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PATTERNS IN NUTRIENT AVAILABILITY AND PLANT DIVERSITY OF TEMPERATE NORTH AMERICAN WETLANDS

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Abstract. Few wetland studies from temperate North America have related either species richness or plant community composition to any direct measure of nutrient availability, or examined changes in species composition following experimental nutrient additions. Studies of wetlands in western Europe and of other terrestrial ecosystems in North America frequently show that nutrient enrichment leads to changes in species composition, declines in overall plant species diversity, and loss of rare and uncommon species. We therefore used an extensive literature survey and analysis of data on plant species composition, species richness, productivity or standing crop, and C:N:P stoichiometry in plant tissues and surface soils to draw conclusions about the nature of nutrient limitation in temperate North American bogs, fens, marshes, and swamps, and to infer their potential response to nutrient enrichment. We searched all major bibliographic data bases for studies containing such data (through March 1998) and added relevant data from our own ongoing research. We analyzed plant and soil data sets by wetland type and by wetland soil type, and the plant data set also by growth form.

Existing studies appear to confirm common generalizations: (1) plant community type changes across broad nutrient gradients; (2) species richness declines as various indicators of nutrient availability increase beyond some threshold; and (3) rare and uncommon species are almost always associated with species-rich communities. However, (1) these generalizations do not always hold within community types; (2) for many community types, the threshold beyond which richness declines has not been established, and high or low diversity may occur below that threshold; and (3) the failure of many studies to include bryophytes precludes drawing strong conclusions about nutrient availability and diversity in peatlands.

Marshes had significantly lower mean nitrogen : phosphorus (N:P) ratios in live tissue than other wetland types (bogs, fens, and swamps), which did not differ significantly from each other. Mean N:P ratios in live tissues were significantly higher in peatlands than in mineral-soil wetlands. Nitrogen : phosporus ratios in litter did not differ significantly between peatlands and mineral-soil wetlands but were higher than in live tissues. Among growth forms, the highest mean N:P ratios in live tissues occurred in bryophytes, and the lowest in vascular herbaceous species. Only bryophyte live tissues differed significantly from other growth forms; litter N:P ratios were not significantly different among growth forms.

Average N:P ratios in surface soils were lower in marshes and swamps than in bogs and fens. Wetlands on mineral soils had lower average N:P ratios than wetlands on peat soils. Average surface soil N:P ratios rose sharply at high soil organic-matter contents ($\geq$90%) and were generally greater than 16 at organic-matter concentrations above 20%.

In combination, plant tissue and surface soil N:P ratios suggest that a large proportion of North American wetlands are either P limited or co-limited by N and P, especially those occurring on organic soils. Only marshes have N:P ratios in both live tissues and surface soils that consistently indicate N limitation, although soils data suggest that the majority of swamps are also N limited. Vascular herbaceous species appear to be N limited, but no pattern is apparent among other growth forms. Inferences drawn from N:P stoichiometry need to be verified by examining ecosystem response to experimental fertilization. High variances in plant and soil N:P ratios suggest that understanding nutrient limitation at both the community and individual-species level may be necessary to predict changes in species composition and richness with nutrient enrichment.

Key words: bryophytes; diversity, wetlands; nitrogen; N:P ratios, wetland nutrient limitation; nutrient enrichment, productivity; nutrient limitation; phosphorus; plant-tissue nutrients; soil nutrients; standing crop and plant species richness; temperate zone wetlands, North America; wetlands, nutrient availability and plant diversity.

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INTRODUCTION

Despite decades of scientific attention (Whittaker 1965), the nature of the relationship between nutrient availability and plant species diversity in wetlands and other ecosystems continues to intrigue ecologists (Tilman and Pacala 1993, Bridgham et al. 1996, Marrs et al. 1996, Hooper and Vitousek 1998, Pollock et al. 1998). Current interest is driven by widespread observation of declines in species diversity associated with nutrient enrichment, especially increased nitrogen (N) flows stemming from human activities (Morris 1991, Vitousek 1994). Changes in species composition, loss of overall plant diversity, conversion of a unique flora to one dominated by a few common species, and replacement of native species by exotics have been reported in connection with nutrient enrichment in several types of wetlands (Aerts and Berendse 1988, Verhoeven et al. 1988, Wassen et al. 1989, Koerselman et al. 1990, Ehrenfeld and Schneider 1991, Kooijman 1992). The most extreme effects have occurred in northern Europe where levels of N deposition range from 30–170 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Berendse et al. 1993). Here many species-rich wetlands have turned to near monospecific stands of nitrophilous species (Verhoeven et al. 1993). Though peak deposition rates are lower in North America (Lovett 1994, Butler and Likens 1995), N deposition is well above background levels, and outputs from agricultural watersheds and urban development can be high (Simmons et al. 1992, Jordan et al. 1997). Some wetlands in North America have already experienced losses of native flora (Ehrenfeld 1983) or shown signs of N saturation (Hanson et al. 1994). With little experimental data available for North American wetlands, predictions of future effects, as well as design of appropriate experiments, depend on a clear understanding of how wetland plant species composition and diversity vary as a function of nutrient availability.

