GEOGRAPHIC VARIATION IN NUTRIENT AVAILABILITY, STOICHIOMETRY, AND METAL CONCENTRATIONS OF PLANTS AND PORE-WATER IN OMBROTROPHIC BOGS IN NEW ENGLAND, USA

Nicholas J. Gotelli[1], Paula J. Mouser[2], Stephen P. Hudman[1,6], Sergio E. Morales[3], Donald S. Ross[4], and Aaron M. Ellison[5,7]

[1]*Department of Biology, University of Vermont*
Burlington, Vermont, USA 05405

[2]*Department of Civil and Environmental Engineering, University of Vermont*
Burlington, Vermont, USA 05405

[3]*Department of Microbiology and Molecular Genetics, University of Vermont*
Burlington, Vermont, USA 05405

[4]*Department of Plant and Soil Science, University of Vermont*
Burlington, Vermont, USA 05405

[5]*Harvard Forest, Harvard University*
324 North Main Street
Petersham, Massachusetts, USA 01366

[6]*Present address:*
University of Kansas, Department of Ecology and Evolutionary Biology
1200 Sunnyside Avenue
Lawrence, Kansas, USA 66045

[7]*Correspondence author e-mail: aellison@fas.harvard.edu*

Abstract: Geographic trends in surface water chemistry and leaf tissue nutrients may reflect gradients of nutrient limitation and broad-scale anthropogenic inputs. In 24 rain-fed (ombrotrophic) peatland bogs in Massachusetts and Vermont, we measured nutrient and metal concentrations in pore-water and in leaf tissues of three common bog plant genera – leather leaf (*Chamaedaphne calyculata*), northern pitcher plant (*Sarracenia purpurea*), and peat moss (*Sphagnum* spp.). The concentrations of N, P, and K were low in leaf tissues of all three plant genera, as were the concentrations of many trace heavy metals, including Cr, Cu, Co, Cd, Mo, and Pb. Stoichiometric ratios of macronutrients (N:P, P:K, and N:K) in plant leaves suggested that plant growth in the sampled bogs was limited by P, or was co-limited by all three macronutrients. N:P and N:K nutrient ratios of *Sarracenia purpurea* and *Sphagnum* spp. increased toward the northwest and with elevation, but stoichiometric ratios of *Chamaedaphne calyculata* did not show any clear geographic trends. A principal components analysis revealed additional distinct differences among the three plant genera in their nutrient and metal concentrations. Furthermore, dissolved organic carbon (DOC), dissolved organic nitrogen (DON), Cu, Mg, NO_3, Al, and K in pore-water increased from the northwest (northwestern Vermont) to the southeast (Cape Cod and eastern Massachusetts near Boston), a gradient of increasing human population density and urbanization. In contrast, pore-water concentrations of SO_4 and Al were highest in the western sites, and SO_4 concentrations increased with elevations. These patterns may reflect atmospheric inputs from the Ohio River Valley leading to increased acidic deposition, causing Al to be leached from soils. Because bogs are naturally low in nutrients and do not receive substantial inputs from surrounding groundwater, the chemical signatures and nutrient stoichiometry of specific bog plant species or genera may provide useful indicators for assessing spatiotemporal changes in atmospheric deposition.

Key Words: atmospheric deposition, *Chamaedaphne calyculata*, nitrogen, phosphorus, potassium, *Sarracenia purpurea*, *Sphagnum*

INTRODUCTION

Nutrient limitation characterizes most terrestrial and wetland plant assemblages (Chapin et al. 1986, Bedford et al. 1999, Aerts and Chapin 2000). Many studies have shown stoichiometric relationships – ratios of critical nutrients in plant tissues – are reliable indicators of which nutrients (co-)limit plant growth and system-wide production (Olde Venterink et al. 2002, 2003, Sterner and Elser 2002, Ågren 2004, Güsewell 2004, 2005, Kerkhoff et al. 2005, Schade et al. 2005). The production of inorganic nitrogen for agriculture, the combustion of fossil fuels, and other industrial processes have resulted in widespread atmospheric deposition of nitrogen (N) as NO_x and NH_4, phosphorus (P) as PO_4, sulfur (S) as SO_4, carbon (C) (e.g., in soot), and a variety of metals, including lead (Pb), copper (Cu), and mercury (Hg). These additional inputs (as well as soil leaching from acidification) alter both the absolute and relative concentrations of nutrients and elements in the environment. Such changes can affect competitive relationships among plants (Tilman 1988, Bobbink et al. 1998) and may directly or indirectly reduce population size or even eliminate species of management concern (Verhoeven et al. 1996).

Bogs are fragile, nutrient-poor ecosystems that receive most or all of their nutrient inputs from precipitation (Gorham et al. 1985, Damman 1986, 1990, Lamers et al. 1999, Holden and Burt 2003). Many plant species that grow in bogs are adapted to low nutrient conditions. Such adaptations include: low photosynthetic rates (Small 1972) and photosynthetic nutrient-use efficiency (Ellison 2006); the ability to take up organic forms of nitrogen (Kielland 1994, Raab et al. 1996, Näsholm et al. 1998); specialized mycorrhizal relationships (Michelsen et al. 1996); and carnivory that provides nutrients from arthropod prey (Givnish 1989). In Europe, where nitrogen deposition rates are 2–10 times higher than in North America (Holland et al. 2005), atmospheric deposition of nutrients and metals is widespread (Steinnes 1997, West et al. 1997) and has dramatically altered plant species composition in bogs (Giller and Wheeler 1988, Bobbink et al. 1998, Heijmans et al. 2002). Changes in nutrient stoichiometry repeatedly have been identified as plausible mechanisms underlying these observed changes in vegetation structure (Hoosbeek et al. 2002, Güsewell 2004, 2005, Limpens et al. 2004).

In North America, implementation of the Clean Air Act of 1969 has significantly reduced continent-wide deposition rates of SO_4, whereas changes in deposition rates of NO_x and NH_4 vary geographically: nitrogen deposition has decreased in the northeastern United States, but it has increased in the Midwest and elsewhere (Lynch et al. 1995, Lehmann et al. 2005). There have also been reductions in the deposition rates of major cations (Ca, Mg, Na, and K). Deposition rates of mercury (Hg) and lead (Pb) have generally declined following the imposition of regulatory controls and the elimination of leaded gasoline (Swain et al. 1992, Norton et al. 1997, Schuster et al. 2002, Vanarsdale et al. 2005). Deposition rates of most other metals are not measured routinely (but see Evans et al. 2005) and are presumed to be extremely low from a regulatory standpoint. These observed (and unobserved) changes in deposition rates also may alter the growth, morphology of individual plants, as well as affect competitive interactions among species.

