willby

et al., 2001; Güsewell *et al.*, 2003), as well as through food webs (Elser *et al.*, 2000). Representing a quick and simple alternative to fertilization (Güsewell & Koerselman, 2002), nutrient ratios have been widely used to test nutrient limitation and nutrient imbalance for upland and wetland ecosystems (see Tessier & Raynal, 2003 for review).

In the light of the current concerns about human-caused global environmental changes, alteration of nutrient cycles can have dramatic implications for the stability of natural ecosystems (Bobbink *et al.*, 1998). It has been shown that human activities have significantly altered the N cycle to such an extent that anthropogenic N released into the biosphere is equal to the N naturally produced by terrestrial biological fixation (Vitousek *et al.*, 1997). Under such a scenario, global alteration of nutrient cycles has the potential to greatly unbalance natural plant communities in relation to the different ability of plant species to acquire nutritional resources (Sala *et al.*, 2000). This threat is particularly high for those ecosystems, such as ombrotrophic mires or bogs, whose nutrient balance depends totally on atmospheric deposition. In fact, ombrotrophic mires are peat-producing ecosystems geochemically characterized for being fed only by atmospheric deposition. High levels of acidity in pore-water, permanently anaerobic conditions of the peat substrate and very low nutrient amounts make ombrotrophic mires very harsh environments for plant growth, so that very few plant species can grow in them.

A genus of plants particularly well adapted to such environmental conditions is *Sphagnum*, whose species usually form the bulk of the dead and living biomass in ombrotrophic mires. Like all bryophytes, *Sphagnum* plants accumulate nutrients through direct influx of the atmospheric loadings into living cells. This makes these mosses extremely sensitive to, and reliable biomonitors of, the present and past atmospheric conditions (e.g. Shotyk *et al.*, 1998; Bragazza *et al.*, 2003). In ombrotrophic mires, the effects of increased N inputs have been studied through short-term fertilization experiments reporting an imbalance between N and P contents in *Sphagnum* plants living under low and high nutrient loadings (Aerts *et al.*, 1992). Unbalanced nutrient uptake in *Sphagnum* plants can result not only in a different competitive ability among *Sphagnum* species or between *Sphagnum* mosses and vascular plants (Twenhöven, 1992; Berendse *et al.*, 2001), but also in an alteration of mire geochemistry, which in turn affects litter quality and decomposition rates (Aerts *et al.*, 2001; Limpens & Berendse, 2003b).

The present paper aims at assessing if and to what extent nutrient balance in ombrotrophic *Sphagnum* plants is limited by different amounts of atmospheric N deposition in Europe in relation to: (a) the different role played by N, P and potassium (K) as growth limiting nutrients in *Sphagnum* plants; (b) the species-related responses to nutritional constraints between hummock and lawn *Sphagnum* plants. Data were field-collected under a natural gradient of atmospheric N deposition with the main advantage of detecting nutrient limitation under

relatively low, but chronic, additions of atmospheric N, thereby avoiding possible toxic effects of abrupt N inputs associated with short-term fertilization experiments. In addition, hummock and lawn *Sphagnum* plants have been analysed separately so to take into account the nutrient tissue variability in relation to different moisture conditions of hummock and lawn microhabitats.

Materials and Methods

Field sampling

Sampling was carried out during 2001–03 at 15 mires in 11 European countries (Fig. 1). At each mire three to six hummocks and, whenever possible, three to six lawns were selected in ombrotrophic sectors of the mire. The sampling was performed in areas with a dense cover of healthy *Sphagnum* plants and a very low, if any, cover of vascular plants. The hummocks had *Sphagnum fuscum* (Schimp.) Klinggr. and/or *S. capillifolium* (Ehrh.) Hedw. (both the species belong to section *Acutifolia*) as the dominant species in the moss layer. The lawns had *Sphagnum magellanicum* Brid. as the dominant species, with