Because of the strong interdependence between species richness and productivity (Tilman and Pacala 1993) and between nutrient supply and productivity, the presumed link between nutrients and species composition is the effect of nutrient enrichment on productivity. For relatively undisturbed wetlands, comparative studies have shown that high species diversity frequently is associated with low nutrient status, that species-rich wetlands typically have moderate productivity and standing crop, and that the optimum range in productivity and standing crop for which species richness is greatest varies among wetland types. These correlations appear robust, having been observed for fens in England (Wheeler and Giller 1982, Wheeler and Shaw 1991) and The Netherlands (Vermeer and Berendse 1983), fens and bogs in Minnesota (Heinselman 1970), riverine wetlands in Ontario (Day et al. 1988), and emergent wetlands in eastern Canada (Moore and Keddy 1989, Moore et al. 1989). Numerous studies, therefore, have sought to identify the nutrients that limit productivity in wetlands and other systems (Vitousek and Howarth 1991, Bridgham et al. 1996, Verhoeven et al. 1996).

However, the relationships among nutrient enrichment, productivity, and species richness in wetlands are not always consistent. Changes in species composition and species richness are not always associated with increases in productivity (Verhoeven et al. 1993). In wet alpine meadows, Bowman et al. (1993) found that nutrient additions led to increases in biomass of graminoid species relative to forbs but had no effect on species richness. In other types of ecosystems, nutrient additions have been shown to reduce plant species diversity (Tilman 1987, Huenneke et al. 1990, Schlesinger 1994).

Furthermore, the question of which nutrient(s) limit(s) plant growth and productivity in wetlands is an open one (Bridgham et al. 1996). Though many freshwater wetlands appear to be N limited (Bowden 1987), phosphorus (P) limitation can occur in fens with high inputs of aluminum- or calcium-rich waters (Richardson and Marshall 1986, Boyer and Wheeler 1989), and in N-enriched fens where annual mowing depletes soil P relative to N (Verhoeven and Schmitz 1991). Bowman et al. (1993) found N and P co-limited production in Colorado wet alpine meadows. Mosses, a major component of many peatlands, appear to be more responsive to alkalinity–acidity gradients than to N or P gradients (Vitt and Chee 1990, Vitt et al. 1995*b*). Few experimental studies of nutrient enrichment in wetlands have been carried out in North America (DiTommaso and Aarssen 1989, Bridgham et al. 1996, Thormann and Bayley 1997*a*, Lockaby and Walbridge 1998), and the prevailing model of vegetation response to enrichment is based primarily on studies of American grasslands (Tilman 1987), arctic tundra (see Jonasson and Shaver 1999), terrestrial forests (Vitousek 1982), and Dutch wetlands (see Verhoeven et al. 1993, Aerts et al. 1999).

The most comprehensive studies of the effects of nutrient enrichment on wetlands are those from The Netherlands. Concerned with the decline in species richness within Dutch wetlands, Koerselman and Meuleman (1996) and Verhoeven et al. (1996) presented data from 45 fertilization studies carried out in European herbaceous wetlands. Their data included both the response of aboveground biomass to fertilization and N:P ratios of live plant tissues in control plots. They concluded that sites with plant N:P <14 were N limited, sites with N:P >16 were P limited, and sites with N:P between 14 and 16 were co-limited by N and P.

While these studies offer insight into potential effects on North American wetlands, their results may not be simply extrapolated to the situation in North America (but cf. Verhoeven et al. [1994]). Rates and forms of N deposition in The Netherlands differ greatly from those in North America, as do other factors likely to influence response to increased nutrient supply—

