Carbon, Nitrogen, Phosphorus, and Potassium Stoichiometry in an Ombrotrophic Peatland Reflects Plant Functional Type

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ABSTRACT

Ombrotrophic bog peatlands are nutrient-deficient systems and important carbon (C) sinks yet the stoichiometry of nitrogen (N), phosphorus (P) and potassium (K), essential for plant growth and decomposition, has rarely been studied. We investigated the seasonal variation in C, N, P, and K concentrations and their stoichiometric ratios in photosynthetically active tissues of 14 species belonging to five plant functional types (PFTs) (mosses, deciduous trees/shrubs, evergreen shrubs, graminoids, and forb) at Mer Bleue bog, an ombrotrophic peatland in eastern Ontario, Canada. Although we observed variations in stoichiometry among PFTs at peak growing season, there was convergence of C:N:P:K to an average mass ratio of 445:14:1:9, indicating N and P co-limitation. Nitrogen, P, and K concentrations and stoichiometric ratios showed little seasonal variation in mosses, evergreens, and graminoids, but in forb and deciduous species were the largest in spring and decreased throughout the growing season. Variations in nutrient concentrations and stoichiometric ratios among PFTs were greater than seasonal variation within PFTs. Plants exhibit N and P co-limitation and adapt to extremely low nutrient availability by maintaining small nutrient concentrations in photosynthetically active tissues, especially for evergreen shrubs and Sphagnum mosses. Despite strong seasonal variations in nutrient availabilities, few species show strong seasonal variation in nutrient concentrations, suggesting a strong stoichiometric homeostasis at Mer Bleue bog.

Key words: bog; deciduous; evergreen; forb; graminoid; Mer Bleue; nutrient limitation; Sphagnum moss; seasonality.

INTRODUCTION

Ecological stoichiometry deals with the elemental balance in ecological interactions and processes, providing an integrative nutrient framework linking biogeochemical patterns at a global scale to physiological constraints that operate at cellular or organismal levels (Sterner and Elser 2002). Compared to aquatic ecosystems, the application of the principles of ecological stoichiometry in terrestrial...
ecosystems is less developed. For example, the nitrogen to phosphorus (N:P) ratios in vegetation are considered reliable indicators of nutrient limitation, with the mass N:P ratio less than 14 or greater than 16 indicating N or P limitation, respectively, and between 14 and 16 indicating N and P co-limitation (Koerselman and Meuleman 1996; Güsewell and Koerselman 2002). Although this approach is often criticized (for example, von Oheimb and others 2010), it has been successfully applied to bryophytes (Aerts and others 1992; Bragazza and others 2004; Jiroušek and others 2011) and vascular plants (Güsewell and Koerselman 2002; Olde Venterink and others 2003). Potassium (K) limitation is rarely studied but could also occur in peatlands, especially after N and carbon dioxide enrichments (Hoosbeek and others 2002).

Most stoichiometric studies in mid- and high-latitude northern regions have been conducted in fen meadows, heathlands, boreal forests, and tundra. Little attention has been given to ombrotrophic peatlands such as bogs, which are nutrient-deficient systems with slow rates of plant production and litter and soil organic matter decomposition (for example, Moore and others 2008) resulting in important C sinks, storing approximately 547 Gt C (Yu and others 2010) and covering about 1 million km$^2$ in Canada (Tarnocai 2006). The resorption of nutrients from senesced leaves and subsequent translocation to newly grown tissues (Killingbeck 1986) is important to reduce the dependence on external nutrient availability (Aerts 1996; Aerts and Chapin 2000). The resorption of nutrients is essential in supporting spring growth in deciduous species and forbs (Chapin and others 1980), which are expected to show strong seasonal variations in nutrient concentrations and stoichiometry, whereas evergreen species can retain leaf nutrients and resorption can occur gradually over the growing season (Chapin and others 1980). Although Sphagnum mosses are able to resorb nutrients (Aldous 2002), these evergreen-like non-vascular species may show little seasonal variation in stoichiometry. The seasonal variation in organic matter mineralization and nutrient release may contribute to the seasonal variation in plant stoichiometry.