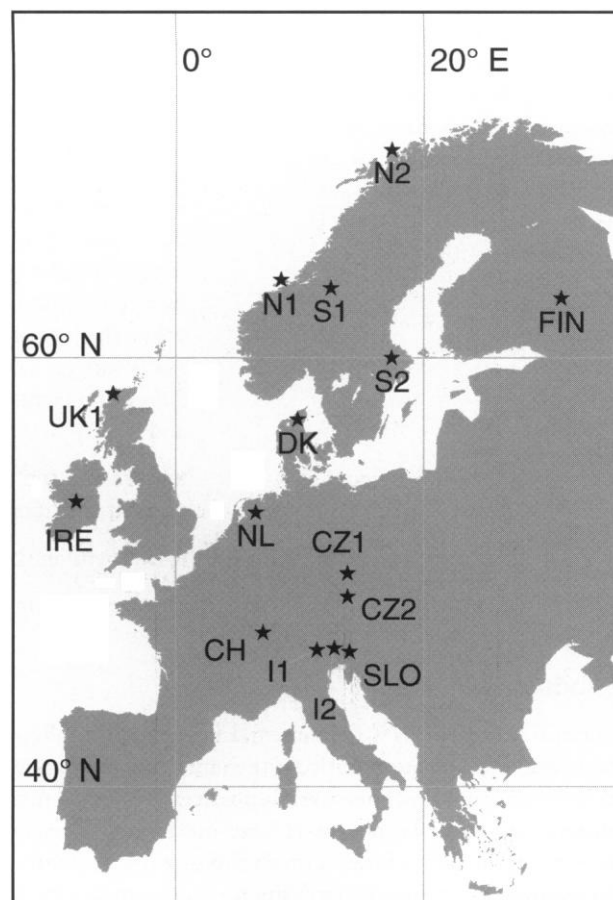


Fig. 1 Geographic location of the mires investigated, with identification codes as in Table 1.

Table 1 List of the mires investigated with identification codes, climatic data, average atmospheric depositions of nitrogen and potassium, and selected habitats

Mire, country and identification code	Annual precipitation (mm)	Mean annual temperature (°C)	N-deposition (g m ⁻² year ⁻¹)	K-deposition (g m ⁻² year ⁻¹)	Type (and number) of selected habitats
Malmmyran – Norway (N1)	1200	+7.0	0.17	0.10	Hummocks (4)
Djupvik – Norway (N2)	760	+3.0	0.08	0.07	Hummocks (3)
Salmisuo – Finland (FIN)	600	+2.0	0.20	0.03	Hummocks (3)
Klockamyran – Sweden (S1)	857	+1.1	0.14	0.07	Hummocks (3) Lawns (3)
Ryggmossen – Sweden (S2)	554	+5.6	0.38	0.10	Hummocks (3) Lawns (3)
Laxford Bridge – Great Britain (UK1)	1430	+8.0	0.22	0.18	Hummocks (3)
Ballinahocun – Ireland (IRE)	820	+10.0	0.22	0.21	Hummocks (3) Lawns (3)
Store Vildmose – Denmark (DK)	853	+8.3	0.68	0.20	Hummocks (3) Lawns (3)
Reigersplas – Netherlands (NL)	780	+8.6	2.0	0.09	Hummocks (3) Lawns (3)
Čihadla – Czech Republic (CZ1)	1476	+4.4	1.9	0.20	Hummocks (6) Lawns (3)
Mrtvý luh – Czech Republic (CZ2)	700	+5.1	0.49	0.10	Hummocks (6) Lawns (3)
Etang de la Gruere – Switzerland (CH)	1200	+6.5	0.58	0.03	Hummocks (3) Lawns (3)
Šijec – Slovenia (SLO)	1580	+3.0	1.11	0.33	Hummocks (3) Lawns (4)
Coltrondo – Italy (I1)	1227	+2.2	0.45	0.05	Hummocks (4) Lawns (4)
Wöfl Moor – Italy (I2)	808	+6.3	0.82	0.31	Hummocks (4)

