Variations in nitrogen, phosphorus and $\delta^{15}\text{N}$ in *Sphagnum* mosses along a climatic and atmospheric deposition gradient in eastern Canada

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Complete List of Authors:	Zivkovic, Tatjana; McGill University, Geography Disney, Kristina; McGill University, Geography Moore, Tim; McGill University, Department of Geography and Global Environmental and Climate Change Centre
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Title: Variations in nitrogen, phosphorus and $\delta^{15}\text{N}$ in *Sphagnum* mosses along a climatic and atmospheric deposition gradient in eastern Canada

Authors: Tatjana Živković, Kristina Disney, and Tim R. Moore

Emails: tatjana.prsa@mail.mcgill.ca, kristina.disney@mail.mcgill.ca, tim.moore@mcgill.ca

Affiliation and address: Department of Geography and Global Environmental & Climate Change Centre, McGill University, 805 Sherbrooke Street West, Montreal, Quebec, Canada H3A 0B9

Corresponding author:

Tatjana Živković, McGill University, 805 Sherbrooke Street West, Montreal, Quebec, Canada H3A 0B9

Telephone number: 438-821-0802

Fax: (514) 398-7437

Email: tatjana.prsa@mail.mcgill.ca

Abstract

We examined concentrations of nitrogen (N) and phosphorus (P) and $\delta^{15}\text{N}$ value in *Sphagnum* sections Acutifolia and Cuspidata inhabiting hummocks and hollows from 8 bogs along a transect from ~ 45 to ~ 55 °N in Ontario/Quebec. The N concentration in *Sphagnum* declined from South to North, correlating with a decrease in atmospheric N deposition. Although the overall N concentration was larger in hollows than hummocks, the pattern was inconsistent across the sites. There was a proportionally larger decline in P concentration from South to North and an overall larger P concentration in hollows than hummocks, but there were inconsistent differences across the sites. The N:P ratio ranged from 12:1 to 29:1, driven primarily by the variation in P concentration. Ratios of N and P concentration in *Sphagnum* capitulum:stem averaged 1.2:1, suggesting nutrient resorption from stem to capitulum during growth; the ratio rose with increasing N and P concentration in the capitulum. The $\delta^{15}\text{N}$ value of *Sphagnum* rose from $\sim -6\text{‰}$ in the South to $\sim -1\text{‰}$ in the North, correlated with the decrease in *Sphagnum* N concentration and with a rise in water table. We interpret this to indicate a greater dependence on N_2 -fixation for N acquisition in the northern and wetter sites.

Key words: peatland, nitrogen (N) and phosphorus (P) deposition, N:P ratio, $\delta^{15}\text{N}$ value, *Sphagnum* capitulum and stem, bog.

Introduction

Sphagnum mosses control several important processes in the functioning of northern peatlands. Two of these processes are plant production and decomposition, which contribute to *Sphagnum* being a primary driver of peat accumulation (Rydin and Jeglum 2006). *Sphagnum* is also the location of microbially-driven biological di-nitrogen (N₂) fixation in peatlands (Larmola et al. 2014; Vile et al. 2014). Plant production and decomposition and N₂ fixation are dependent on the nutrient content of the moss tissues, in particular nitrogen (N) and phosphorus (P) (e.g. Vitousek and Field 1999; Bragazza et al. 2009). Human activities have increased the rates of atmospheric deposition of N and P (e.g. Holland et al. 1997; Tipping et al. 2014), so that peatlands, particularly ombrotrophic bogs, are subject to ‘eutrophication’, ultimately resulting in changes in rates of moss production, decomposition, and carbon (C) accumulation (Juutinen et al. 2010).

Atmospheric N deposition increases N content in *Sphagnum* mosses (Aerts et al. 1992; Bragazza et al. 2005; Granath et al. 2009; Jiroušek et al. 2011). Less is known about rates of atmospheric P deposition, which have a high degree of spatial variation (Tipping et al. 2014) and are thus more difficult to assess in terms of their impact on *Sphagnum* P concentration. Peatland ecosystems can be limited either by N, P, or by N-P co-limitation in combination with a third nutrient, potassium (Walbridge and Navaratnam 2006). Koerselman and Meuleman (1996) found that plants in peatland ecosystems are most likely limited by N if N:P < 14:1, by P if N:P > 16:1, and N and P co-limited if 14 < N:P < 16, though Güsewell (2004) notes the variable nature of this ratio in influencing plant production. *Sphagnum* mosses are able to translocate nutrients from the stem to the capitulum for photosynthetic activities (Aldous 2002a) and their exposure to chronically elevated N supply results in a decrease in the difference in N concentration between

stem and capitulum (Bragazza et al. 2004; Limpens et al. 2006; Limpens and Heijmans 2008). Many peatlands have a distinct microtopography resulting in ‘hummocks’ and ‘hollows’ with varying distances from the water table, and inhabited by different *Sphagnum* species as well as vascular plants. This microtopographic variability can also affect nutrient acquisition by mosses: *Sphagnum* in hollows may have a larger access to nutrients than hummocks due to their proximity to the water table (Jiroušek et al. 2011).