Nitrogen limitation is often prevalent in bogs under low atmospheric N deposition (Aerts and others 1992; Gunnarsson and Rydin 2000). Increased N availability from atmospheric deposition and accelerated organic matter decomposition may shift nutrient limitation types and stimulate plant growth in the short term (Aerts and others 1992; Verhoeven and others 1996; Bragazza and others 2004) and alter community composition and ecosystem nutrient cycling in the long term (Aerts and Berendse 1988; Bobbink and others 1998; Berendse and others 2001; Bubier and others 2007).

In this study, we examined the seasonal variation in nutrient concentrations and their stoichiometric ratios in photosynthetically active tissues (that is, leaves of vascular plants and capitula of Sphagnum mosses) in 14 species belonging to five plant functional types (PFTs) (moss, deciduous tree/shrub, evergreen shrub, graminoid, and forb) at Mer Bleue bog, an ombrotrophic peatland in eastern Ontario, Canada. Atmospheric N deposition at Mer Bleue is about 0.8 g N m$^{-2}$ y$^{-1}$ (Turunen and others 2004), close to the critical value of 1 g N m$^{-2}$ y$^{-1}$, above which Sphagnum mosses in Europe shifted from N limitation to co-limitation by P or K (Gunnarsson and Rydin 2000; Bragazza and others 2004). We hypothesized that plant growth at Mer Bleue bog is co-limited by N and P or K, as indicated by the N:P:K ratios in photosynthetically active tissue at the peak growing season. In addition, we hypothesized that deciduous species, forbs, and graminoids would show stronger seasonal variation in their nutrient concentrations and stoichiometric ratios than evergreen species and Sphagnum mosses.

**Materials and Methods**

**Study Sites and Species Description**

This study was conducted at Mer Bleue peatland located 10 km east of Ottawa, eastern Ontario, Canada (45.40°N, 75.50°W). Mean annual temperature is 6.0°C with monthly averages of −10.8°C in January and 20.9°C in July (Bubier and others 2007). Mean annual precipitation is 943 mm (76% as rainfall), 350 mm of which falls from May to August (Canadian Climate Normals 1981–2010). The atmospheric wet inorganic N deposition in this site was about 0.8 g N m$^{-2}$ y$^{-1}$ (Turunen and others 2004) and the total wet P deposition in eastern Canada is estimated to range from 6 to 26 mg P m$^{-2}$ y$^{-1}$ (R. Vet, personal communications).

The central portion of the peatland is an ombrotrophic bog with hummock and hollow micro-topography and a beaver pond. There are deciduous trees—birch (Betula populifolia Marshall) and tamarack (Larix laricina (Du Roi) K. Koch.). On the bog hummock, the dominant shrubs are evergreens Chamaedaphne calyculata (L.) Moench, Rhododendron groenlandicum (Oeder) K.A. Kron and W.S. Judd (formerly Ledum groenlandicum Oeder)
and Kalmia angustifolia L., with the deciduous Vaccinium myrtillusoides Michx. Sphagnum capillifolium (Ehrh.) Hedw. occurs in hummocks and hollows contain S. magellanicum Brid., S. fallax (Klinggr.) Klinggr. and S. angustifolium (C.E.O. Jensen ex Russow) C.E.O. Jensen, with sedge (Eriophorum vaginatum L.) and forb (Maianthemum trifolium (L.) Sloboda). Typha latifolia L. and S. cuspidatum Ehrh. ex Hoffm. occur in the beaver pond, with S. fallax at the edge of the beaver pond. The classification of PFTs and species scientific names was based on the United State Department of Agriculture (USDA) plant database (http://plants.usda.gov/) with the exception of T. latifolia, which was classified as a graminoid rather than a forb (for example, Koncalova 1990; Kercher and Zedler 2004; Verne- scu and others 2005). Fine-scale vegetation distribution and biomass at Mer Bleue were investigated by Bubier and others (2007) whereas Moore and others (2002) estimated net primary productivity.