Notes: Precipitation chemistry sources (and selected monitoring stations) were: NILU-Norsk Institutt for Luftforskning (Kårvatn and Karasjok); Finnish Meteorological Institute (Hietajärvi); IVL-Svenska Miljöinstitutet (Sandnässet and Ryda Kungsgård); NETCEN – AEA Technology Env. (Strathvaich Dam); Jordan (1997); Ellermann *et al.* (2002); Rijksinstituut voor Volksgezondheid en milieu (Eibergen and Valthermond); Český hydrometeorologický ústav (Jizerka and Spalenc); OFEFP/NABEL (Chaumont); Slovenian Forestry Institute (Pokljuka); Regione Veneto-ARPAV (Monte Chertz); Tait & Thaler (2000).

the only exception of one mire site (i.e. Čihadla) where the dominant species was *Sphagnum papillosum* Lindb. (both the species belong to section *Sphagnum*). In each of the sampling areas, a 10 × 10 cm plot was set up, from which all *Sphagnum* plants were picked up.

As seasonal variability of nutrient tissue content can alter the nutrient content in plants (Güsewell & Koerselman, 2002), *Sphagnum* plants were sampled at the end of the growing season, mostly between mid-September and mid-October.

Precipitation chemistry

Mean atmospheric depositions of N-NO₃⁻, N-NH₄⁺, K⁺, Ca²⁺, and Mg²⁺ were calculated based on data obtained, whenever possible, during the three years preceding the sampling, primarily from national organizations responsible for deposition monitoring (Table 1). Bulk deposition usually is sampled by means of funnels permanently open to the atmosphere, in order to collect wet deposition as well as part of dry deposition. Due to the complex physical and chemical processes involved in dry deposition (Sehmel, 1980), the contribution of dry deposition to total deposition is generally estimated by large-scale models taking into account ambient atmospheric concentrations of gaseous and aerosol components, and depositional velocity (Erisman *et al.*, 2001). Even if an average ratio of wet-only to bulk precipitation for selected ions has been obtained over Europe (Van Leeuwen *et al.*, 1996), and even if we are aware that in highly polluted areas dry deposition can account for a

great portion of total deposition in close vicinity to the emission source (Whelpdale *et al.*, 1997), we decided to use bulk depositional values for the following reasons: (1) the existence of an extensive network of bulk deposition monitoring stations in many European countries permitted us to select a monitoring station as close as possible to the study mires (in this study the mean distance was *c.* 40 km), so to obtain atmospheric depositional fluxes much more reliable than the fluxes estimated from large-scale models (Erisman *et al.*, 1998); (2) the bulk deposition measured with permanently open funnels can partly compensate for the amount of total dry deposition (Cape & Leith, 2002); (3) bulk deposition measurements are based on the same sampling method (i.e. open funnels) which makes large-scale comparisons practicable and reliable.

For monitoring stations where precipitation chemistry data referred only to wet deposition, we used the ratio reported by van Leeuwen *et al.* (1996) to obtain the bulk deposition value.

Chemical analyses

Concentrations of major nutrients were determined in the capitula, that is, the apical youngest tissues of the *Sphagnum* plants where N, P, and K are more concentrated (Malmer, 1988). Compared to nutrients, which are supposed to be more concentrated inside the cells, calcium (Ca) and magnesium (Mg) are mainly accumulated on the exchange sites of the moss and are therefore here defined as 'mineral elements' (Malmer, 1988).

After collection, all *Sphagnum* plants were cut into two parts: the apical portion (the capitulum) and the next 2-cm long portion (the stem). The weight of capitula (i.e. capitulum biomass) as well as the weight of stem portions at each sampling plot were determined after air drying.

Before performing chemical analyses, all *Sphagnum* capitula were ground in a titanium mill through a 0.2 mm screen to ensure homogeneity of the sample. Sub-samples of powdered material were oven-dried for 48 h at 70°C to convert air dry weight as well as element concentrations to standard oven dry conditions.