Analysis of the ^{15}N isotope in *Sphagnum* mosses may provide information on the source of N. N_2 fixation by cyanobacteria and other microbes involves a small change in $\delta^{15}\text{N}$ value, close to 0‰ (Kendall and Doctor 2004; Deane-Coe and Sparks 2015). Atmospheric deposition of NH_4^+ , created mainly by agricultural activities, has a negative $\delta^{15}\text{N}$ value, while N emitted from industrial activities (NO_x) has a more positive $\delta^{15}\text{N}$ value, though there is considerable variability (e.g. Pearson et al. 2000; Bragazza et al. 2005; Kendall and Doctor 2004; Skinner et al. 2006; Zechmeister et al. 2008; Novak et al. 2014). Peat in the surface layers has a negative $\delta^{15}\text{N}$ value, being derived from the decomposition of plants with a negative $\delta^{15}\text{N}$ value (Novak et al. 2014; Moore, unpublished data). Thus, N (NH_4^+ , NO_3^- or dissolved organic nitrogen) absorbed from mineralization of the peat will likely also decrease the $\delta^{15}\text{N}$ value in the *Sphagnum* tissue.

We sampled *Sphagnum* mosses from hummocks and hollows at eight sites along a latitudinal transect in Ontario and Quebec from ~45 to ~55 °N, with inferred variations in atmospheric deposition of N and P and climate (Table 1). We analyzed the samples to test the following hypotheses:

1. N and P concentration in *Sphagnum* will decrease with increasing latitude, associated with a decline in atmospheric deposition of these two elements along the climatic gradient. N and P

concentrations will be larger in hollows than hummocks, as the former are closer to the water table and have a greater access to nutrients mineralized by peat decomposition. The N:P ratio in *Sphagnum* will vary with latitude and microtopography, depending on the relative availability of the two elements.

2. As nutrient availability and concentration in bogs is limited, N and P concentrations in *Sphagnum* capitula will be larger than in stems, suggesting nutrient resorption during growth. Furthermore, the ratio between the capitulum and stem for both N and P will be negatively correlated with N or P concentration in the stem, suggesting the importance of translocation as a mechanism to supply nutrients needed for growth.
3. The $\delta^{15}\text{N}$ value of *Sphagnum* will reflect the origin of N and will be less negative with increasing latitude, suggesting a greater dependence of northern sites on N_2 fixation.

Material and methods

Site selection and sampling

Eight sites in Quebec and Ontario were sampled (Fig. 1, Table 1). At each site, two hollows and two hummocks were selected, based on the dominant *Sphagnum* species in each microtopographic feature, and moss samples were collected from a block 40 x 30 cm and 20 cm deep. The samples were transported to the laboratory and kept at 4°C until analyzed. As *Sphagnum* species varied across the sites along the gradient, we classified moss into sections. The hummocks comprised mosses from section Acutifolia (*Sphagnum fuscum* and *Sphagnum capillifolium*) and Palustria (*Sphagnum magellanicum*), while hollows were mainly dominated by Cuspidata (*Sphagnum angustifolium*, *Sphagnum fallax*) or Palustria (*S. magellanicum*). Palustria section was represented by *S. magellanicum* at only two sites, inhabiting two

hummocks (at LLT) and a hollow (at MB), and thus was not used for statistical analyses owing to a small sample size. We chose to plot *Palustria* in figures to keep the information available to the reader.

Upon the arrival at the site, we installed perforated PVC wells into each hummock and hollow and used the blow tube method to measure water table depth prior to extracting moss blocks. We collected pore water from the water wells and measured pH in the field with a calibrated pH meter (PC300 waterproof portable meter, Eutech/Oakton Instruments).

We summarized site-specific environmental, climatic and atmospheric N and P deposition data at each site along the gradient (Table 1). We used the model ensemble-mean with a resolution of 1 degree for total annual N deposition derived by the Task Force on Hemispheric Transport of Atmospheric Pollutants (HTAP 2010, www.htap.org) summarized by Vet et al. (2014, 2017). We estimated total annual N deposition based on the model estimates for the grid-cells covering each site location. P deposition data are estimated values based on models by Mahowald et al. (2008) and Tipping et al. (2014).

Chemical analyses

Five subsamples (diameter 7.2 cm) were extracted from hummocks and hollows and cut in 6 cm stem lengths, oven dried at 50°C, and then separated into capitulum (the top 1 to 2 cm) and stem (the lower 4 to 5 cm). The *Sphagnum* was finely ground through a 40 mesh sieve (Wiley Mini Mill 3383-L10, Thomas Scientific, USA), dried at 50°C for 24 h before acid digestion was performed following procedures from Parkinson and Allen (1975) using concentrated H₂SO₄ and H₂O₂ with Se and Li₂SO₄ as catalysts. Samples were then analyzed for

total N and P colorimetrically (Murphy and Riley 1962) on a LachatQuick-Chem AE flow injection autoanalyzer (Lachat Instruments, Milwaukee, WI).