**Vegetation Sampling and Chemical Analyses**

Samples of 14 species were collected with five replicates (1 × 1 m plots) for each species and 70 plots in total. The plots for T. latifolia and S. cuspidatum were located in the open water of the beaver ponds with the plots of S. fallax at the edge of the beaver pond. All the other 55 plots were located in the central portion of the bog. For each species, the five plots were randomly chosen and separated as far as possible to cover a large spatial extent. All the plots were chosen to include a monoculture of each species if possible. Fully expanded and sun-exposed current year’s leaves (exclusive of petioles) of the shrubs (C. calyculata, R. groenlandicum, K. angustifolia, and V. myrtillusoides), forb (M. trifolium) and tree species (B. populifolia and L. liricina), the leaf blades of graminoids (E. vaginatum and T. latifolia) and the capitula of Sphagnum mosses (S. capillifolium, S. angustifolium, S. magellanicum, S. fallax and S. cuspidatum) were sampled on July 6 and September 27 of 2010, May 18, June 17, July 18, August 18, September 16 and October 30 of 2011. A subset of samples were collected and covered by aluminum foil immediately after defoliation to determine chlorophyll concentration after being stored at −20°C until analyzed. The rest of the tissues were oven-dried at 60°C to a constant weight and ground (Wiley Mini Mill 3383-L10, Thomas Scientific, USA) to fine powder (60-mesh sieve). Carbon and N concentration was determined by dry combustion on an elemental analyzer (Leco CNS 2000, Leco Corporation, St. Joseph, Michigan, USA). Total P was determined colorimetrically by the ammonium molybdate–ascorbic acid method (Murphy and Riley 1962) on a Lachat Quik-Chem AE flow-injection auto-analyzer (Lachat Instruments, Milwaukie, Wisconsin, USA), after digested in concentrated sulphuric acid and hydrogen peroxide with selenium and lithium sulfate as catalysts (Parkinson and Allen 1975). Digested samples were filtered through 0.45 μm glass fiber filters (MN 85/90, MACHEREY-NAGEL GmbH & Co. KG, Germany) before analysis. Total iron (Fe) and K concentration was measured on an atomic absorption spectrophotometer (PerkinElmer model 2380, PerkinElmer Inc., USA). The chlorophyll concentration was extracted by the dimethyl sulphoxide (DMSO) (Hiscox and Israelstam 1979) with the absorbance being measured by a visible spectrophotometer (GENESYS™ 10 Scanning UV/Visible, Thermo Electron Corporation, USA) under two different wavelengths 645 and 663 nm, respectively. The total chlorophyll concentration (g L−1) is calculated according to the equation from Arnon (1949):

\[
\text{Total chlorophyll concentration} = 0.0202 \times A_{645} + 0.00802 \times A_{663},
\]

where \(A_{645}\) and \(A_{663}\) are the absorbance under the wavelength of 645 and 643 nm, respectively. Total chlorophyll concentration is reported as mg g−1 dry mass.

**Statistics**

Shapiro–Wilk and Levene’s tests were used to examine the normality of data and the homogeneity of variance, respectively. All data were logarithmically transformed before statistical analyses but the raw (untransformed) data were reported in the figures. As there was no significant difference in nutrient concentrations and stoichiometric ratios in July and September between 2010 and 2011 (t test, \(P > 0.05\)), we considered 2011 a typical year (Online Appendix 1) and do not show data from 2010. The variation among PFTs and seasonal variation in nutrient concentrations and stoichiometric ratios were examined by a coefficient of variation (CV) derived from log10-transformed data (Güsewell and Koerselman 2002):

\[
\text{CV}_{\log_{10}-\text{normal}} = \frac{1/2(10^{\bar{x} + \text{SD}}) - 10^{\bar{x} - \text{SD}})}{10^\bar{x} - 10^{-\text{SD}}} = \frac{10^{\text{SD}} - 10^{-\text{SD}}}{2},
\]
where \( \bar{X} \) and SD are the mean and standard deviation of log_{10}-transformed data. Compared to the usual calculation of CV, this approach has the advantage that \( \bar{X} \) and SD are derived from normally distributed data and hence the CV follows a normal distribution (Güsewell and Koerselman 2002).