Total N concentration was determined with an elemental analyzer (EA 1110, Carlo Erba, Milan, Italy). Total P, K, Ca, and Mg were extracted by acid digestion using a microwave oven (Mars 5, CEM, Bergamo, Italy). K, Ca, and Mg were determined, on the extract, by atomic absorption spectrophotometry (Solaar 969, ThermoOptek, Rodano, Italy), whereas P was determined colorimetrically using a continuous-flow autoanalyser (FlowSys, Systea, Rome, Italy). Standard reference material (NIST Citrus leaves 1572, National Bureau of Standards, Washington, DC, USA) was analyzed along with *Sphagnum* samples to ensure accuracy within 5% of known N, P, K, Ca, and Mg concentrations.

Data analyses

The retention coefficient of Ca and Mg was calculated as the ratio between mineral element content in *Sphagnum* capitula per square meter and corresponding amount of atmospheric deposition.

Linear and non-linear regression was applied to explain the relationships between atmospheric deposition and *Sphagnum* tissue chemistry. The regression model with the best fit, that is, the highest r^2 , was then selected. All statistical analyses were performed using Statistica for Windows ver. 6.0 (StatSoft Italia, Padova, Italy).

Results

Atmospheric inputs over the study mires

The geographical location of the mires investigated is shown in Fig. 1, whereas data on climate and precipitation chemistry are summarized in Table 1. The gradient of atmospheric N input ranged from *c.* 0.1 g/m² year⁻¹ to 2 g/m² year⁻¹. Less N polluted sites were located in Fennoscandia, whereas the most N polluted sites were found in the Czech Republic and the Netherlands. Total K deposition ranged from 0.03 g/m² year⁻¹ to *c.* 0.3 g/m² year⁻¹ without any correlation with total N deposition ($r = 0.33$; $P = 0.23$; $n = 15$).

Nutrient content, nutrient ratios and mineral retention in relation to precipitation chemistry

In hummock and lawn *Sphagnum* plants the N : P ratio and the N : K ratio showed a much steeper increase across the N input

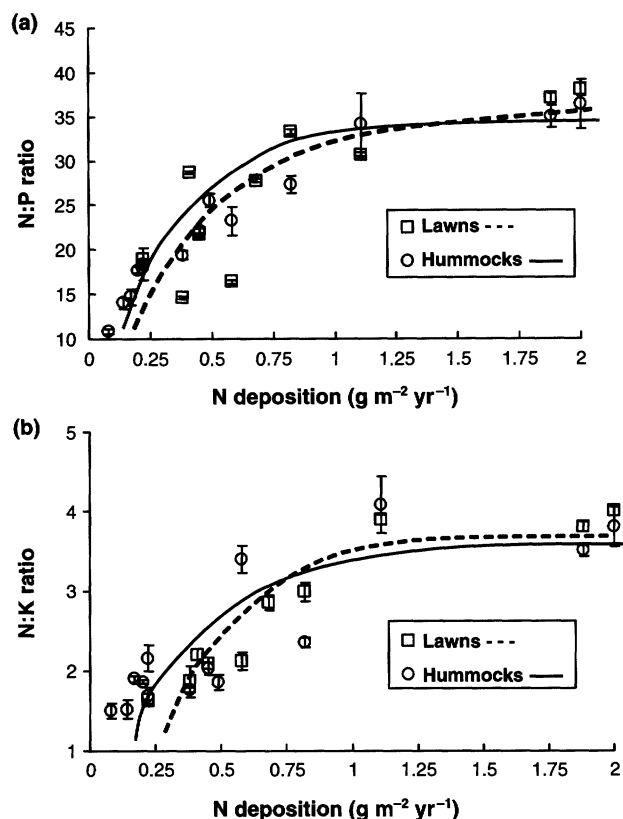


Fig. 2 Mean values (± 1 SE) of (a) N : P and (b) N : K ratios in hummock and lawn *Sphagnum* plants at each mire in relation to atmospheric N deposition. Dashed and continuous lines represent the theoretical patterns based on regression model (see text for details).