In northeastern North America, the morphology of the pitcher plant *Sarracenia purpurea* L. (a bog specialist) changes in response to experimental nutrient additions. Moreover, variation in plant morphology among populations is correlated with a variation in pore-water nutrient concentrations among bogs (Ellison and Gotelli 2002). Higher levels of pore-water NH_4 are associated with reduction in pitcher diameter, an increase in the area of the plant's flattened ''keel'', and concomitant increases in photosynthetic rates (Ellison and Gotelli 2002). At very high levels of N deposition, however, plants senesce faster, seedlings are ''burned'' by excessive N, and populations may go locally extinct (Gotelli and Ellison 2002b). Additional species of bog plants might serve as indicators of deposition rates of other nutrients or metals. A prerequisite for finding such indicator species is determining baselines of nutrient and mineral composition in plants and identifying specific differences between them.

Here, we report such baselines for pitcher plants and two other common plant genera in bogs – leatherleaf (*Chamaedaphne calyculata* (L.) Moench.) and sphagnum moss (*Sphagnum* spp., primarily *S. magellanicum* Brid. and *S. rubellum* Wils.) – in 24 bogs across Massachusetts and Vermont. We simultaneously measured pore-water chemistry in these bogs, and we used those data to identify ''hot spots'' of deposition of nutrients and metals in our study region, to quantify stoichiometric relationships among key nutrients, and to identify which nutrient or nutrients likely limit the growth of each of these taxa. Our results suggest how bog communities in northeastern North America might respond to additional changes in atmospheric inputs.

METHODS

Study Genera

Leatherleaf (*Chamaedaphne calyculata*) is an evergreen, perennial ericaceous shrub that forms large, dense stands in bogs and poor fens. It ranges from southern Canada and the northern midwestern United States south to Georgia in the eastern United States (Niering 1998). This shrub has extensive root systems and predictably expands through *Sphagnum* mats by vegetative proliferation. Leatherleaf's vegetative growth can consolidate bog mats rapidly and promotes the successful establishment of other woody plants (Swan and Gill 1970).

The northern pitcher plant (*Sarracenia purpurea*) is a perennial, rosette-forming, carnivorous herb that is common in bogs and poor fens throughout the eastern coastal plain of North America. It ranges from Georgia northward into Newfoundland and Labrador, and westward across Canada east of the Rocky Mountains and in the northern Midwestern United States (Schnell 2002). *Sarracenia* is shallowly rooted, and like other carnivorous plants it obtains most of its nutrients from captured prey (Ellison et al. 2003). It also collects rainwater in its pitchers. In places where atmospheric deposition rates are high, more than 40% of the plant's nutrient budget can come from inorganic nutrients dissolved in precipitation (Błędzki and Ellison 1998).

Sphagnum mosses are the characteristic foundation genera of temperate-zone bogs in both hemispheres (Andrus 1986) and function as ''keystone genera'' or ''ecosystem engineers'' in these habitats (Svensson 1995, Rochefort 2000). *Sphagnum* has a high water-holding capacity and acidifies the bog habitat by taking up cations (including critical elements such as Ca and Mg) and releasing hydrogen ions into the surrounding water. The most common species of *Sphagnum* in our study sites, accounting for ~80% of all collected material, were *S. magellanicum*, *S. rubellum*, *S. angustifolium* (Russ.) C. Jens., and *S. fallax* (Klinggr.) Klinggr. We did not distinguish among *Sphagnum* species in our analysis of plant nutrient content.

Sample Collection and Analysis

Samples of *C. calyculata*, *S. purpurea*, *Sphagnum*, and pore-water were collected at 24 bogs in Vermont and Massachusetts (Figure 1) over a two-week period in June 2002. All of these bogs have well-developed *Sphagnum* mats and woody vegetation dominated by *Chamaedaphne* (Gotelli and Ellison 2002a, Błędzki and Ellison 2003). We collected leaves (5–10 g fresh mass) for analysis that were representative of new growth produced in the current growing season, and that were from plants growing in the *Sphagnum* mat where the density of pitcher plants was highest. *Sphagnum* samples were not identified to species, but we did collect the most abundant morphotype of *Sphagnum* at each site.

All plant tissue samples collected were of young, fully expanded leaves of similar age – approximately 25% through their life cycle. Although macronutrient and elemental contents of leaves change through time, young, fully expanded leaves are at a point in their growth when leaf performance is at its peak (Reich et al. 1995). Such leaves act as competing sinks for many nutrients, including calcium (McLaughlin and Wimmer 1999), which is known to show pronounced seasonality in concentration. Nonetheless, our focus in this work is on biogeographic patterns of nutrient content, and there is no a priori reason to expect that temporal changes in nutrient status would be affected by a statistical interaction between leaf age and elevation, longitude, or latitude, so our biogeographic comparisons should still be valid.

The leaf samples were bagged individually in the field and immediately returned to the laboratory where they were dried at 60°C to constant mass, ground in a Udy Cyclone Sample Mill (1-mm screen), and microwave-digested with nitric acid for chemical analysis. Nutrient and metal content (C, H, N, Al, B, Ca, Cd, Co, Cr, Cu, Fe, K, Mg, Mn, Mo, Na, Ni, P, Pb, S, and Zn; elemental abbreviations defined in Table 1) of the digested samples were determined at the University of Vermont Agricultural and Environmental Testing Laboratory using a Perkin-Elmer Optima 3000 DV inductively-coupled plasma atomic emission spectrometer (ICP-AES; PerkinElmer, Wellesley, Massachusetts, USA). Analysis for C, H, and N was performed on separate sub-samples using a Leeman Lab model 440 CHN elemental analyzer (Teledyne Technologies, Los Angeles, California, USA). All analyses were conducted using standard methods and quality control, including blanks, duplicates, and NIST traceable standard materials.