Standard deviations were calculated in different ways to quantify the variation among PFTs and the seasonal variations in nutrient concentrations and stoichiometric ratios. For “among functional type means” (Table 1), nutrient concentrations and stoichiometric ratios from all sampling months were first averaged for each PFT (moss, evergreen, deciduous, graminoid, and forb) and SD was then calculated with the means of each PFT. For “among sampling month means,” SD was calculated for each PFT separately. For example, for “mosses,” the nutrient concentrations and stoichiometric ratios of all mosses were averaged within one sampling month, and SD was calculated with the means of individual sampling month. For “across all functional types and months,” SD was calculated with all individual PFTs from all sampling months.

The overall variation among different species in nutrient concentrations and stoichiometric ratios was examined by principal component analysis (PCA), using the means from all sampling months for each species. Linear mixed model with repeated measures was conducted to examine the seasonal variation in nutrient concentrations and stoichiometric ratios among PFTs in 2011. Compound symmetry covariance structure was adopted to minimize Schwarz’s Bayesian Criterion (BIC). If the interaction between PFTs and sampling month (PFT \( \times \) M) was significant \((P < 0.05)\), multiple comparisons were conducted to discriminate the difference among PFTs within each sampling month and among different sampling months for each PFT with Bonferroni adjustment. As there was only one species in forb \((M. \text{trifolia})\) and only one of the graminoids \((E. \text{vaginatum})\) grew in May, forb in all months and graminoids in May were excluded from all statistical analyses and only means are shown for visual comparison.

PCA was conducted using PC-ORD for Windows (Version 5.0, MJM Software, Glenden Beach, Oregon, USA) and all other analyses were conducted in IBM SPSS Statistics Version 20.0 for Windows (IBM Corp., Armonk, New York, USA).

**RESULTS**

**Principal Component Analysis**

The 14 plant species were separated by their nutrient concentrations and stoichiometric ratios and converged in PFTs (Figure 1). The first and second principal axes explained 51 and 36% of the total variation among species, respectively. The first axis separated the graminoids, forb, and \( S. \text{cuspidatum} \) (pond moss) from the other species, reflecting larger N, P, K, and chlorophyll concentrations and smaller C:N, C:P, and N:P ratios. The second axis separated mosses and forb from the other PFTs, reflecting smaller C concentrations and N:K ratios and larger Fe concentrations and K:P ratios (that is, poorer in structural C and richer in K and Fe).

**Stoichiometric Ratios at Peak Growing Season and Over the Full Season**

The N:P:K stoichiometric ratios at peak growing season (July) converged to the boundary of N and P co-limitation (Figure 2A). Forbs and mosses were richer in K than other PFTs. No substantial

**Table 1.** Coefficients of Variation (%) for Carbon (C), Nitrogen (N), Phosphorus (P), Potassium (K), Iron (Fe), and Chlorophyll (Chl) Concentrations and C:N, C:P, N:P, N:K, and K:P Ratios

<table>
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<tr>
<th>Coefficients of variation (%)</th>
<th>C</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Fe</th>
<th>Chl</th>
<th>C:N</th>
<th>C:P</th>
<th>N:P</th>
<th>N:K</th>
<th>K:P</th>
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<th>SE</th>
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<td>13.6</td>
<td>17.5</td>
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<td>52.7</td>
<td>20.4</td>
<td>44.3</td>
<td>42.9</td>
<td>45.7</td>
<td>6.1</td>
</tr>
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Different letters indicate significant difference in mean CV of all nutrient concentrations and stoichiometric ratios among PFTs at \( P = 0.05 \). See “Materials and Methods” section for details of calculations.