Four additional moss subsamples (6 cm in length and 7.2 cm in diameter; comprised of both capitulum and stem) from two hummocks and two hollows at each site were oven dried at 50°C, finely ground and analyzed for total N content and $\delta^{15}\text{N}$ value on a continuous flow Isotope Ratio Mass Spectrometer (IRMS) (UC Davis Stable Isotope facility, USA). The analytical long-term standard deviation for $\delta^{15}\text{N}$ and N is 0.3‰ and 0.5%, respectively.

Statistical analysis

We averaged the capitula and stem N and P concentrations and N:P ratio for each *Sphagnum* plant. We used multiple regression method to best predict N and P concentration in *Sphagnum* mosses by considering representative climatic variables (MAT and MAP) and atmospheric deposition (N_{dep} or P_{dep} for N and P concentration, respectively) in two *Sphagnum* sections (Acutifolia from hummocks and Cuspidata from hollows). We log₁₀ transformed *Sphagnum* P content data to achieve the normality and all other assumptions for all multiple regression analyses were met.

Linear regressions were performed to evaluate the change in N and P concentrations and N:P ratio in *Sphagnum* mosses with the latitude. We used the Shapiro-Wilk's test for the normal distribution of N, P concentrations and N:P ratio in moss samples. N concentration data were normally distributed ($W = 0.99$, $p = 0.763$) and for P concentration and N:P ratio datasets, normality was achieved after log₁₀ transformation ($W = 0.99$, $p = 0.661$ and $W = 0.99$, $p = 0.650$, respectively). We used linear regression on transformed data, where appropriate. The assumption of homogeneity of variance for each of the variables used in the linear regressions

was tested and met using Levene's test. We used the Mann-Whitney U test to assess whether the N and P concentrations and N:P ratios were different between hummocks and hollows within each site.

We calculated the ratios between capitulum and stem of N concentration ($N_{\text{cap}}:N_{\text{stem}}$), P concentration ($P_{\text{cap}}:P_{\text{stem}}$) and N:P ratio $[(N:P)_{\text{cap}}:(N:P)_{\text{stem}}]$. The Kruskal-Wallis test was used on pooled data from hummocks and hollows to compare cap-stem ratios of N, P and N:P ratios among the sites. Because there were no significant differences between the sites, we used the Mann-Whitney U test to compare these ratios between hummocks and hollows within each site. Linear regressions were used to test whether stem nutrient concentrations were the main drivers of cap-stem ratios along the gradient. As above, $\log_{10}$ transformations were performed to achieve normal distributions of datasets where appropriate, and all assumptions needed for linear regression analyses were met.

We used linear regression to test the relationship between $\delta^{15}\text{N}$ in *Sphagnum* mosses and latitude, and to determine the effect of N concentration in *Sphagnum* tissue and water table depth on *Sphagnum* $\delta^{15}\text{N}$ in hummocks and hollows. All data were normally distributed and the assumption of homogeneity of variance of the variables for each of the linear regression was met.

All statistical analyses were performed using JMP (JMP v.11.2.0, SAS Institute Inc., Cary, NC, USA).

Results

Study sites were chosen along a climatic gradient spanning from the temperate (MB, MIR, LLT), to the boreal (DES, NEL, NOR) and the subarctic zones (VIC, SCH; Table 1). This climatic gradient is indicated by the decrease in mean annual temperature (MAT) and growing

degree days (GDD) from the South to the North (Table 1). Mean annual precipitation (MAP) generally decreased northwards while snowfall precipitation (SP) increased slightly. Both estimates of N and P deposition followed the decreasing trend towards the North (Table 1) most likely associated with the smaller human population and lesser anthropogenic disturbances compared to the southern sites. There is a strong correlation among these atmospheric variables along the transect (supplementary Table S1).

Water table depth was variable within and across sites, with hummocks and hollows being 31 to 49 cm and 7 to 25 cm above the water table, respectively; the average difference in elevation between hummocks and hollows was 24 cm (Table 1). Water table pH ranged from 3.7 to 4.1 in all but one site, Schefferville (pH 5.1). This was a poor fen, but samples were collected from the peatland margin where vegetation was more similar to bogs.