Pore-water samples were taken by pressing a 500 mL sample bottle into the surface of the *Sphagnum* mat. The collected water was immediately filtered in the field through glass-fiber filter paper (Whatman GFF), separated into four subsamples for separate analyses, placed on ice, and transported to the University of Vermont Agricultural and Environmental Testing Laboratory. The first subsample, used to determine concentration of soluble Al, Ca, Cu, Fe, K, Mg, Mn, Na, Si, and Zn, was preserved with nitric acid (final concentration 0.1 N) and
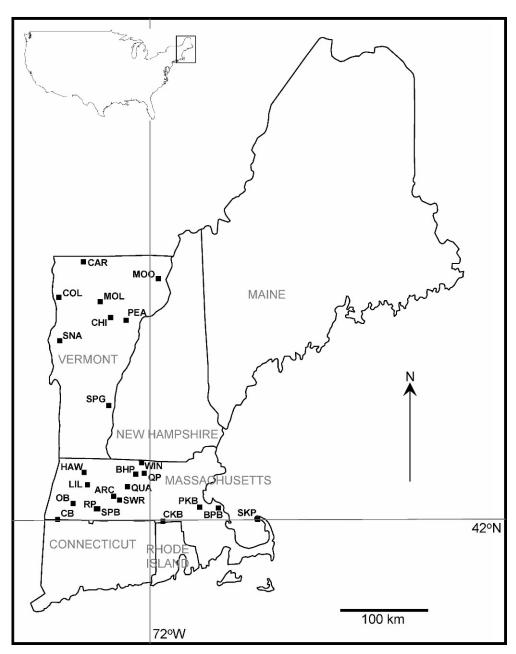
Figure 1.   Map of sampled bogs. Abbreviations are: CAR – Carmi Bog; MOO – Moose Bog; MOL – Molly Bog; COL – Colchester Bog; PEA – Peacham Bog; CHI – Chickering Bog; SNA – Snake Mountain Bog; SPG – Springfield Bog; HAW – Hawley Bog; LIL – Lily Pond Bog; OB – Otis Bog; CB – Clayton Bog; WIN – Lake Jones Bog; BHP – Bourne-Hadley Ponds; QP – Quag Pond; QUA – Quabbin Bog; ARC – Arcadia Bog; SWR – Swift River Bog; RP – Round Pond; SPG – Snake Pond Bog; PKB — Ponkapoag Bog; CKB – Chockalog Bog; BPB – Black Pond Bog; SKP – Shankpainter Ponds. Detailed geographic information about these bogs can be found in Gotelli and Ellison (2002a) and Błędzki and Ellison (2003).

stored at 4°C until analyzed using an Optima 300 DV ICP-AES (Perkin-Elmer Inc., Norwalk, CT). The second subsample, used to determine concentrations of NH_4-N and NO_3-N, was preserved with sulfuric acid (to pH 2) and stored at 4°C until analyzed on a Flow Injection Auto-Analyzer (Lachat QuikChem AE, Loveland, CO) using the salicylate-nitroprusside methods and cadmium reduction, respectively. The third subsample, used to measure pH, dissolved organic carbon (DOC), and dissolved organic nitrogen (DON), was stored at −20°C. The pH of thawed samples was measured with an Orion pH electrode (Thermo Electron, Waltham, MA). DOC and DON were measured using the persulfite

Table 1. Concentrations (mg/kg) of metals in leaf tissue of *Chamaedaphne calyculata*, *Sarracenia purpurea*, and *Sphagnum* spp. Values given are means ± 1 SD. For each metal, superscript letters indicate significant differences among species (P < 0.05; Tukey's HSD test for multiple comparisons among means). If no letters are given, then there were no significant differences in metal concentration among the three genera.

	Chamaedaphne	*Sarracenia*	*Sphagnum*
Calcium (Ca)	10,304.90 (1,976.67)[a]	1,038.37 (526.38)[c]	2,236.05 (771.40)[b]
Magnesium (Mg)	1,414.62 (416.83)[b]	2,084.39 (871.14)[a]	897.83 (337.11)[c]
Iron (Fe)	64.79 (29.69)[b]	95.66 (44.84)[b]	590.07 (392.13)[a]
Chromium (Cr)	2.85 (4.13)	3.50 (5.99)	1.58 (3.09)
Copper (Cu)	2.31 (2.26)	2.56 (3.32)	4.88 (5.46)
Aluminum (Al)	224.92 (95.68)[b]	61.59 (39.52)[c]	333.74 (189.92)[a]
Cobalt (Co)	1.13 (1.79)	0.90 (0.84)	0.70 (0.34)
Boron (B)	10.66 (9.35)[a]	1.57 (2.55)[b]	0.66 (0.43)[b]
Cadmium (Cd)	0.77 (0.57)	1.57 (1.43)	1.38 (1.76)
Molybdenum (Mo)	15.35 (24.42)	5.46 (11.80)	5.33 (11.96)
Manganese (Mn)	991.81 (472.48)[a]	92.16 (60.42)[b]	151.18 (115.22)[b]
Sodium (Na)	18.85 (26.69)[b]	375.47 (242.71)[a]	606.90 (536.62)[a]
Nickel (Ni)	3.39 (5.36)[b]	4.59 (4.72)[a,b]	8.32 (9.00)[a]
Lead (Pb)	1.88 (3.07)	2.69 (4.66)	17.96 (64.48)
Sulfur (S)	1,539.59 (264.45)[a]	786.44 (161.93)[c]	1,030.24 (219.67)[b]
Zinc (Zn)	31.16 (7.98)[a]	19.39 (6.68)[b]	26.76 (8.35)[a,b]

oxidation method (Clesceri et al. 1998). The fourth subsample, used for SO_4, Cl, and soluble reactive P, was stored at $-20°C$ until analyzed by ion chromatography (for SO_4, Cl) or using the stannous chloride molybdate blue procedure (for P) (Clesceri et al. 1998). Random duplicate samples and field blanks, consisting of 500 mL filtered distilled water, were taken at several sites and processed as described above. Latitude, longitude, and elevation (meters above sea-level [m a.s.l.]) of each bog were determined in the field using a Trimble Global Positioning System unit (Trimble Instruments, Sunnyvale, CA). Latitude and longitude are reported here only to the nearest degree in order to protect these sensitive sites. Access to sites and sample collection was permitted by private landowners and by state Natural Heritage programs.

Data Analysis

Initial analysis focused on geographic patterns in nutrient and mineral availability (in pore-water), genus-specific differences in nutrient and mineral content, and how these differences varied with latitude, longitude, and elevation. Key stoichiometric relationships – C:N, N:P, N:K, and K:P ratios in plant tissues – were also examined within and among sites and across plant taxa. Koerselman and Meuleman (1996) and Aerts and Chapin (2000) have suggested that N limitation is implied by N < 20 mg/g (2%) and N:P < 14 mg/mg, whereas P limitation is implied by P < 1 mg/g (0.1%) and N:P > 16. Co-limitation of N and P is implied when concentrations of N and P are both individually limiting and when $14 \leq N:P \leq 16$. Olde-Venterink et al. (2002, 2003) expanded the concept of nutrient limitation in wetland plants to include K limitation and suggested that if K is less than 8 mg/g (0.8%) then its availability can limit plant growth. They further suggest critical ratios for P or P+N limitation (N:P > 14.5, K:P > 3.4), K or K+N limitation (N:K > 3.1, K:P < 3.4), and pure N limitation (N:P < 14.5, N:K < 2.1). We used these a priori thresholds to determine whether growth of *Chamaedaphne*, *Sarracenia*, or *Sphagnum* is likely to be limited by N, P, or K.

To compare tissue nutrient concentrations, we used a randomized block ANOVA (Gotelli and Ellison 2004), with each bog as a block. For each plant genus, geographic trends in average nutrient content were identified with stepwise multiple regression models, using latitude, longitude, and elevation as the predictor variables. We used principal component analysis (PCA) as a data reduction technique to reveal whether suites of nutrients and minerals covaried among genera or sites. All data were standardized by conversion to standard deviation units for the PCA. Data analyses were conducted with R version 2.6.1 (http://www.r-project.org/).