wetland history, water budgets, hydroperiods and water chemistry, watershed characteristics, management practices, and the diversity of wetland types in the landscape. The successional stage of Dutch wetlands, a key variable controlling plant response to nutrient additions (Verhoeven and Schmitz 1991), is determined by long-term manipulation of sites through peat cutting, water control, and mowing. Most North American wetlands have not been subjected to these types of manipulations. Though influenced by land-use changes in their watersheds, their successional stage is largely a function of glacial history, long-term climatic patterns, and harvesting in the case of some forested wetlands. The relative contributions of groundwater, surface water, and precipitation to water budgets of many North American wetlands are controlled largely by physiographic and climatic factors (Winter 1992), while the different sources of water to Dutch wetlands are highly altered and intensively managed (Wassen et al. 1990, Verhoeven et al. 1993). Hence, hydroperiods and water chemistry in North America largely reflect climatic and watershed variables; these characteristics of Dutch wetlands are a function of human control of water sources and timing. With The Netherlands containing the highest population density in the world and one of the highest densities of domesticated animals, most Dutch wetlands are surrounded by intensively used land, and few natural wetlands remain. In contrast, North America still supports many relatively undisturbed wetlands, as well as a high diversity of wetland plant communities (Dahl and Johnson 1991, Wilen and Tiner 1993).

Our goal was to determine the extent to which different types of temperate freshwater wetlands in North America conform to the general model, strongly influenced by research in The Netherlands, relating nutrient enrichment to plant species composition and diversity. To achieve this goal, we conducted an extensive review of the North American wetland literature to: (1) examine relationships among nutrient availability, plant species composition, primary productivity or biomass, and species richness; (2) synthesize results of experimental studies on responses to nutrient enrichment (i.e., changes in species or community-level productivity that indicate whether N or P limits plant growth); and (3) examine N:P stoichiometry in vascular and bryophyte plant tissues and soils as indices of N vs. P limitation. We included herbaceous and forested wetlands occurring on both peat and mineral soils in our review, and focused on the relationship between increased nutrient supply and plant community composition and diversity. Fertilization effects on nutrient-use efficiency, decomposition, and other nutrient-related soil processes in temperate freshwater wetlands are covered by Aerts et al. (1999).

METHODS

We searched all major bibliographic data bases (as of March 1998) for studies containing data on biomass, net primary productivity, plant species richness, and carbon (C), N, and P in plant tissues and soils for temperate freshwater wetlands of North America. To these we added relevant data from our own on-going research. We excluded studies from northern boreal and arctic regions of North America (Jonasson and Shaver 1999), and from the sub-tropical region (Richardson et al. 1999), since these are dealt with in companion papers. We also excluded studies from coastal areas in which freshwater sites could not be differentiated from saltwater sites. We included studies from the southern boreal region because of the affinity of these wetlands to those of temperate North America. As we were interested in the stoichiometry of C, N, and P, we excluded plant tissue data that reported values for only C, N, or P, and soils data that did not report values for both N and P. When studies included a fertilization treatment, we used only values reported for unfertilized controls. Fifty-two studies contained data on plant tissue nutrients (Appendix A); 24 contained soils data (Appendix B). Only four studies contained data on plant C and P or C and N; only 14 studies included data on soil C, N, and P. For a list of all studies see Appendix C.

All relevant data were entered into spreadsheets and analyzed by categories: (1) broad wetland types; (2) wetlands with peat vs. mineral soils; (3) plant growth forms; (4) depth interval from which soil was collected; (5) species identity and plant part; (6) time of year data were collected; and (7) live vs. dead material for tissue nutrients. We excluded data where growth form or plant parts were combined. When data for more than one soil depth were available, we took a weighted average of nutrient concentrations for the upper 30 cm of the soil profile. We defined wetland type as defined by the author(s) of a study, recognizing that wetland types are not defined consistently in the literature (Mitsch and Gosselink 1993, Bridgham et al. 1996). In general, however, bogs and fens are true peat-accumulating ecosystems while swamps and marshes occur on mineral soils or shallow peats (Vitt 1994). Bogs are acidic peatlands dominated by mosses of the genus *Sphagnum*. True bogs are ombrotrophic systems that receive all water inputs from the atmosphere and typically have pH's <4.0, low alkalinity, and negligible concentrations of base cations in surface waters. Poor fens also are acidic, *Sphagnum*-dominated peatlands but have somewhat higher surface water pH's (4.0–5.5) than bogs, presumably because they receive some minerotrophic drainage in addition to precipitation. Rich fens are alkaline peatlands that receive significant inputs from groundwater and/or surface water. They have surface water pH's >5.5, higher alkalinity, and distinctly higher concentrations of base cations than bogs and poor fens. Brown mosses (true mosses, largely of the Amblystegiaceae) and sedges of the genus *Carex* dominate the ground layer of rich fens. Rich fens with pH's of 5.5–7.0 are termed "moderate-rich fens" while extreme-rich fens have pH's >7.0 (Vitt 1994). Swamps are forested wetlands; marshes are dominated by herbaceous vegetation, notably cattails (*Typha* spp.) and large sedges of the genus *Carex*. Neither has a well-developed moss layer; both receive significant inputs of surface and/or groundwater and usually occur on mineral soils. Greater water-level fluctuations and surface-water inputs generally lead to higher concentrations of base cations and nutrients in swamps and marshes than in bogs and fens. We grouped forested bogs with bogs.