Sphagnum N and P concentration and N:P ratio

Along the latitudinal gradient where climatic variables (MAT and MAP) and atmospheric chemistry (N_{dep} or P_{dep}) were analysed to explain the variability of N or P nutrient in *Sphagnum* sections, the multiple regressions indicated strong multicollinearity between the variables. This was shown by Pearson's correlations (Supplementary Table S1) and variance inflation factor ($VIF > 10$) (Zuur et al. 2010; Supplementary Table S2). To test the importance of each of the strongly collinear variables, especially MAT and $N_{\text{dep}}/P_{\text{dep}}$, we performed two separate multiple regression analyses. The first excluded MAT, but included $N_{\text{dep}}/P_{\text{dep}}$ and MAP, and the second excluded $N_{\text{dep}}/P_{\text{dep}}$ but included MAT and MAP. Each of the analyses was performed on Acutifolia (hummocks) and Cuspidata (hollows) sections separately. We found that N_{dep} explained about 23% and MAT about 26% of the variance in N content in Acutifolia (Table 2a, b). Similarly, about 31 and 34% of N content in Cuspidata was explained by N_{dep} and MAT, respectively (Table 2a, b). MAP had no explanatory power in any of the regressions testing N content in *Sphagnum* (Table 2a, b). The best explanatory variables for P content in *Sphagnum* were P_{dep} and MAT, although only about 10-15% of variance was explained by either (Table 2c, d). MAP only had a small influence on P content in Acutifolia and none in Cuspidata (Table 2c, d).

The two most represented *Sphagnum* sections across sites (Acutifolia and Cuspidata, hummocks and hollow species, respectively) showed a significant decrease in N concentration with increasing latitude, from ~10 to 6.5 mg g⁻¹ between 45 and 55°N, though R^2 values were small (0.28 and 0.25, respectively; Fig. 2a). Overall, hummock samples had a significantly

smaller N concentration than hollow samples and within the sites, four (VIC, NEL, MIR and MB) had a significantly smaller N concentration in the hummocks than hollows (Table 3).

The P concentration in *Sphagnum* decreased with increasing latitude in both *Acutifolia* and *Cuspidata* (~ 0.6 to 0.2 mg g^{-1} from 45 to 55°N , Fig. 2b), proportionally larger than the decrease in N concentration. Overall, the hummock samples had a significantly ($p = 0.013$) smaller P concentration than the hollows (0.48 versus 0.53 mg g^{-1} ; Table 3). Three sites had a significantly smaller P concentration in hummocks than hollows and two other sites, the southernmost MIR and MB, showed a reverse pattern.

The N:P ratio was not significantly related to latitude in both *Sphagnum* sections (Fig. 2c). There was no significant difference in N:P ratio between hummock and hollow samples pooled across all the sites. Within sites, significant ($p < 0.05$) differences between hummock and hollow samples occurred at six of the eight sites: at three sites (SCH, NOR and NEL), hummocks had a higher N:P ratio than hollows and the pattern was reversed at VIC, MIR and MB (Table 3). Assuming that the N:P ratio reflects limitations of these two nutrients, in general the hollow *Sphagnum* species are more P limited (N:P ratio > 16), whereas in the hummocks there may be co-limitation of N and P, though the pattern varies across the sites. Concentration of P is more variable than that of N, so that the N:P ratio is driven more by P than N (Fig. 3a and b).

Sphagnum N and P concentration and N:P ratio in capitulum and stem

Separation of the *Sphagnum* samples into capitulum (top 1 to 2 cm) and stem (4-5cm in length) revealed cap:stem ratios ≥ 1 for N and P. $N_{\text{cap:stem}}$ ratios ranged from 1.0 to 1.5 with hummocks having significantly larger ratios than hollows in the northern sites (Mann-Whitney U test, $p < 0.05$ for DES, NEL, NOR and VIC; Fig 4a). $P_{\text{cap:stem}}$ ratios ranged from 1.1 to 1.9 and

showed no significant differences among sites or between hummock and hollow (Fig. 4b).

$N:P_{\text{cap:stem}}$ ratios ranged from 0.8 to 1.32 and were significantly larger in hummocks than hummocks at MB, NOR and VIC (Mann-Whitney U test, $p < 0.05$; Fig. 4c). The $N_{\text{cap:stem}}$, $P_{\text{cap:stem}}$ and $N:P_{\text{cap:stem}}$ ratios were negatively correlated with the N and P concentrations and N:P ratio in the stem, respectively (Fig. 5a, b and c).

Sphagnum $\delta^{15}\text{N}$ value

Subsampling of the *Sphagnum* (combined capitulum and stem) showed a significant increase in the $\delta^{15}\text{N}$ value with latitude in both hummocks and hollows (Fig. 6a). Overall, the $\delta^{15}\text{N}$ value at 45°N was -5.9 and -4.9 ‰ for hummocks and hollows, respectively, and this increased to -2.5 and -0.9 ‰ at 55°N. There were no significant differences in $\delta^{15}\text{N}$ between hummock and hollow at the sites. There was a weak but significant relationship between the $\delta^{15}\text{N}$ value and N concentration, with $\delta^{15}\text{N}$ becoming more negative (from -2 to -5 ‰) with an increase in N concentration from 5 to 10 mg g⁻¹, but the overall relationship was mostly driven by hummock species (Fig. 6b). The $\delta^{15}\text{N}$ value increased with a rise in water table depth, increasing from about -5 ‰ at 50 cm to about -3 ‰ at 10 cm beneath the surface (Fig. 6c). This relationship was mainly driven by a significant increase of the $\delta^{15}\text{N}$ value in hollow species as a response to a lower water table (Fig. 6c).