*The CV for forb is calculated from M. trifolia only.*
Variation was observed among species within the same PFT, except for *S. cuspidatum*, which was in the N-limited section (Figure 2A) owing to smaller N:P ratios than other *Sphagnum* mosses (Online Appendix 2). The average mass ratios of C:N:P:K in moss, evergreen, deciduous, graminoid, and forb at peak growing season were 612:13:1:11, 708:16:1:8, 640:16:1:7, 292:14:1:8, and 303:14:1:12, respectively, giving an overall average of 445:14:1:9.

The N:P:K stoichiometric ratios also converged to the boundary of N and P co-limitation throughout the growing season for mosses, evergreens, and graminoids (Figure 2B). For forb and deciduous species, the N:P:K stoichiometric ratios in May deviated from other months, showing a richer P than other PFTs.

**Seasonal Variations in Nutrient Concentrations and Stoichiometric Ratios**

The interactions between PFTs and sampling months were significant in all nutrient concentrations and stoichiometric ratios (*P* < 0.05; Figures 3, 4). Mosses, evergreens, and graminoids showed little seasonal variation. In contrast, deciduous species showed significant seasonal variation in all nutrient concentrations and stoichiometric ratios (*P* < 0.01) except for N:K (*P* = 0.710) and K:P ratios (*P* = 0.061). Specifically, N, P, and K concentrations were the largest in May and decreased throughout the growing season to the smallest in October (*P* < 0.001; Figure 3A–C). The C:N and C:P ratios were the smallest in May, increased to the largest in October (*P* < 0.001; Figure 4A, B) and the smallest N:P ratios occurred in May (*P* < 0.001; Figure 4C). A similar trend was observed for forb (Figures 3, 4). There was little seasonal variation in Fe concentration (Figure 3D). Chlorophyll concentration was the largest in May for forb and significantly smaller in October for deciduous species (*P* < 0.001; Figure 3E).

As the seasonal variation was mainly related to varied nutrient concentrations and stoichiometric ratios in May for forb and in May and October for deciduous species (Figures 2B, 3, 4), we excluded these sampling months from the calculation of CV resulting in a substantially reduced seasonal variation. Specifically, the seasonal variation was significantly reduced by approximately 20% when May was excluded for forb (CV = 16.7 ± 2.1%, mean ± 1 SE; *t* test, *P* = 0.019) and by ~80% when May and October were excluded for deciduous species from the calculation of CV (CV = 10.6 ± 1.7%; *P* = 0.010), in which there was no seasonal variation from June to September (*P* > 0.05; Figures 3, 4).

**Variation Among PFTs**

There were more substantial differences among PFTs in nutrient concentrations and stoichiometric ratios than seasonal variation (Table 1; Figures 3, 4). Graminoids and forb showed a trend of larger N and P concentrations and smaller C:N and C:P ratios than mosses, evergreen, and deciduous species, except for May and October, when deciduous species showed the largest N and P concentrations and smallest C:N and C:P ratios in May (*P* < 0.001), and the smallest N and P concentrations and the largest C:N and C:P ratios in October (*P* < 0.05; Figures 3A, B, 4A, B). There was no significant difference among PFTs in chlorophyll concentration (*P* > 0.5; Figure 3E) and N:P ratios except in May when the N:P ratio was significantly larger in mosses and evergreen species than in deciduous species (*P* < 0.05; Figure 4C). In general, mosses showed the largest Fe concentration across all PFTs (*P* < 0.05; Figure 3D), and smaller N:K ratio (Figure 4D) and larger K:P ratios (Figure 4E) than evergreen and deciduous species.
The variation in nutrient concentrations and stoichiometric ratios among PFTs (that is, “among functional type means”) was generally larger than among species within each PFT (Online Appendix 3). The variation among PFTs was also significantly larger than the seasonal variation (that is, “among sampling month means, all functional types”) (t test, \( P = 0.002 \); Table 1). The overall variation (that is, “across all functional types and months”) in N concentration was smaller than in P and K concentrations; Fe and chlorophyll concentrations varied the most. The ratios of N:P, N:K, and K:P varied less than did N, P, and K concentration. The variation in C:N and C:P ratios was comparable to that in N and P concentration, respectively, with C concentration varying the least. On average, mosses and evergreen species showed significantly lower seasonal variation than deciduous species (\( P < 0.05 \); Table 1).