We analyzed plant and soil data sets by wetland type and by wetland soil type. We further analyzed the vegetation data set by growth form. Our response variables were the stoichiometric ratios of N:P, C:P, and C:N in vegetation, and N:P in soils. Where we found heteroscedasticity across categories, we log-transformed data prior to analysis. We present all data non-transformed except where specifically indicated. Most data sets conformed to assumptions of normality; we log-transformed those that did not. We analyzed our own balanced data sets using simple regression models.

Data sets derived from literature reviews are likely to be unbalanced. Different studies have different numbers of data points, and data points within individual studies are likely to be correlated. To overcome these problems, we used SAS PROC MIXED, a mixed linear-model procedure where data may exhibit correlation and nonconstant variability (SAS 1996). In this way, we were able to group data into clusters, each consisting of data from one site of an individual published study, i.e., data points that are correlated. We considered data from one site, reported by the same author in separate studies, as a single cluster.

In our analyses comparing wetland types, soil types, or plant growth forms (see Tables 1 and 2), we used least-squares means (means of the cluster means), rather than simple means. This approach weights each cluster equally rather than weighting each data point equally. To compare differences among categories (e.g., wetland types), we used the Tukey option, adjusted for unbalanced data. While not as conservative as some other adjustments available, this test may find no significant differences among groups that appear to have different means. This may be because one of the groups being compared has a much lower number of degrees of freedom than the others.

RESULTS

Species composition and diversity vs. nutrient availability/NPP

Few North American studies have quantified species composition or diversity with respect to direct measures of nutrient availability (Bridgham et al. 1996, but see Walbridge 1991). The more common approach has been to relate composition and/or diversity to hydrologic and ionic gradients (e.g., Heinselmann 1970, Vitt and Slack 1975, Slack et al. 1980, Glaser et al. 1981, Paratley and Fahey 1986, Chee and Vitt 1989, Motzkin 1994, Walbridge 1994, Pollock et al. 1998). Those interested in vegetation–nutrient relations of herbaceous wetlands have often inferred nutrient supply from community biomass, less commonly from net primary productivity (NPP), or from some other variable (e.g., soil organic matter) presumed to relate to nutrient flux (e.g., Wisheu and Keddy 1989, Johnson and Leopold 1994). In peatlands the acidity–alkalinity gradient from bogs to rich fens is often interpreted as a nutrient-availability gradient, with associated changes in species composition, richness, and productivity presumed to be caused by changes in nutrient availability (Bridgham et al. 1996). Species richness and productivity of mosses are frequently ignored even in systems where they dominate the ground layer. Seldom are species composition, nutrient status, and productivity quantified in the same study. (See Grace and Pugesek [1997] for an exception from a coastal wetland.)

Species richness and surrogate measures of nutrient availability.—The most extensive North American work relating species richness to biomass is that of Keddy and his associates on herbaceous emergent wetlands (Day et al. 1988, Wilson and Keddy 1988, Moore and Keddy 1989, Wisheu and Keddy 1989, Shipley et al. 1991). This work and related studies from Europe have recently been reviewed (Marrs 1993, Marrs et al. 1996). In general, Keddy's work conforms to the "hump-shaped" model of the relationship between species richness and biomass (Grime 1979, Tilman 1986), i.e., richness is greatest at some intermediate value of community biomass and lower at both ends of the biomass gradient. More correctly, close inspection of the data shows that while species richness may be high or low at intermediate points on the gradient, high diversity never occurs at either very high or very low biomass. The trick is in identifying where on the gradient any particular community is located. Keddy and others (e.g., Wisheu and Keddy 1989, Shipley et al. 1991) have identified important constraints on the model, and research now focuses on identifying controlling mechanisms (e.g., McJannet et al. 1995, Twolan-Strutt and Keddy 1996).

For purposes of predicting responses to nutrient enrichment, three constraints on the species richness–biomass model are particularly relevant. First, the relationship breaks down when examined within wetland community types. Moore and Keddy (1989) found no pattern when they looked at species richness and biomass within 15 different herbaceous wetlands. We also found no relationship between species richness and biomass in two rich fens in New York (B. Bedford, *unpublished data*). Nor did we find any strong relationship between species richness and more direct indicators of nutrient availability such as soil C:N, C:P, or N:P ratios within another New York rich fen (Fig. 1). These results raise the question of how studies based on natural gra-

TABLE 1. Nitrogen (N) and phosphorus (P) concentrations in live tissues and litter of wetland plants (see *Methods*).