Discussion

The results of multiple regressions indicate that both MAT and atmospheric deposition chemistry could equally explain the *Sphagnum* nutrient content of N and P along our transect. Mean annual precipitation did not play a role in any of the cases, except in explaining P content

in Cuspidata section (Table 2). Due to strong collinear relationships between the latitude, climatic variables and atmospheric chemistry (see Supplementary Table S1), it is difficult to determine which of the factors plays the strongest role.

We show a significant trend of decreasing N concentration along the latitudinal gradient from South to North in both *Sphagnum* sections, with no differences between the Acutifolia and Cuspidata (Fig. 2a). Mosses from Cuspidata section dominate wetter hollows, and Acutifolia as well as Palustria are often found on drier hummocks or in the transitional zones between hummocks and hollows. Studies focusing on similar gradients (Lamers et al. 2000; Bragazza et al. 2005; Zechmeister et al. 2008; Jiroušek et al. 2011) indicate that *Sphagnum* species can be used as good proxies for atmospheric deposition and their nutrient content is less driven by the climate.

Collation of data on N concentration in hummock *Sphagnum* from a wide range of temperate and boreal sites under natural and fertilized conditions (Bragazza et al. 2005; Jiroušek et al. 2011; Moore, unpublished data) shows a strong correlation between moss N content and atmospheric wet N deposition, represented by equation:

$$\text{N concentration (\%)} = 0.327 \ln N_{\text{dep}} + 1.103, R^2 = 0.75, n = 134 \quad (1)$$

The wet atmospheric deposition rates ranged from 0.2 to 0.6 g N m⁻² yr⁻¹ along the gradient of our sites (Turunen et al. 2004; Vet et al. 2014, 2017), and applying the equation above, the predicted *Sphagnum* N concentration is between 0.6 and 0.9%, similar to the range we observed (0.55 to 1.00%, Table 3). The southernmost bogs (MB, MIR and LLT, Fig. 1) are located near major cities (Ottawa and Montreal), highways and airport (Mirabel) and have been exposed to larger, anthropogenically-derived N loads from the atmosphere, compared to more pristine bogs in northern latitudes (HBL and SCH) (Turunen et al. 2004).

Given that our *Sphagnum* N concentrations fit well within the models by Bragazza et al. (2005) and our own, as shown above, we believe that *Sphagnum* nutrient content follows a declining trend from the South to the North along this transect as a result of decreasing nutrient loads from the atmosphere.

Phosphorus concentration follows a similar trend, decreasing along the latitudinal gradient in both *Acutifolia* and *Cuspidata* *Sphagnum* sections (Fig. 2b). Most of the P in peatlands likely entered these ecosystems during their early formation as a result of bedrock weathering processes (Walbridge and Navaratnam 2006). The small atmospheric P deposition and lack of additional P inputs in ombrotrophic bogs results in P recycling and high C:P ratios in the peat profile (Wang et al. 2014) as well as P becoming a limiting nutrient (Toberman et al. 2015). Atmospheric deposition of P is rarely measured, although human activities have been known to increase local P inputs (Tipping et al. 2014) and modelling suggests a decline northwards in Canada (Mahowald et al. 2008). Our results suggest the existence of a latitudinal P gradient, likely due to increased anthropogenic activities in the South and hence larger amounts of P in the moss tissue. The 67% decrease in P concentration (from 0.6 to 0.2 mg g⁻¹) was twice as large as the 35% decrease in N concentration. Walbridge and Navaratnam (2006) report similar ranges for both P (0.25-1.5 mg g⁻¹) and N (5-10 mg g⁻¹) in *Sphagnum spp.* from bogs across North America and Europe.

We found large variations in P concentration between hummocks and hollows (Table 3), but the patterns are inconsistent: in the South, hummocks > hollows (MB and MIR), hollows > hummocks (DES, NEL and SCH), and there was no difference in VIC, LLT and NOR. Our analyses excluded species differences across sites as an explanatory variable for these trends, but our interpretation is that recycled P from the decomposition may be more available in the

hollows than hummocks due to the proximity of the water table and the form of P that is available to microbes and *Sphagnum*, though the direct mechanisms remain unclear. The activity of phosphatases (enzymes that release P bound to organic matter and make it available to microbes and plants) measured across different *Sphagnum* species has been shown to play an important role in P-limited conditions (Press and Lee 1982) and phosphatase activities could explain some of the observed trends.