gradient at low atmospheric N input, whereas for atmospheric N input > 1 g/m² year⁻¹ the trend reached a saturation (Fig. 2). The trend of N : P ratio was better expressed by the equation $Y = 37.5(1 - e^{(-2X)})$ for lawn *Sphagnum* plants ($r^2 = 0.67$), and by $Y = 34.3(1 - e^{(-2.9X)})$ for hummock *Sphagnum* plants ($r^2 = 0.88$). The trend of N : K ratio was better expressed by the equation $Y = 4.9(1 - e^{(-1.2X)})$ for lawn *Sphagnum* plants ($r^2 = 0.92$), and by $Y = 3.5(1 - e^{(-2.8X)})$ for hummock *Sphagnum* plants ($r^2 = 0.56$).

Atmospheric K deposition was not significantly correlated with the K : N and K : P ratios either in hummock *Sphagnum* plants ($r = -0.37$, $P = 0.19$ and $r = 0.06$, $P = 0.84$, respectively), or in lawn *Sphagnum* plants ($r = -0.38$, $P = 0.20$ and $r = 0.05$, $P = 0.88$, respectively). Along the atmospheric K depositional gradient, the K : N ratio spanned a range between 0.2 and 0.7, whereas the K : P ratio ranged between 6 and 15 (data not shown).

N concentration, N : P ratio and N : K ratio in both hummock and lawn *Sphagnum* plants were all significantly lower under non-saturating conditions, that is, under N deposition < 1 g/m² year⁻¹ (Table 2). For *Sphagnum* plants forming hummocks, K concentration did not vary significantly in relation to atmospheric N supply, whereas in lawns K concentration was significantly higher in *Sphagnum* plants collected in

Table 2 Mean values (± 1 SE) and range of variation (in brackets) of nutrient tissue concentrations and nutrient ratios in hummock and lawn *Sphagnum* plants under non-saturating and saturating conditions expressed by a threshold of atmospheric N input of $1 \text{ g/m}^2 \text{ year}^{-1}$ as observed in Fig. 2

Mire code	Hummock <i>Sphagnum</i> plants		Lawn <i>Sphagnum</i> plants	
	N < $1 \text{ g/m}^2 \text{ year}^{-1}$ ($n = 11$) N1, N2, FIN, S1, S2, UK1, IRE, CZ2, CH, I1, I2	N > $1 \text{ g/m}^2 \text{ year}^{-1}$ ($n = 3$) NL, CZ1, SLO	N < $1 \text{ g/m}^2 \text{ year}^{-1}$ ($n = 7$) S2, UK1, DK, CZ2, CH, I1, I2	N > $1 \text{ g/m}^2 \text{ year}^{-1}$ ($n = 3$) NL, CZ1, SLO
N (mg g^{-1})	8.2 ± 0.4^a (5.6–10.0)	12.2 ± 1.0^b (9.5–13.6)	9.2 ± 0.7^a (5.3–10.8)	11.6 ± 0.6^b (10.0–12.5)
P (mg g^{-1})	0.41 ± 0.02^a (0.33–0.51)	0.36 ± 0.02^a (0.33–0.41)	0.44 ± 0.06^a (0.26–0.70)	0.35 ± 0.02^a (0.30–0.40)
K (mg g^{-1})	4.0 ± 0.2^a (3.0–5.2)	3.3 ± 0.4^a (2.6–4.0)	4.4 ± 0.3^a (3.0–5.1)	2.8 ± 0.2^b (2.5–3.3)
N: P	18.9 ± 1.4^a (10.6–26.6)	33.8 ± 1.5^b (31.0–36.3)	22.8 ± 2.9^a (14.5–34.0)	33.6 ± 3.7^b (26.5–39.2)
N: K	2.0 ± 0.1^a (1.4–3.3)	3.7 ± 0.2^b (3.4–4.0)	2.3 ± 0.2^a (1.5–3.0)	4.0 ± 0.4^b (3.0–4.7)

Different superscripts indicate significant differences ($P < 0.05$) within hummock and lawn *Sphagnum* plants based on *t*-test. (n , number of mires). Mire code follows Table 1.

