INTRODUCTION

Nutrient limitation characterizes most terrestrial and wetland plant assemblages (Chapin et al. 1986,

METHODS

Study Genera

Leatherleaf (*Cha a a h- a a a*) is an evergreen, perennial ericaceous shrub that forms large, dense stands in bogs and poor fens. It ranges from southern Canada and the northern mid-western United States south to Georgia in the eastern United States (Niering 1998). This shrub has extensive root systems and predictably expands through *ha* 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 (*a a a a*)

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 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 concentrations of these nutrients suggest that all three genera are limited by N and K and that *a a a* and *la* 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

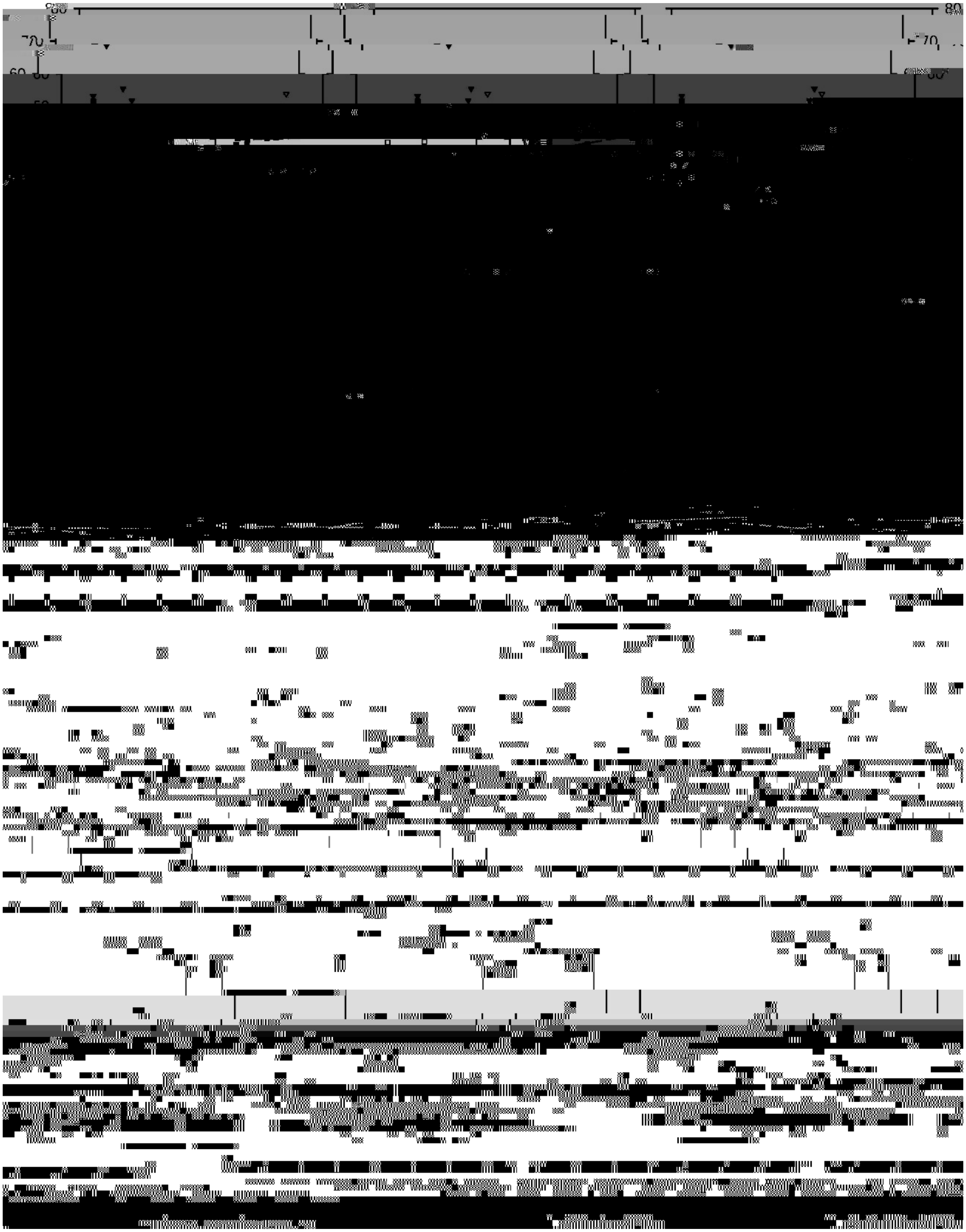

Figure 3. Stoichiometric relationships for the three plant taxa. – [illegible] (circles, solid regression lines); [illegible] (inverted triangles, dashed regression lines); [illegible] spp. (squares, dotted regression lines) – as a function of latitude, longitude, and elevation. Solid symbols indicate plants sampled from bogs in Massachusetts and open symbols are plants sampled from bogs in Vermont. Dark grey lines indicate c