Phosphorus is lost at a faster rate than either C and N during peat decomposition resulting in larger C:P and N:P ratios with depth in profiles (Wang et al. 2014). The larger concentration of P in moss capitulum than in the stem by 1.1 to 2.6 times (Fig. 4b) may suggest P transport from the stem into the capitulum in all *Sphagnum* sections along the gradient and the importance of P recycling in these peatlands. We observed a larger N:P ratio in Acutifolia than Cuspidata sections, a trend also described by Jiroušek et al. (2011). Assuming that the N:P ratio reflects limitations of these two nutrients, in general the hollow *Sphagnum* species were more P limited (N:P ratio > 16), whereas in the hummocks there may be co-limitation of N and P, though the pattern varied across the sites.

While strong retention and re-translocation of N from the moss stem to the capitulum has been found to play an important role in bogs (Aldous 2002a, 2002b), under large N loading N is leached downward to the moss stem (Lamers et al. 2000; Novak et al. 2014). Our study shows a similar relationship between capitulum and stem N concentration to that found at the low end of the atmospheric N deposition gradient in Europe (Bragazza et al. 2005). The ratio of N concentration in capitulum to stem in *Sphagnum* was negatively correlated with stem N concentration which suggests that N inputs from the atmosphere are inversely linked with N relocation from the stem to capitulum to maintain *Sphagnum* growth and functioning (Limpens

and Heijmans 2008). The significant differences in the ratio of N concentration in capitulum to stem between hummocks and hollows in more northern sites could be due to hollows in pristine environments having larger N_2 fixation rates than hummocks (Stewart et al. 2011; Leppänen et al. 2015). The proximity of the water table could physically facilitate the transfer of N from either N_2 fixation or decomposition, decreasing the difference between N concentration in capitulum and stem in hollows. Hummocks, on the other hand, may depend more on the translocation and retention of N in capitula to support the growth and photosynthetic activity (Aldous 2002a, 2002b) increasing the $N_{\text{cap:stem}}$ ratio. The atmospheric N deposition in our bogs never reached the high values found in parts of Europe (Bragazza et al. 2005).

The N:P ratio has been used as an indicator of N-, P- or NP co-limitation of plant productivity in peatlands (Koerselman and Meuleman 1996), though the critical value may vary (Bragazza et al. 2004; Walbridge and Navaratnam 2006). *Sphagnum* from five of the eight bogs in our study had a N:P ratio > 16 , ranged between 14 and 16 in two bogs and one bog (NOR) had $N:P < 14$, when hummocks and hollows were pooled (Table 3). This suggests a general P limitation and P is known to control biomass growth and functioning of microbial activities in peatlands, such as N_2 fixation (Fritz et al. 2012; Larmola et al. 2014; Toberman et al. 2015).

The *Sphagnum* $\delta^{15}N$ value can be driven by environmental controls such as water table depth (Asada et al. 2005) and increased N deposition along an altitudinal gradient in Europe (Zechmeister et al. 2008). In our data, latitude explained more variation in *Sphagnum* $\delta^{15}N$ than the water table (Fig. 6a and 6c). A trend of decreasing $\delta^{15}N$ value with N concentration in *Sphagnum* tissue in hummocks (Fig. 6b) supports a similar trend found in European *Sphagnum* sampled along the gradient of increasing atmospheric N deposition (Bragazza et al. 2005). The

$\delta^{15}\text{N}$ value of the top 5 cm of photosynthetically active *Sphagnum* significantly increased from $\sim -6\text{‰}$ in the South to $\sim -1\text{‰}$ in the North (Fig. 6a).

Sphagnum receives N from either wet or dry deposition, as $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$ or dissolved organic nitrogen, biological N_2 fixation or re-translocation of N from decomposing litter. The $\delta^{15}\text{N}$ value may be used as an indicator of the primary source of N to vegetation although reports show a large variability in N fractionation during biologically-mediated processes (*e.g.* denitrification, nitrification and litter decomposition; Nadelhoffer et al. 1996). When the primary source of N is $\text{NH}_4\text{-N}$, it generally leads toward more negative $\delta^{15}\text{N}$ values. More positive $\delta^{15}\text{N}$ values are attributed to NO_3 as a source of N, while biological N_2 fixation keeps $\delta^{15}\text{N}$ values near 0‰. Assuming that there is no fractionation of N to organic N, NH_4 or NO_3 , N from litter and peat decomposition in bogs would have a $\delta^{15}\text{N}$ value between -4 and -8‰ (Moore, unpublished data). The low *Sphagnum* $\delta^{15}\text{N}$ values in the southernmost bogs (MIR and MB, -6 and -5.4 ‰, respectively) may indicate the combination of two sources, atmospheric $\text{NO}_3\text{-N}$ deposition associated with locations near cities and translocation of N from decomposition. Bogs in the mid-latitudes (DES, NEL, NOR) with $\delta^{15}\text{N}$ values of -4.3, -4.2 and -3.9‰, respectively) may reflect more equal contributions of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$, N_2 fixation and recycling of mineralized N, in regions where wet N deposition does not exceed $0.5 \text{ g N m}^{-2} \text{ y}^{-1}$ and at the northernmost site (SCH) the $\delta^{15}\text{N}$ value of $\sim -1\text{‰}$ may suggest domination by N_2 fixation. The addition of N downregulates N_2 fixation in boreal forests stands in similar moss- N_2 fixing bacteria associations (DeLuca et al. 2008; Ackermann et al. 2012). Although we suggest that these $\delta^{15}\text{N}$ patterns may indicate differences in the source of N acquired by *Sphagnum* mosses, further studies in which different sources of N are systematically added to *Sphagnum* mosses may better explain changes in $\delta^{15}\text{N}$ value.