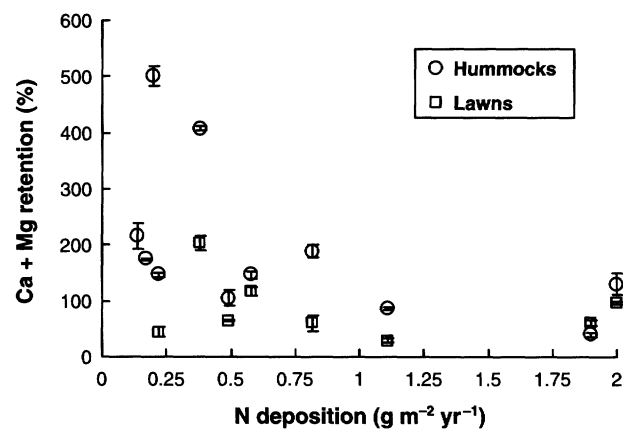


Fig. 3 Mean retention coefficients (± 1 SE) of Ca and Mg by *Sphagnum* capitula across the N depositional gradient in hummocks and lawns. Retention coefficients take into account atmospheric Ca and Mg input as well biomass of *Sphagnum* capitula at each mire (see text for details).

mires having N input < $1 \text{ g/m}^2 \text{ year}^{-1}$ (Table 2). Phosphorus concentration in *Sphagnum* plants was always higher, although not significantly, in mires subject to atmospheric N deposition < $1 \text{ g/m}^2 \text{ year}^{-1}$ (Table 2).

Retention of Ca + Mg in the *Sphagnum* capitula decreased exponentially for both hummock ($Y = 50 + e^{(5.8-1.6X)}$, $r^2 = 0.36$) and lawn ($Y = 99 + e^{(4.1-2.8X)}$, $r^2 = 0.30$) *Sphagnum* plants across the N depositional gradient (Fig. 3). Mineral retention coefficients were similar for hummock and lawn mosses at very high N inputs, but they were more than 2-times greater for hummock *Sphagnum* plants at low N inputs compared to lawn plants (Fig. 3).

Sphagnum biomass in relation to N deposition

Hummocks located in mires subjected to atmospheric N input < $1 \text{ g/m}^2 \text{ year}^{-1}$ showed significantly higher stem volumetric density compared to hummocks subjected to higher N deposition (Table 3). Partial correlation between N deposition and stem volumetric density was significant ($r = -0.72$, $P = 0.049$, $n = 8$) also when considering the effect of annual rainfall amount. Capitula biomass of hummock *Sphagnum* plants was higher at low N deposition, but not significantly so than that at higher N deposition. Lawns did not show any significant difference for capitula biomass and stem volumetric density in relation to the amount of atmospheric N deposition (Table 3).

Table 3 Mean (± 1 SE) capitulum biomass and stem volumetric density for hummock and lawn *Sphagnum* plants in mires subjected to N input, respectively, below and above the threshold of $1 \text{ g/m}^2 \text{ year}^{-1}$ as observed in Fig. 2

	Hummocks		Lawns	
	N input < $1 \text{ g/m}^2 \text{ year}^{-1}$ ($n = 5$)	N input > $1 \text{ g/m}^2 \text{ year}^{-1}$ ($n = 3$)	N input < $1 \text{ g/m}^2 \text{ year}^{-1}$ ($n = 4$)	N input > $1 \text{ g/m}^2 \text{ year}^{-1}$ ($n = 3$)
Capitulum biomass (g dm^{-2})	2.2 ± 0.4^a	1.1 ± 0.2^a	1.0 ± 0.2^a	1.5 ± 0.1^a
Stem volumetric density (g dm^{-3})	16.5 ± 2.0^a	8.8 ± 0.3^b	7.7 ± 0.6^a	8.7 ± 1.1^a

Different superscripts indicate significant differences ($P < 0.05$) within each microhabitat based on *t*-test (n is the number of mires).