principal axes accounted for 26%, 15%, and 11% of

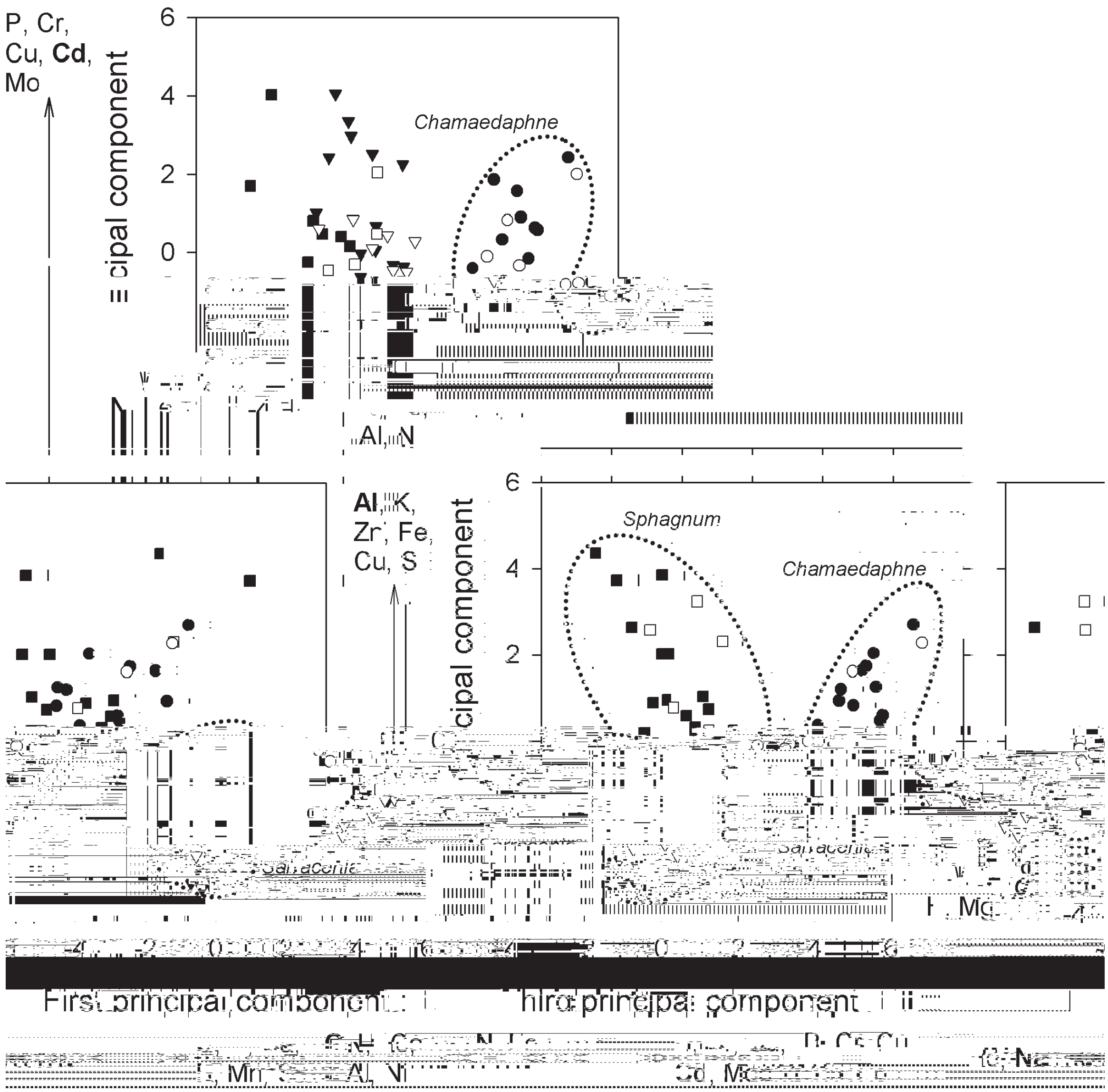

Figure 5. Principal component biplots of the three plant taxa –

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 pore-water 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 *h a* mat

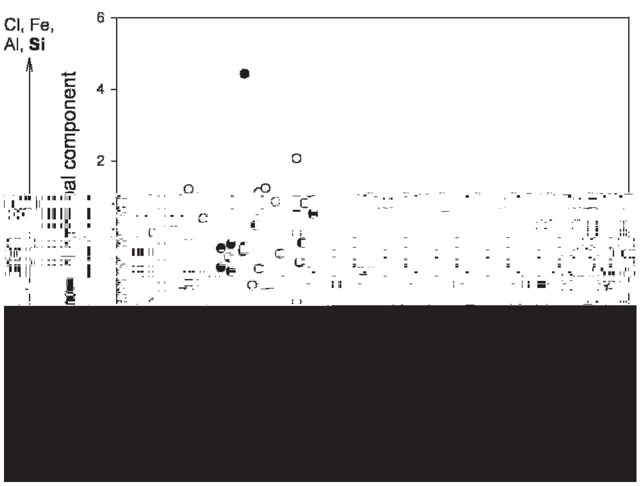

Figure 6. Principal component biplots of the 24 sites as a function of pore-water chemistry. Solid circles indicate Massachusetts bogs and open circles indicate Vermont

was poorly developed, *a a a* densities were low, and the site is accumulating a leaf litter layer and is being invaded by woody vegetation (especially saplings of speckled alder *A a a* (L.) Moench. and gray birch *B a a* 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. *a a a a* and *h a* 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 *a a a* 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 B

elements between surface water concentrations in bogs and plant tissue concentrations in samples of *ha* and *r* *h-* 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 peatlands. Moreover, it also suggests that different plant taxa may be useful indicators for deposition rates of particular nutrients or metals. However, the indicator status of any species will have to be confirmed with experimental studies that demonstrate shifts in stoichiometry in response to particular environmental conditions.

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