This study strengthens previously established evidence that N concentration in *Sphagnum* tissues can be used as an indicator of increased background N inputs, especially areas where N deposition data are scarce. Our findings suggest that declining P content in *Sphagnum* mosses may also be a good indicator of decreasing P inputs along the gradient. Most bogs along the South-North gradient seem to be P-limited and *Sphagnum* actively recycles P by re-translocation from the stem to the capitulum. N:P ratios are mostly driven by P content and they are highly variable across sites and microtopography. The $\delta^{15}\text{N}$ value increased from South to North, suggesting different sources of N: peat decomposition and atmospheric NO_3 deposition in the South and N_2 fixation in the North.

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Table 1. Site location (and abbreviation), latitude and longitude, mean annual temperature (MAT, and in parentheses growing degree days above 5° C; GDD), mean annual precipitation (MAP) and in parentheses growing season precipitation (GSP) and snowfall precipitation (in *italics*, *SP*) 1981-2000, pore water pH, estimated total atmospheric N and P deposition, and hummock and hollow water table depth beneath surface at time of sampling (with SD in the parentheses), *Sphagnum* section dominating hummocks and hollows.

^a estimated from Vet et al. 2014, 2017 ^b estimated from modeled P values from Mahowald *et al.* (2008) and Tipping *et al.* (2014).

Site	Latitude (N)	Longitude (W)	MAT	MAP	pH	N dep ^a (g m ⁻² y ⁻¹)	P dep ^b (g m ⁻² y ⁻¹)	Water table depth (cm)		<i>Sphagnum</i> sections	
			(GDD) (°C)	(GSP, <i>SP</i>) (mm)				Hummock	Hollow	Hummock	Hollow
Schefferville (SCH)	54°48'23"	66°48'07"	-3.1 (817)	840 (397, 337)	5.1	0.13	0.01	43 (9)	7 (4)	Acutifolia	Cuspidata
Victor (VIC)	52°41'47"	83°56'55"	-0.5 (1192)	704 (396, 201)	4.1	0.19	0.01	33 (3)	17 (2)	Acutifolia	Cuspidata
Norembega (NOR)	48°58'55"	80°42'32"	1.8 (1456)	835 (408, 276)	3.9	0.37	0.02	31 (7)	16 (2)	Acutifolia	Cuspidata
Nellie (NEL)	48°46'13"	80°49'23"	1.8 (1456)	835 (408, 276)	3.9	0.46	0.02	44 (5)	15 (2)	Acutifolia	Cuspidata
Despinassy (DES)	48°45'50"	77°21'33"	1.5 (1423)	929 (499, 253)	3.7	0.47	0.02	49 (11)	25 (3)	Acutifolia	Cuspidata
Lac à la Tortue (LLT)	46°31'59"	72°40'00"	5.2 (1927)	1123 (620, 259)	3.8	0.92	0.04	36 (4)	18 (0)	Palustria	Cuspidata
Mirabel (MIR)	45°41'05"	74°02'50"	5.3 (1931)	1068 (654, 232)	3.7	1.06	0.04	46 (4)	22 (0)	Acutifolia	Acutifolia
Mer Bleue (MB)	45°24'32"	75°31'03"	6.6 (2182)	920 (597, 164)	3.7	1.06	0.04	40 (1)	14 (3)	Acutifolia	Palustria

Table 2. The results of multiple regression models predictors for N content a) excluding MAT, b) excluding N_{dep} and for P content in *Sphagnum* along the gradient c) excluding MAT and d) excluding P_{dep}.