RESULTS

Nutrient and Metal Content of Plants

In all bogs, nutrient content (percent N, P, K) was low in the three plant genera (Figure 2). Absolute
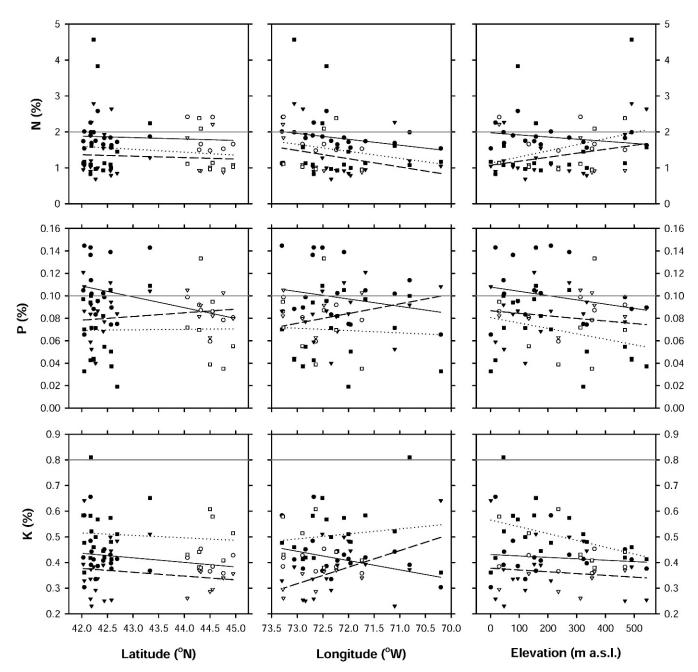
Figure 2.   Macronutrient content of the three plant taxa – *Chamaedaphne calyculata* (circles, solid regression lines); *Sarracenia purpurea* (inverted triangles, dashed regression lines); *Sphagnum* spp. (squares, dotted regression lines) – as a function of latitude, longitude, and elevation. Solid symbols indicate plants sampled from bogs in Massachusetts and open symbols are plants sampled from bogs in Vermont. Dark grey lines indicate critical values at which N, P, or K become limiting (after Aerts and Chapin 2000, and Olde Venterink 2002, 2003).

concentrations of these nutrients suggest that all three genera are limited by N and K and that *Sarracenia* and *Sphagnum* are also limited by P (Figure 2). Across all sites, *Chamaedaphne* leaves had significantly higher concentrations of N and P than leaves of either *Sarracenia* or *Sphagnum* ($P < 0.05$, Tukey's HSD post-hoc test for multiple comparisons among means). *Sphagnum* also had significantly

more K than did *Sarracenia* ($P < 0.05$). There were no clear geographic trends in absolute concentrations of nutrients in plant tissues (Figure 2).

Among the three genera, *Chamaedaphne* had the highest concentrations of Ca, B, Mn, S, and Zn, *Sarracenia* had the highest concentrations of Mg, and *Sphagnum* had the highest concentrations of Fe, Al, Na, and Ni (Table 1). The three genera all had

Table 2. Geographic variables associated with nutrient and cation concentrations in pore-water samples of 24 New England bogs. For each nutrient or cation, we used stepwise multiple regression to determine which of the three geographic variables explained a significant proportion of the variance in the observations. The entry in each cell is the value of the coefficient (β_i) in the model $X = \beta_0 + \beta_1 \times$latitude $+ \beta_2 \times$longitude $+ \beta_3 \times$elevation, where X is the nutrient or cation. An entry labelled "ns" means that that variable was not included in the final model ($P > 0.1$ in the stepwise regression). Note that longitude was coded in the data as a negative number (thus sites located further west have smaller [more negative] values for longitude). Consequently, if $\beta_2 < 0$, that nutrient or cation increased in concentration towards the west. The r^2 value is the proportion of variance explained by the final model; the P-value indicates the significance of the final model.

	Lat	Long	Elev	r^2	P-value
DOC	11.5	−20.4	−0.10	0.52	0.002
DON	ns	−1.02	−0.004	0.58	0.0001
Cu	0.01	ns	ns	0.21	0.08
Mg	ns	−0.52	−0.002	0.26	0.04
Na	ns	ns	ns	0.09	0.15
NO_3	0.11	−0.10	−0.0004	0.42	0.01
Zn	ns	ns	ns	0.11	0.51
SO_4	−0.22	−0.08	0.001	0.32	0.04
Al	ns	−0.04	−0.0002	0.27	0.04
K	0.55	−0.77	−0.005	0.58	0.0006

similar, low concentrations of the heavy metals Cr, Cu, Co, Cd, Mo, and Pb (Table 1), all of which can be toxic to plants at high concentrations.

Geographic Patterns in Pore-water Nutrient Availability

Stepwise multiple regressions revealed common geographic patterns in nutrient and cation availability in pore water (Table 2). Concentrations of DOC, DON, Cu, Mg, NO_3, Al, and K all generally increased from northwest (northwestern Vermont sites) to southeast (eastern Massachusetts sites near Boston). Concentrations of DOC, DON, Mg, NO_3, Al, and K also all decreased with elevation (Table 2). Concentrations of SO_4 were highest in the northwestern sites, and increased with elevation (Table 2). There were no geographic patterns in pore-water pH, or pore-water concentrations of P, Mn, NH_4, Ca, Fe, and Si.

Stoichiometric Relationships

Nutrient ratios in plant tissues generally suggested that plant growth was limited by P or co-limited by all three macronutrients (N, P, and K) (Figure 3), given the relatively low levels of N and K available (Figure 2). The relatively high N:P ratio of all three genera implied P-limitation, and it did not differ among the three genera (P = 0.22, ANOVA). Observed high ratios of N:P and K:P further indicated P limitation (Figure 3). N:K ratios were also above the critical threshold, implying some degree of K limitation (Figure 3). *Sphagnum* appeared to be the

least K- (most P-) limited: its K:P ratio was significantly higher (P < 0.05, Tukey's HSD post-hoc test for multiple comparisons among means) than that of either *Chamaedaphne* or *Sarracenia*; the K:P ratios of the latter did not differ significantly (P > 0.05). Similarly, *Sphagnum* had the lowest N:K ratio of the three genera (Figure 3). A ternary plot (Figure 4) confirmed these patterns. All genera were either P-limited or N-P-K co-limited. C:N ratios of *Sarracenia* and *Sphagnum* were significantly higher than the C:N ratio of *Chamaedaphne* (P < 0.05).