Discussion

Atmospheric deposition chemistry and *Sphagnum* nutrient imbalance

The rates of change in nutrient ratios across the N depositional gradient reflect cumulative effects of atmospheric N enrichment on ombrotrophic mires, with the advantage of representing a natural, long-term field fertilization. The steep increase of N : P and N : K ratios in *Sphagnum* tissues under low atmospheric N inputs is related to the steady adsorption of N by *Sphagnum* plants as N supply increases (Baxter *et al.*, 1992; Rudolph *et al.*, 1993). Above a depositional threshold of *c.* 1 g N m⁻² year⁻¹ the N : P ratio and the N : K ratio in both hummock and lawn *Sphagnum* species increased very slowly with increasing N deposition as a consequence of N saturation (Lamers *et al.*, 2000; Berendse *et al.*, 2001). N saturation in *Sphagnum* tissues is accompanied by and can account for nutrient imbalance caused by reduced uptake of elements, other than N, under high levels of N deposition (Pearson & Stewart, 1993; Kooijman & Bakker, 1994; Geßler & Rennenberg, 1998). Indeed, the saturating trend in nutrient ratios across the N depositional gradient could be interpreted as a shift from N limited conditions to P and K colimited conditions. Similarly, field fertilization experiments showed as the response of bryophytes to N input is highly dependent on the availability of other nutrients, especially P (Heijmans *et al.*, 2001; Hoosbeek *et al.*, 2002; Limpens *et al.*, 2003a).

Relatively lower P concentration in *Sphagnum* plants under higher N deposition suggests that exogenous N does not stimulate phosphatase activity in *Sphagnum* plants or, at least, that any eventual stimulation of phosphatase activity does not keep pace with *Sphagnum* N absorption. Press and Lee (1983) did not observe any relationship between solute enrichment and phosphatase activity in *Sphagnum* mosses, whereas Williams and Silcock (2001) observed a habitat- and time-related variation in total dissolved P in N fertilization experiments.

Lower Ca and Mg retention can be explained as a means for alleviating the effects of excess inorganic ions associated with N deposition through the mobility of highly exchangeable ions, specifically Ca and Mg (Kooijman & Bakker, 1994; Soares & Pearson, 1997).

The constant trend of K : N and K : P ratios along the gradient of K deposition indicates that atmospheric K input did not affect the nutrient balance in *Sphagnum* plants. Although often disregarded in ombrotrophic mire fertilization experiments, K has been found to limit plant growth in fen meadows as much as P (Olde Venterink *et al.*, 2001). K colimitation has been found to be more frequent in drained fen meadows under high K output through hay cropping or leaching (Øien & Moen, 2001; Olde Venterink *et al.*, 2001). As all of the mires investigated in our survey are not subjected to drainage or hay cropping, K alone probably did not affect the nutritional status of *Sphagnum* plants, but it could

become a colimiting nutrient under excess N inputs enforced by microhabitat conditions favouring its leaching (Kooijman & Bakker, 1994).

Increasing amounts of N input have been demonstrated to alter *Sphagnum* growth (e.g. Gunnarsson & Rydin, 2000; Van der Heijden *et al.*, 2000; Heijmans *et al.*, 2001; Limpens *et al.*, 2003a). Our data showed that increasing amount of atmospheric N deposition appears responsible for causing a decrease of stem volumetric density in hummocks. In the long run, this may determine a loss of hummock firmness with negative effects on water capillary transport through the *Sphagnum* stems (Luken, 1985). Hence, hummocks appear more sensitive to increasing amounts of atmospheric N input in terms of structural stability (Jauhiainen *et al.*, 1998b; Gunnarsson & Rydin, 2000).