a)				
Variable	Coefficient	St Error	t ratio	Prob < t
Acutifolia ($R^2_{adj} = 0.23, p < 0.0001, n = 80$)				
Intercept	5.93	1.64	3.62	0.0005
N _{dep}	1.61	0.61	2.63	0.0104
MAP	0.00	0.00	0.4	0.6913
Cuspidata ($R^2_{adj} = 0.31, p < 0.0001, n = 60$)				
Intercept	10.53	1.95	5.39	<.0001
N _{dep}	5.30	1.34	3.96	0.0002
MAP	-0.01	0.00	-1.88	0.0654
b)				
Variable	Coefficient	St Error	t ratio	Prob < t
Acutifolia ($R^2_{adj} = 0.26, p < 0.0001, n = 80$)				
Intercept	5.54	1.42	3.91	0.0002
MAT	0.19	0.06	3.11	0.0026
MAP	0.00	0.00	1.13	0.2607
Cuspidata ($R^2_{adj} = 0.34, p < 0.0001, n = 60$)				
Intercept	7.95	1.57	5.05	<.0001
MAT	0.32	0.09	3.48	0.001
MAP	0.00	0.00	-0.06	0.9551
c)				
Variable	Coefficient	St Error	t ratio	Prob < t
Acutifolia ($R^2_{adj} = 0.10, p < 0.0001, n = 80$)				
Intercept	-0.06	0.17	-0.34	0.737
P _{dep}	7.16	2.20	3.26	0.0017
MAP	0.00	0.00	-2.3	0.0242
Cuspidata ($R^2_{adj} = 0.09, p < 0.0001, n = 60$)				
Intercept	-0.35	0.04	-9.25	<.0001
P _{dep}	4.38	1.72	2.55	0.0133
d)				
Variable	Coefficient	St Error	t ratio	Prob < t
Acutifolia ($R^2_{adj} = 0.14, p < 0.0001, n = 80$)				
Intercept	-0.09	0.15	-0.64	0.52
MAT	-0.02	0.07	3.78	0.0003
MAP	-0.00	0.00	-2.06	0.0424
Cuspidata ($R^2_{adj} = 0.08, p < 0.0001, n = 60$)				
Intercept	-0.28	0.02	-15.26	<.0001
MAT	0.02	0.01	2.59	0.0122

Table 3. Mean (and $\pm$ standard error) of N and P concentrations and N:P ratio by site and overall. Significant differences among hummocks (Hu) and hollows (Ho) (Mann-Whitney U test, $p < 0.05$, $n = 10$) by site and overall are indicated in bold.

Site	N concentration (mg g ⁻¹)			P concentration (mg g ⁻¹)			N:P ratio		
	Hu	Ho	p value	Hu	Ho	p value	Hu	Ho	p value
SCH	7.23 (0.33)	7.20 (0.24)	0.447	0.36 (0.039)	0.53 (0.024)	0.015	21.6 (1.31)	13.4 (0.49)	0.004
VIC	5.50 (0.31)	7.86 (0.50)	0.007	0.38 (0.018)	0.34 (0.023)	0.212	20.4 (1.13)	23.7 (0.89)	0.049
NOR	8.89 (0.43)	7.97 (0.25)	0.048	0.63 (0.060)	0.73 (0.075)	0.361	14.9 (0.98)	12.1 (0.69)	0.030
NEL	7.96 (0.30)	8.87 (0.21)	0.031	0.50 (0.022)	0.73 (0.037)	< 0.001	16.1 (0.58)	12.5 (0.51)	< 0.001
DES	6.69 (0.37)	7.69 (0.34)	0.140	0.45 (0.042)	0.55 (0.026)	0.049	15.7 (0.58)	14.2 (0.64)	0.187
LLT	9.99 (0.38)	9.78 (0.37)	0.734	0.58 (0.046)	0.56 (0.032)	0.791	18.7 (1.11)	18.0 (0.65)	0.850
MIR	7.60 (0.31)	9.25 (0.40)	0.001	0.41 (0.025)	0.34 (0.023)	0.049	19.4 (1.04)	29.1 (1.71)	< 0.001
MB	8.10 (0.25)	9.19 (0.36)	0.036	0.59 (0.030)	0.48 (0.031)	0.013	14.0 (0.49)	20.2 (0.92)	< 0.001
Overall	7.75 (0.15)	8.47 (0.14)	<0.001	0.48 (0.016)	0.53 (0.017)	0.013	18.0 (0.38)	17.7 (0.55)	0.521

Figures

Fig. 1. Location of study sites. Source of information: © 2003. Government of Canada with permission from Natural Resources Canada. Data can be downloaded here:

<http://geogratis.gc.ca/api/en/nrcan-rncan/ess-sst/b754e4f9-3cdc-439e-9b4a-9aecd057a244.html>

Fig. 2. Relationships between (a) N concentration (b) P concentration and (c) N:P ratio presented as means and latitude in three *Sphagnum* sections (Acutifolia, Cuspidata and Palustris); error bars are standard errors of the mean.

Fig. 3. Relationships between *Sphagnum* N:P ratio and (a) N concentration and (b) P concentration in *Sphagnum* sections.

Fig. 4. Mean capitulum:stem ratio for *Sphagnum* (a) N concentration, (b) P concentration and (c) N:P ratio across sites for hummocks and hollows; error bars are standard error of the mean, the asterisk shows significant differences between hummocks and hollows at each site.

Fig. 5. Relationship between (a) $N_{\text{cap:stem}}$ ratio and N_{stem} concentration, (b) $P_{\text{cap:stem}}$ ratio and P_{stem} , and (c) $N:P_{\text{cap:stem}}$ ratio and $N:P_{\text{stem}}$.

Fig. 6. Relationships between *Sphagnum* $\delta^{15}\text{N}$ value and (a) latitude for moss section, (b) N concentration and (c) water table depth.