Stoichiometric relationships of *Chamaedaphne* did not vary consistently with geographic variables (P > 0.15; Figure 3). However, the N:P and N:K ratios of *Sarracenia* and *Sphagnum* increased significantly to the northwest (P = 0.01), with the highest N:P ratios in plants at the high elevation sites of Hawley Bog (543 m a.s.l.) and Otis Bog (491 m a.s.l.) in western Massachusetts (Figure 3). Hawley Bog also had the highest N:K ratio (Figure 3). N:P ratios of *Sphagnum* also were highest at two high elevation sites, Otis Bog in western Massachusetts and Lake Jones Bog (323 m a.s.l.) on the Worcester Plateau of Massachusetts (Figure 3). The stoichiometry of the pore water did not differ geographically (P > 0.1, stepwise multiple regressions). The N:P ratio in pore water was 16.2 ± 28.01 (SD), N:K was 0.3 ± 0.17, and K:P was 44.6 ± 47.50.

Data Reduction and PCA Profiles

Principal components analysis clearly separated the three plant taxa on the basis of nutrient and mineral composition (Figure 5). The first three
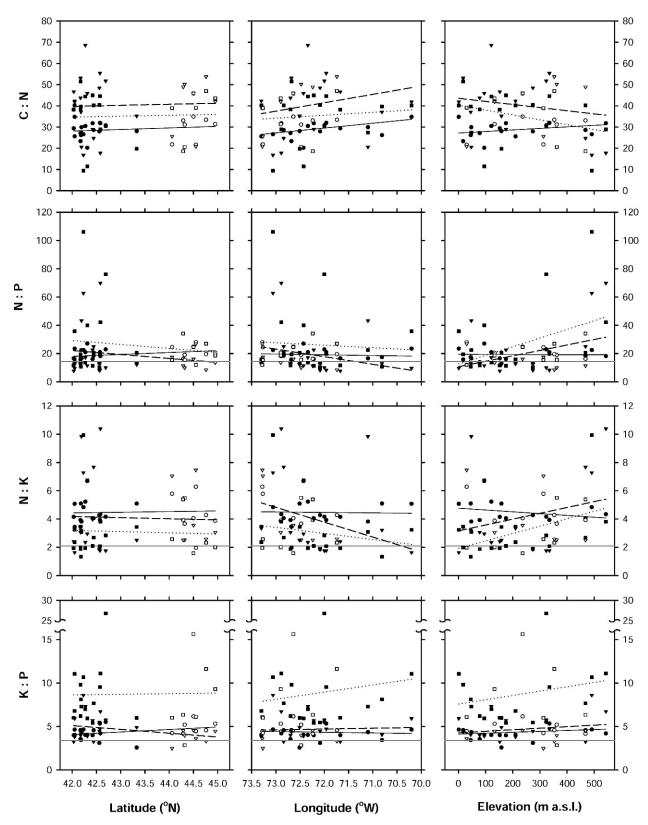
Figure 3.   Stoichiometric relationships for the three plant taxa. – *Chamaedaphne calyculata* (circles, solid regression lines); *Sarracenia purpurea* (inverted triangles, dashed regression lines); *Sphagnum* spp. (squares, dotted regression lines) – as a function of latitude, longitude, and elevation. Solid symbols indicate plants sampled from bogs in Massachusetts and open symbols are plants sampled from bogs in Vermont. Dark grey lines indicate critical values at which N, P, or K become limiting (Olde Venterink 2002, 2003). Please note vertical axis break on the plots of K:P.

Figure 4. Ternary plot illustrating joint N, P, and K limitation in the three plant taxa – *Chamaedaphne calyculata* (circles); *Sarracenia purpurea* (inverted triangles); *Sphagnum* spp. (squares). Solid symbols indicate plants sampled from bogs in Massachusetts and open symbols are plants sampled from bogs in Vermont. Nutrient limitation boundaries in the plot are based on the criteria of Olde Venterink et al. (2003).

principal axes accounted for 26%, 15%, and 11% of the variance, respectively (cumulative variance explained = 52%); visual inspection of the PCA scree plot suggested that higher-order axes were not informative. The largest loadings were for C (positive) and Na (negative) on the first axis; Al (positive) and Mg (negative) on the second axis; and Cd (positive) and N (negative) on the third axis (Figure 5; complete loadings are given in Table 3). All three genera separated out clearly in a biplot of principal axis 1 versus principal axis 2. *Chamaedaphne* had generally positive scores for both principal axes, indicating high C, H, Ca (on the first axis), and K (on the second axis); *Sarracenia* had generally negative scores for both principal axes, indicating high Na, H, and Mg, but low Al, K, Zn, Cu, and S; and *Sphagnum* had generally negative scores for principal axis 1 and positive scores for principal axis 2, indicating low C and high Al and K. *Chamaedaphne* also separated out from the other two genera in the biplot of principal axis 1 versus principal axis 3 (Figure 5); this shrub had intermediate scores on principal axis 3. *Sarracenia* separated out from the other genera in the biplot of principal axis 2 versus principal axis 3 (Figure 5). Geographic position – latitude, longitude, and elevation – was not significantly correlated (P > 0.24, all cases) with any of the three principal axis scores for any of the three plant taxa.

Overall patterns in water chemistry were generally less dramatic (Figure 6). Initial principal components analysis and visual inspection of the scree plot suggested that only the first principal axis was informative; it accounted for 43% of the variance (loadings in Table 4). This PCA also identified Colchester Bog (near Burlington, Vermont) as a clear outlier on principal axis 1. This bog had the highest pH (6.37) and highest DOC, DON, P, Al, Cu, K, Mg, Na, and Zn of all the bogs sampled; the values for DOC, DON, and these nutrients and metals exceeded those values in the other bogs by more than 2-fold on average (range 1 to 5-fold). Because it was possible that these extreme values found at Colchester Bog may have hidden other geographic patterns in water chemistry among bogs, we ran another PCA with Colchester Bog removed from the analysis. As in the PCA that included Colchester Bog, only the first principal axis was informative, and the scores for the first principal axis were highly correlated between the two analyses (r = 0.93; data in Table 4). In this latter analysis, the first principal axis only accounted for 25% of the variance in the data. In both analyses, the second principal axis accounted for 11%–12% of the variance. Principal component scores, either with or without Colchester Bog data included, were not significantly correlated with latitude, longitude, or elevation (P > 0.15, all comparisons).

Pore-water chemistry profiles (i.e., the first principal axis score of water chemistry data) were not significantly correlated (P > 0.16, all cases) with the plants' nutrient content profiles (i.e., the three principal axis scores of the three plant taxa).