Nutritional thresholds and nutrient concentration in *Sphagnum* plants

Güsewell *et al.* (2003) recently showed that N : P ratios in vegetation are closely related to plant responses to N or P fertilization and to the actual nutrient availability in wetland habitats. On this basis, we could assess that P is limiting at N : P ratio > 30–32 and K is limiting at N : K ratio > 3.3–3.4 for both hummock and lawn *Sphagnum* species. The proposed thresholds are in accordance with the patterns reported in Fig. 2 showing N saturation above a N deposition threshold of *c.* 1 g/m² year⁻¹ due to nutrient limitation by P and K. The proposed N : P ratio of *c.* 30 as an index of P limitation is twice that proposed by Koerselman and Meuleman (1996). This difference is not surprising if we consider that the ratio proposed by Koerselman and Meuleman (1996) was obtained after bulking the whole above-ground biomass of vascular plants from different wetland communities.

The average N concentrations in *Sphagnum* tissues in the absence of N limitation were 12.2 mg/g for hummock species and 11.6 mg/g for lawn species (see Table 2), very close to the threshold of 12 mg/g suggested by Lamers *et al.* (2000) for N-saturated *Sphagnum* plants. Very high N concentrations can be toxic for *Sphagnum* plants (Baxter *et al.*, 1992; Nordin & Gunnarsson, 2000; Van der Heijden *et al.*, 2000), which has often been regarded as the main cause of *Sphagnum* decline in several highly polluted regions in Europe (e.g. Greven, 1992; Hogg *et al.*, 1995). Berendse *et al.* (2001) proposed a maximum N content in *Sphagnum* tissues of 20 mg/g, whereas Van der Heijden *et al.* (2000) suggested a tissue N concentration of 15 mg/g as an indication of N pollution stress in bogs.

A slight increase in N concentration for the Dutch and the Czech *Sphagnum* plants can still be expected if N deposition increases as suggested by N tissue concentrations observed in short-term fertilization experiments where the external N loading was well above the highest atmospheric N deposition observed in our survey (Jauhiainen *et al.*, 1998a; Williams *et al.*, 1999; Berendse *et al.*, 2001; Heijmans *et al.*, 2001; Limpens

et al., 2003a). In fact, under gradual increase of atmospheric N deposition *Sphagnum* plants are supposed to adapt to changing atmospheric chemistry through, for example, higher N tissue content, reduced N uptake, reduced nitrate reductase activity, and increased free amino acid concentration in tissue (Jauhiainen *et al.*, 1998a; Nordin & Gunnarsson, 2000; Limpens & Berendse, 2003c).

N critical load for ombrotrophic mires in Europe

The concept of 'critical load' has been used since the 1980s as an index of ecosystem susceptibility to N input (Jefferies & Maron, 1997). For ombrotrophic *Sphagnum* plants, we can define the 'critical load' as the amount of N bulk deposition above which *Sphagnum* plants experience nutrient imbalance to such an extent to greatly decrease the absorption of exogenous N. In this sense, N deposition levels above the critical load cause a N saturation of the *Sphagnum* layer, that is, the removal of N limitation associated with a decrease of N retention capacity. The atmospheric N input shifting ombrotrophic *Sphagnum* plants from being N limited to being P + K colimited is *c.* 1 g/m² year⁻¹, a critical load value consistent with the value suggested by other authors (Bobbink & Roelofs, 1995; Gunnarsson & Rydin, 2000).

The major ecological consequences expected for European ombrotrophic mires receiving an atmospheric N input above the critical load are: (1) increased availability of N to the rooting system of vascular plants with consequent shifts in the plant competitive equilibria (Berendse *et al.*, 2001; Bragazza *et al.*, 2003; Limpens *et al.*, 2003a); (b) higher potential decay rates of plant litter with effects on the carbon balance of peat ecosystems (Aerts *et al.*, 2001; Limpens & Berendse, 2003b).

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