**DISCUSSION**

**N and P Co-limitation**

Foliar stoichiometric ratios can suggest nutrient limitation, especially N, P, and K, in wetlands (Koerselman and Meuleman 1996; Güsewell and Koerselman 2002; Hoosbeek and others 2002; Olde Venterink and others 2003; Güsewell 2004). Güsewell (2004) suggested re-setting the critical value of N and P limitation to be N:P less than 10 and greater than 20, respectively, instead of N:P less than 14 and greater than 16 suggested by Koerselman and Meuleman (1996). Our N:P ratios suggest a consistent pattern of N and P co-limitation at Mer Bleue bog based on the critical ratio suggested by Güsewell (2004) (Figure 2), supporting P limitation or N and P co-limitation in temperate North American wetlands (Bedford and others 1999). Nitrogen and P co-limitation is supported by the long-term fertilization experiment at Mer Bleue bog: the addition with only N or P+K did not significantly change species abundance of *C. calyculata* and *R. groenlandicum* after a decade compared to the control, whereas their abundance was increased by approximately 50% when N, P, and K were applied together (Larmola and others 2013). Under lower atmospheric N deposition than their European equivalents, Canadian bogs are either N limited (Malmer and others 1992; Thor mann and Bayley 1997) or co-limited by N and P (Pakarinen and Gorham 1983; Malmer and others 1992), based on the foliar stoichiometry of the dominant species.

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**Figure 2.** Ternary diagram showing the stoichiometric relationship of nitrogen (N), phosphorus (P), and potassium (K) in moss, graminoids, deciduous, forb, and evergreen species at peak growing season (A) and over the full season (B). Each symbol represents one species within each PFT in A and the average of all species for each PFT in B. Dashed lines indicate the critical ratios of N:P (14.5), N:K (2.1), and K:P (3.4) (Olde Venterink and others 2003). These lines divide the plot into four parts, and three of them indicate N-limitation (N section), P or P, N-co-limitation (P or P+N section), and K or K, N-co-limitation (K or K+N section), respectively. For the central triangle section, the stoichiometric ratio cannot be used to determine the type of nutrient limitation or this is non-NPK limitation. For visual reasons, the P concentration is multiplied by a factor of 10.
With foliar N:K ratio below 2.1 and K:P ratio above 3.4 (Olde Venterink and others 2003) at peak growing season, none of the PFTs showed K limitation at Mer Bleue bog. However, under elevated CO$_2$ and/or N deposition, K could primarily limit the potential growth of bog vegetation (Hoosbeek and others 2002) and the depletion of K could result under acidic conditions (Rydin and Jeglum 2006).

Although most ecosystems in the northern hemisphere are N limited (Walker and Syers 1976; LeBauer and Treseder 2008), ombrotrophic
peatlands are weakly connected to the underlying mineral soil, impeding the upward replenishment of mineral nutrients and P may occur as occluded P or organic P, leaving it less available to plants and microbes (Rydin and Jeglum 2006; Walbridge and Navarathnam 2006). A in situ soil mineralization study at Mer Bleue bog revealed that 4.9 ± 0.7 and 0.4 ± 0.02% of the total soil N and P was available, as potassium chloride extractable ammonium and nitrate, and Mehlich III extractable orthophosphate, respectively (M. Wang, personal observations). Nitrogen was mineralized but P was either immobilized by soil microorganisms or occluded by soil organic matter after 3 months’ incubation and strong P immobilization by soil microorganisms has been reported in fen and pocosin peatlands Figure 4. The seasonal course of carbon: nitrogen (C:N), C:phosphorus (P), N:P, N:potassium(K), and K:P ratios (means ± 1 SE) in moss, evergreen, deciduous, graminoids, and forb. Linear mixed model with repeated measures analyzing the difference among functional type (PFT), sampling months (M), and the interaction (PFT × M) in stoichiometric ratios is shown. NS, P < 0.05; *, 0.01 ≤ P < 0.05; **, 0.001 ≤ P < 0.01; ***, P < 0.001. Standard error is not calculated for graminoid in May and forb, as they contain only one species, respectively. **Different upper case letters indicate significant difference between sampling months for each PFT. Different lower case letters indicate significant difference among PFTs for each sampling month. **M. Wang and T. R. Moore
Well-Constrained C:N:P:K Stoichiometry