DISCUSSION

This work provides baseline analytical data for pore-waters and plant tissue sampled in 24 New England bogs. Our results suggest that, in spite of the relatively narrow geographic extent of the samples, there are complex geographic gradients of nutrients and elements in the pore-water of these bogs that are related to the latitude, longitude, and elevation of each site. Although nutrient deposition rates at small spatial scales typically increase with elevation (Miller et al. 1993), the main effects of elevation in our regression models were mostly negative, suggesting that deposition of many nutrients and elements decreases at higher elevations. This pattern probably reflects the confounding geographic gradient of human population density and urbanization which is greater at low elevation
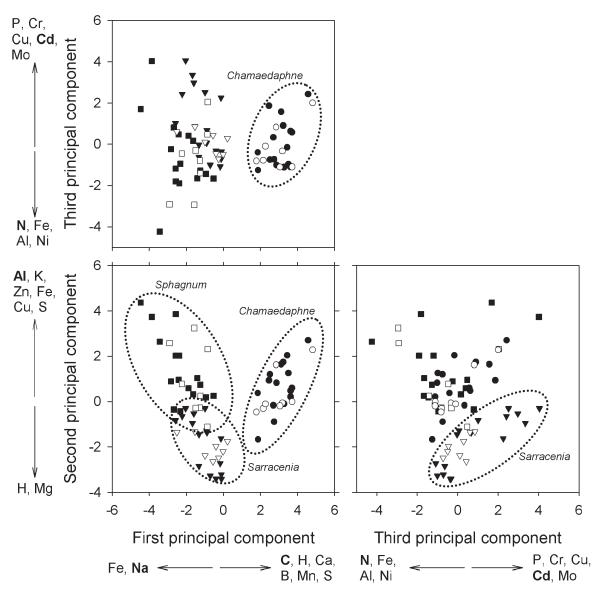
Figure 5. Principal component biplots of the three plant taxa – *Chamaedaphne calyculata* (circles); *Sarracenia purpurea* (inverted triangles); *Sphagnum* spp. (squares). Solid symbols indicate plants sampled from bogs in Massachusetts and open symbols are plants sampled from bogs in Vermont. The axes are annotated with the minerals and metals that loaded most heavily (|loading| > 0.2); the dominant element loading on each axis is indicated in bold. All loadings are reported in Table 3.

sites in our study (Cape Cod and eastern Massachusetts near Boston) than at high elevations (the Berkshire Mountains of Massachusetts and the Green Mountains of Vermont). However, the increasing concentrations of SO_4 to the west and K to north may reflect deposition of pollutants that originate in the Ohio River Valley (Malm et al. 2002). In bogs of Britain and Ireland, there are similar geographic gradients in chemical composition that are related to inputs from sea-spray and local pollution and terrestrial sources (Proctor 1992). In western Canada, elemental concentrations in pore water samples also varied on a longitudinal

gradient (Malmer et al. 1992). In our study, sea-spray inputs may also be important in accounting for nutrient profiles of Ponkapoag Bog, Black Pond Bog, and Shankpainter Ponds, all of which are near the coast of eastern Massachusetts.

Because of these geographic gradients in porewater chemistry, there was considerable variability among individual bogs, and the first two principal components accounted for 55% of the variance. In contrast, the first two principal components of a similar analysis of pore-water chemistry in bogs of Britain and Ireland accounted for almost 80% of the variance (Proctor 1992), although that study was

Table 3. Variable loadings of each element on the first three principal components constructed from tissue concentrations of the three plant genera (see Figure 5).

Element	First principal component	Second principal component	Third principal component
C	0.398	−0.033	−0.026
H	0.296	−0.212	−0.062
N	0.138	0.039	−0.301
P	0.180	0.142	0.224
K	−0.114	0.364	0.054
Ca	0.374	0.191	−0.002
Mg	0.062	−0.295	0.140
Fe	−0.238	0.312	−0.281
Cr	0.023	0.049	0.414
Cu	−0.116	0.235	0.364
Al	−0.044	0.450	−0.234
Co	0.086	0.087	0.182
B	0.263	0.079	0.023
Cd	−0.166	0.142	0.418
Mo	0.116	0.154	0.298
Mn	0.336	0.190	0.032
Na	−0.290	0.085	0.020
Ni	−0.124	0.173	−0.277
Pb	−0.106	0.162	0.084
S	0.312	0.214	−0.110
Zn	0.189	0.341	0.007

conducted on a much larger geographic scale. Moreover, Colchester Bog in northwestern Vermont had the highest levels of pH, DOC, and DON, and nutrient and metal concentrations were 2 to 5 times greater than average. This site was also unusual in that its vegetation was atypical: the *Sphagnum* mat
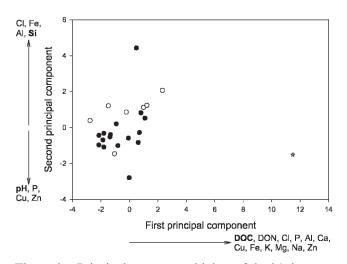

Figure 6. Principal component biplots of the 24 sites as a function of pore-water chemistry. Solid circles indicate Massachusetts bogs and open circles indicate Vermont bogs. The grey star is Colchester Bog in northwestern Vermont. The axes are annotated with the minerals and metals that loaded most heavily (|loading| > 0.2); the dominant element loading on each axis is indicated in bold. All loadings are reported in Table 4.

was poorly developed, *Sarracenia* densities were low, and the site is accumulating a leaf litter layer and is being invaded by woody vegetation (especially saplings of speckled alder *Alnus incana* (L.) Moench. and gray birch *Betula populifolia* Marsh.; N. J. Gotelli, unpublished data).

Across the sample of 24 New England bogs, the three plant genera show clear evidence of nutrient limitation, both in absolute levels of N, K, and P, and in the stoichiometry of nutrient ratios. These results are consistent with the findings of Bedford et al. (1999) and Olde-Venterink et al. (2003) that wetland plants are generally nutrient limited.

An unexpected finding of this work was the lack of correspondence between geographic trends in pore-water chemistry and nutrient concentrations in plant tissues. Nutrient and metal content of pore-water varied geographically, and all three plant genera appeared to be nutrient limited. *Sarracenia purpurea* and *Sphagnum* spp. showed significant geographic variation in stoichiometric ratios: N:P and N:K ratios of these taxa increased significantly towards the northwest. Previous experimental work has shown that tissue nutrient ratios of *Sarracenia* can shift in response to food additions, which supply both N and P, or to additions of soluble inorganic N, either as NH_4Cl or NH_4NO_3 (Ellison and Gotelli 2002, Wakefield et al. 2005). Malmer et al. (1992) reported a similar lack of correlation for most

Table 4. Variable loadings of each element on the first two principal components constructed from pore-water samples of the 24 bogs (see Figure 6). Analyses are shown with and without Colchester Bog VT. This site was an outlier with extreme values for measured nutrients and metals.

Variable	First principal component		Second principal component	
	With Colchester	Without Colchester	With Colchester	Without Colchester
pH	0.084	−0.246	−0.520	−0.060
DOC	0.341	0.424	0.060	−0.058
DON	0.271	0.264	−0.001	−0.104
NH_4	0.049	0.047	−0.081	−0.146
NO_3	0.153	0.200	0.163	−0.111
SO_4	−0.086	−0.123	−0.055	0.037
Cl	0.219	0.241	0.253	0.075
P	0.263	0.086	−0.229	−0.285
Al	0.259	0.393	0.370	0.133
Ca	0.230	0.067	−0.106	0.295
Cu	0.301	−0.080	−0.224	−0.375
Fe	0.221	0.299	0.299	0.125
K	0.322	0.336	0.007	−0.236
Mg	0.332	0.269	−0.114	0.222
Mn	0.197	0.228	0.017	−0.004
Na	0.252	0.198	−0.071	−0.257
Si	0.124	0.163	0.431	0.382
Zn	0.248	0.098	−0.286	−0.531

elements between surface water concentrations in bogs and plant tissue concentrations in samples of *Sphagnum* and *Tomenthypnum* mosses from western Canada.

In a simple model, we would expect geographic trends in pore-water to be reflected in the chemical composition of some or all plant tissues. However, all three genera clearly exhibited distinct chemical profiles of both nutrients and metals that were independent of geographic location. This finding indicates that each plant genus may be capable of outcompeting others for specific groups of macro- or micro-nutrients that are plant-specific rather than location-specific, even within nutrient-poor peat-lands. Moreover, it also suggests that different plant taxa may be useful indicators for deposition rates of particular nutrients or metals. However, the indica-tor status of any species will have to be confirmed with experimental studies that demonstrate shifts in stoichiometry in response to particular environmen-tal conditions.

LITERATURE CITED

Aerts, R. and F. S. Chapin. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Advances in Ecological Research 30:1–67.

Ågren, G. I. 2004. The C:N:P stoichiometry of autotrophs – theory and observations. Ecology Letters 7:185–91.

Andrus, R. E. 1986. Some aspects of *Sphagnum* ecology. Canadian Journal of Botany 64:416–26.

Bedford, B. L., M. R. Walbridge, and A. Aldous. 1999. Patterns of nutrient availability and plant diversity of temperate North American wetlands. Ecology 80:2151–69.

Błędzki, L. A. and A. M. Ellison. 1998. Population growth and production of *Habrotrocha rosa* Donner (Rotifera: Bdelloidea) and its contribution to the nutrient supply of its host, the northern pitcher plant, *Sarracenia purpurea* L. (Sarracenia-ceae). Hydrobiologia 385:193–200.

Błędzki, L. A. and A. M. Ellison. 2003. Diversity of rotifers from northeastern USA bogs with new species records for North America and New England. Hydrobiologia 497:53–62.

Bobbink, R., M. Hornung, and J. G. M. Roelofs. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. Journal of Ecology 86:717–38.

Chapin, F. S., P. M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. American Naturalist 127:48–58.

Clesceri, L. S., A. E. Greenberg, and A. D. Eaton. 1998. Standard Methods for the Examination of Water and Wastewater, twentieth edition. American Public Health Association, Wa-shington, DC, USA.

Damman, A. W. H. 1986. Hydrology, development, and biogeochemistry of ombrogenous peat bogs with special reference to nutrient relocation in a western Newfoundland bog. Canadian Journal of Botany 64:384–94.

Damman, A. W. H. 1990. Nutrient status of ombrotrophic peat bogs. Aquilo Serie Botanica 28:5–14.

Ellison, A. M. 2006. Nutrient limitation and stoichiometry of carnivorous plants. Plant Biology 8:740–47.

Ellison, A. M. and N. J. Gotelli. 2002. Nitrogen availability alters the expression of carnivory in the northern pitcher plant *Sarracenia purpurea*. Proceedings of the National Academy of Sciences, USA 99:4409–12.

Ellison, A. M., N. J. Gotelli, J. S. Brewer, D. L. Cochran-Stafira, J. Kneitel, T. E. Miller, A. C. Worley, and R. Zamora. 2003. The evolutionary ecology of carnivorous plants. Advances in Ecological Research 33:1–74.

Evans, G. C., S. A. Norton, I. J. Fernandez, J. S. Kahl, and D. Hanson. 2005. Changes in concentrations of major elements and trace metals in northeastern US-Canadian sub-alpine forest floors. Water, Air, and Soil Pollution 163:245–67.

Giller, K. E. and B. D. Wheeler. 1988. Acidification and succession in a flood-plain mire in the Norfolk broadland, U.K. Journal of Ecology 76:849–66.

Givnish, T. J. 1989. Ecology and evolution of carnivorous plants. p. 243–90. *In* W. G. Abramson (ed.) Plant - Animal Interactions. McGraw-Hill Publishers, Toronto, Canada.

Gorham, E., S. J. Eisenreich, J. Ford, and M. V. Santelman. 1985. The chemistry of bog waters. p. 339–63. *In* W. Stumm (ed.) Chemical Processes in Lakes. John Wiley & Sons, Inc., New York, NY, USA.

Gotelli, N. J. and A. M. Ellison. 2002a. Biogeography at a regional scale: determinants of ant species density in bogs and forests of New England. Ecology 83:1604–09.

Gotelli, N. J. and A. M. Ellison. 2002b. Nitrogen deposition and extinction risk in the northen pitcher plant *Sarracenia purpurea*. Ecology 83:2758–65.

Gotelli, N. J. and A. M. Ellison. 2004. A Primer of Ecological Statistics. Sinauer Associates, Sunderland, MA, USA.

Güsewell, S. 2004. N:P ratios in terrestrial plants: variation and functional significance. New Phytologist 164:243–66.

Güsewell, S. 2005. High nitrogen:phosphorus ratios reduce nutrient retention and second-year growth of wetland sedges. New Phytologist 166:537–50.

Heijmans, M. M. P. D., H. Klees, and F. Berendse. 2002. Competition between *Sphagnum magellanicum* and *Eriophorum angustifolium* as affected by raised CO_2 and increased N deposition. Oecologia 97:415–25.

Holden, J. and T. P. Burt. 2003. Hydrological studies on blanket peat: the significance of the acrotelm-catotelm model. Journal of Ecology 91:86–102.

Holland, E. A., B. H. Braswell, J. Sulzman, and J-F. Lamarque. 2005. Nitrogen deposition onto the United States and Western Europe: synthesis of observations and models. Ecological Applications 15:38–57.

Hoosbeek, M. R., N. van Breeman, H. Vasander, A. Buttler, and F. Berendse. 2002. Potassium limits potential growth of bog vegetation under elevated atmospheric CO_2 and N deposition. Global Change Biology 8:1130–38.

Kerkhoff, A. J., B. J. Enquist, J. J. Elser, and W. F. Fagan. 2005. Plant allometry, stoichiometry and the temperature-dependence of primary productivity. Global Ecology and Biogeography 14:585–98.