Although the C:nutrients, N:K and K:P ratios at peak growing season may vary (up to threefold among PFTs), the N:P ratio varies within a narrow range, and on average, the mass C:N:P:K ratio (445:14:1:9) is convergent at Mer Bleue bog. This ratio is similar to the global average of C:N:P = 469:13:1 in forest foliage (McGroddy and others 2004), 427:17:1 in Canadian forest litter with 20% original C remaining (Moore and others 2011), the average of global terrestrial plants of 375:13:1 (Elser and others 2000) and 384:13:1 in subarctic flora (Aerts and others 2012). This convergence in stoichiometry, especially N:P ratio, in our ombrotrophic bog may have a cause: Loladze and Elser (2011) suggested that the Redfield mass ratio of N:P = 7:1 was not a coincidence but rather a consequence of the conservative balance between protein and ribosome RNA (rRNA) synthesis in prokaryotic and eukaryotic microbes with intrinsic cell N:P ratio around 7:1 under optimal growth conditions. Although the N:P ratio of 14:1 in photosynthetically active tissues at peak growing season at Mer Bleue bog slightly declined to 12:1 after senescence (Wang and others 2014), the plastic allocation of plant biomass to organs with distinct stoichiometry may shift the ratios, preventing an ubiquitous optimum stoichiometric ratio.

A similar convergence in C:N:P stoichiometry has been observed in soil microbial biomass in the top 30 cm peat at Mer Bleue bog (mass ratio 31:3:1) (Basiliko 2004), supporting the convergence of C:N:P stoichiometry in both total soil pools (72:6:1) and soil microbial biomass (23:3:1) globally (Cleveland and Liptzin 2007). The C:N, C:P, and N:P ratios are substantially smaller in soil microbes than in plant tissues, the imbalance between which governs the overall nutrient cycling and C sequestration (Sterner and Elser 2002; Hessen and others 2004). In ombrotrophic bogs, the imbalance between the C:N:P stoichiometry in soil microbes and C-rich plant litters may immobilize N and P by soil microorganisms, while mineralizing C until critical C: nutrients ratios are reached, for examples litter mass C:N ratio between 33 and 68 and C:P ratio between 800 and 1200 in Canadian forest litter (Moore and others 2011). The larger N:P ratios in plant tissues than in soil microbes indicate the mineralization of organic matter in bogs is primarily limited by P, as supported by the immobilization of P in our in situ mineralization study discussed above.

Overall at Mer Bleue bog, N concentration varied less than P and K concentrations, consistent with the results from broad reviews of wetland plants (Bedford and others 1999; Guéswell and Koerselman 2002; Olde Venterink and others 2003). Guéswell and Koerselman (2002) attributed these more variable P and K plant concentrations to a larger variation in P and K availability in soil. Our results suggest that the overall variation in nutrient concentration and stoichiometry is mainly driven by PFTs coexisting in similar habitats. This implies either little variation in soil nutrient availability or weak relationships between soil nutrient availability and nutrient concentration in plants, which is strong homeostasis (Sterner and Elser 2002). The variation in P concentration among PFTs was consistently larger than in N, probably because of the inherently tighter physiological regulation on N than on P (Aerts and Chapin 2000). The smaller variation of stoichiometric ratios than nutrient concentrations for N, P, and K may be explained by the fact that the stoichiometric ratios are not affected by C-rich structural materials. The variation in C:N and C:P ratios was largely caused by the variation in N and P concentrations, shown by the negative correlations ($r = -0.973$ and $-0.984$, $P < 0.001$, respectively).