Kielland, K. 1994. Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. Ecology 75:2373–83.

Koerselman, W. and A. F. W. Meuleman. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. Journal of Applied Ecology 33:1441–50.

Lamers, L. P. M., C. Farhoush, J. M. van Groenendael, and J. G. M. Roelofs. 1999. Calcareous groundwater raises bogs; the concept of ombrotrophy revisited. Journal of Ecology 87:639–48.

Lehmann, C. M. B., V. C. Bowersox, and S. M. Larson. 2005. Spatial and temporal trends of precipitation chemistry in the United States, 1985–2002. Environmental Pollution 135:347–61.

Limpens, J., F. Berendse, and H. Klees. 2004. How phosphorus availability affects the impact of nitrogen deposition on *Sphagnum* and vascular plants in bogs. Ecosystems 7:793–804.

Lynch, J. A., J. W. Grimm, and V. C. Bowersox. 1995. Trends in precipitation chemistry in the United States - a national perspective, 1980–1992. Atmospheric Environment 29:1231–46.

Malm, W. C., B. A. Schichtel, R. B. Ames, and K. A. Gebhart. 2002. A 10-year spatial temporal trend of sulfate across the United States. Journal of Geophysical Research-Atmospheres 107(D22): Article Number 4627.

Malmer, N., D. G. Horton, and D. H. Vitt. 1992. Element concentrations in mosses and surface waters of western Canadian mires relative to precipitation chemistry and hydrology. Ecoography 15:114–28.

McLaughlin, S. B. and R. Wimmer. 1999. Tansley Review No. 104: Calcium physiology and terrestrial ecosystem processes. New Phytologist 142:373–417.

Michelsen, A., I. K. Schmidt, S. Jonasson, C. Quarmby, and D. Sleep. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia 105:53–63.

Miller, E. K., A. J. Friedland, E. A. Arons, V. A. Mohnen, J. J. Battles, J. A. Panek, J. Kadlecek, and A. H. Johnson. 1993. Atmospheric deposition to forests along an elevational gradient at Whiteface Mountain, NY, USA. Atmospheric Environment A–27:2121–36.

Näsholm, T., A. Ekblad, A. Nordin, R. Giesler, M. Högberg, and P. Högberg. 1998. Boreal forest plants take up organic nitrogen. Nature 392:914–16.

Niering, W. A. 1998. Wetlands. Alfred A. Knopf, New York, NY, USA.

Norton, S. A., G. C. Evans, and J. S. Kahl. 1997. Comparison of Hg and Pb fluxes to hummocks and hollow of ombrotrophic Big Heath Bog and to nearby Sargent Mt. Pond, Maine, USA. Water, Air, and Soil Pollution 100:271–86.

Olde Venterink, H., N. M. Pieterse, J. D. M. Belgers, M. J. Wassen, and P. C. De Ruiter. 2002. N, P, and K budgets along nutrient availability and productivity gradients in wetlands. Ecological Applications 12:1010–26.

Olde Venterink, H., M. J. Wassen, A. W. M. Verkroost, and P. C. De Ruiter. 2003. Species richness-productivity patterns differ between N-, P-, and K-limited wetlands. Ecology 84:2191–99.

Proctor, M. C. F. 1992. Regional and local variation in the chemical composition of ombrogenous mire waters in Britain and Ireland. Journal of Ecology 80:719–36.

Raab, T. K., D. A. Lipson, and R. K. Monson. 1996. Non-mycorrhizal uptake of amino acids by roots of the alpine sedge *Kobresia myosuroides*: implications for the alpine nitrogen cycle. Oecologia 108:488–94.

Reich, P. B., D. S. Ellsworth, and C. Uhl. 1995. Leaf carbon and nutrient assimilation and conservation in species of differing successional status in an oligotrophic Amazonian forest. Functional Ecology 9:65–76.

Rochefort, L. 2000. *Sphagnum* – a keystone genus in habitat restoration. The Bryologist 103:503–08.

Schade, J. D., J. F. Espeleta, C. A. Klausmeier, M. E. McGroddy, S. A. Thomas, and L. Zhang. 2005. A conceptual framework for ecosystem stoichiometry: balancing resource supply and demand. Oikos 109:40–51.

Schnell, D. E. 2002. Carnivorous plants of the United States and Canada, second edition. Timber Press, Portland, OR, USA.

Schuster, P. F., D. P. Krabbenhoft, D. L. Naftz, L. D. Cecil, M. L. Olson, J. F. Dewild, D. D. Susong, J. R. Green, and M. L. Abbott. 2002. Atmospheric mercury deposition during the last 270 years: a glacial ice core record of natural and anthropogenic sources. Environmental Science and Technology 36:2303–10.

Small, E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. Canadian Journal of Botany 50:2227–33.

Steinnes, E. 1997. Trace element profiles in ombrogeneous peat cores from Norway: evidence of long range atmospheric transport. Water, Air, and Soil Pollution 100:405–13.

Sterner, R. W. and J. J. Elser. 2002. Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. Princeton University Press, Princeton, NJ, USA.

Svensson, B. M. 1995. Competition between *Sphagnum fuscum* and *Drosera rotundifolia*: a case of ecosystem engineering. Oikos 74:205–12.

Swain, E. B., D. R. Engstrom, M. E. Brigham, T. A. Hennig, and P. L. Brezonik. 1992. Increasing rates of atmospheric mercury deposition in midcontinental North America. Science 257: 784–87.

Swan, J. M. and A. M. Gill. 1970. The origins, spread, and consolidation of a floating bog in Harvard Pond, Petersham, Massachusetts. Ecology 51:829–40.

Tilman, D. 1988. Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, NJ, USA.

Vanarsdale, A., J. Weiss, G. Keeler, E. Miller, G. Boulet, R. Brulotte, and L. Poissant. 2005. Patterns of mercury deposition and concentration in northeastern North America (1996–2002). Ecotoxicology 14:37–52.

Verhoeven, J. T. A., C. E. Johnson, and C. T. Driscoll. 1996. Nitrogen- or phosphorus-limited growth in herbaceous wet vegetation: relations with atmospheric inputs and management regimes. Trends in Ecology and Evolution 11:494–97.

Wakefield, A. E., N. J. Gotelli, S. E. Wittman, and A. M. Ellison. 2005. The effect of prey addition on nutrient stoichiometry, nutrient limitation, and morphology of the carnivorous plant *Sarracenia purpurea* (Sarraceniaceae). Ecology 86:1737–43.

West, S., D. J. Charman, J. P. Grattan, and A. K. Cherburkin. 1997. Heavy metal in Holocene peats from south west England: detecting mining impacts and atmospheric pollution. Water, Air, and Soil Pollution 100:343–53.