Seasonal Variation Among PFTs

A more pronounced seasonal variation of nutrient concentration and stoichiometry was found in deciduous species than in evergreen species and mosses, whereas graminoids and forb showed intermediate variation (Table 1). We did not observe significant differences in N:P ratio among PFTs, in contrast to graminoids having a larger N:P ratio than forbs (Guéswell 2004), and herbaceous plants having a smaller N:P ratio than woody plants (Kerkhoff and Enquist 2006). Although statistically insignificant, N, P, and K concentrations in graminoids and forb tended to decrease, and therefore C:N and C:P ratios increased, over the growing season, as noted in sedges by Konings and others (1992) and Thomann and Bayley (1997). Mosses, deciduous, or evergreen species showed little seasonal variation in nutrient concentrations and
stoichiometry over the major part of the season (June–September). Ion-exchange resin membranes (PRSTM, Western Ag Innovations of Saskatchewan, Canada) captured the seasonal variation in available N (ammonium and nitrate), P (orthophosphate), and K in peat soil at Mer Bleue bog in May, July, and September: N availability was doubled and tripled, and K availability was increased by 40 and 80% in July and September compared to May, whereas no change in P availability was observed (Online Appendix 4). This supports our earlier argument of strong homeostasis in bog plants, especially evergreens and mosses, which can keep their tissue stoichiometry stable, despite the changes in the chemical composition of the environment (Sterner and Elser 2002). The uniformly small concentrations of Fe in all PFTs except for mosses are within the range of Fe deficiency (0.05–0.15 mg g$^{-1}$) (Marschner 1995). The larger Fe concentrations indicate either their greater physiological need or Fe is just left behind as Fe-rich water which is drawn up from the water table and is evaporated, leaving Fe in the mosses.

The substantial seasonal variation in nutrient concentration in deciduous species at the beginning (May) and the end (October) of the growing season is attributed to nutrient translocation and resorption, respectively, as is suggested in tundra (Chapin and others 1980). Deciduous species translocate a substantial amount of N, P, and K into new leaves in the beginning of the growing season and then resorb a large portion of them at the end of the growing season. Evergreen species translocate these nutrients into new leaves gradually throughout the growing season, especially in the second year’s leaves, resulting in a relatively stable nutrient concentration and stoichiometry (Chapin and others 1980). We observed a 10–50% decrease in N, P, and K concentration in the second year’s leaves of $C.\ calyculata$ and $R.\ groenlandicum$ during senescence, compared to mature leaves (Wang and others 2014), supporting the relationship between seasonal variation and nutrient resorption. The lack of seasonal variation in evergreen species and resorption-induced seasonality in deciduous species has been widely reported in arctic and subarctic tundra (Chapin and others 1980; Arndal and others 2009).

Implications for Bogs

Bogs, covering 760,000 km$^2$ in Canada, are important C sinks with low productivity and slow rates of litter and peat decomposition. Located in a region of relatively high atmospheric N deposition in Canada (~0.8 g N m$^{-2}$ y$^{-1}$), Mer Bleue bog shows N and P co-limitation. The absence of significant external P inputs and historically elevated atmospheric N deposition may trigger a further shift to P-limitation of Canadian bogs, as demonstrated in Europe, and a restraint on organic matter mineralization which is primarily P-limited. By adapting to extremely low nutrient availability, bog plants at Mer Bleue maintain small nutrient concentrations in photosynthetically active tissues, especially in evergreen species and $Sphagnum$ mosses. Unlike deciduous species, the dominant evergreen shrubs and $Sphagnum$ mosses at Mer Bleue do not show a strong seasonal variation in plant stoichiometry, despite seasonal variations in nutrient availability, indicating a strong ecological homeostasis.

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