	N					P				
Sample	Mean (%)	Range (%)	1 SE (%)	*n*	*N*	Mean (%)	Range (%)	1 SE (%)	*n*	*N*
All samples										
Live tissue	1.34	0.08–4.20	0.08	215	65	0.14	0.004–0.64	0.01	215	65
Litter	1.05	0.10–2.08	0.08	66	20	0.13	0.002–0.68	0.04	56	15
Wetland types										
Bogs										
Live tissue	0.85	0.08–2.08	0.10	61	18	0.07	0.004–0.17	0.01	61	18
Litter	0.66			1	1				0	0
Poor Fens										
Live tissue	0.80	0.28–1.37	0.11	22	6	0.06	0.02–0.12	0.01	22	6
Litter	1.01	0.24–2.08	0.08	11	2	0.06	0.02–0.11		8	2
Moderate Fens										
Live tissue	1.46	0.44–3.85	0.22	34	12	0.12	0.01–0.26	0.02	34	12
Litter	1.21	0.36–1.91	0.20	11	3	0.11	0.03–0.20	0.03	11	3
Rich Fens										
Live tissue	1.33	0.84–1.65	0.11	12	5	0.11	0.06–0.16	0.02	12	5
Litter	1.00	0.42–2.04	0.10	17	5	0.08	0.03–0.15	0.002	11	2
Marshes										
Live tissue	1.97	0.83–4.20	0.11	41	13	0.29	0.10–0.64	0.03	41	13
Litter	1.22	0.75–1.58	0.36	5	2	0.16	0.06–0.22	0.06	5	2
Swamps										
Live tissue	1.48	0.69–2.41	0.09	45	12	0.12	0.03–0.25	0.02	45	12
Litter	1.04	0.10–1.81	0.16	21	7	0.16	0.002–0.68	0.09	21	7
Plant growth form										
Bryophytes										
Live tissue	0.65	0.24–0.96	0.06	23	11	0.04	0.01–0.12	0.01	23	11
Litter	0.60	0.24–0.78	0.05	12	7	0.04	0.02–0.10	0.01	8	3
Evergreen species										
Live tissue	0.99	0.08–1.95	0.07	85	28	0.09	0.004–0.26	0.01	85	28
Litter	1.31	0.90–1.77	0.24	5	3	0.10	0.07–0.12	0.01	5	3
Vascular herbs										
Live tissue	1.71	0.64–4.20	0.11	65	26	0.20	0.03–0.64	0.02	65	26
Litter	1.15	0.74–1.94	0.08	22	10	0.10	0.05–0.22	0.02	18	6
Deciduous species										
Live tissue	1.48	0.10–2.40	0.11	43	21	0.10	0.004–0.25	0.01	43	21
Litter	1.28	0.10–2.08	0.14	27	13	0.14	0.07–0.68	0.06	25	11
Soil type										
Mineral soil										
Live tissue	1.89	0.83–4.20	0.08	53	17	0.25	0.10–0.64	0.03	53	17
Litter	1.06	0.10–1.81	0.16	22	8	0.17	0.002–0.68	0.08	22	8
Peat soil										
Live tissue	1.14	0.08–3.85	0.08	163	48	0.09	0.004–0.26	0.01	163	48
Litter	1.05	0.24–2.08	0.07	44	12	0.09	0.02–0.20	0.01	34	7

Note: *N* is the number of clusters from which the least-squares means are derived, and *n* is the number of all data points.

dients that cross community types apply to gradients imposed within a single community by human enrichment of ecosystems. Comparisons across undisturbed communities may not provide a good analog for predicting effects of anthropogenic nutrient additions unless such enrichment produces nutrient levels and ratios similar to natural gradients. Furthermore, as Moore and Keddy's (1989) work indicates, controls operating within communities may differ from those controlling richness among communities.

Second, any productivity gradient is likely to be complex and incorporate other variables related to species diversity (Day et al. 1988, Grace and Pugesek 1997). The set of interacting variables along the gradient will differ among wetland types, confounding efforts to extrapolate results from one type to another. Third, as Marrs (1993, Marrs et al. 1996) points out, increases or decreases in species richness with enrichment cannot be predicted with this model unless the biomass threshold beyond which species density declines is known. Empirical data show that this threshold varies among community types, and data exist for only

TABLE 2. Nitrogen (N) and phosphorus (P) concentrations and N:P ratios of surface soils by wetland type and soil type.

	N (%)			P (%)			N:P ratio			
Sites	Mean	Range	1 SE	Mean	Range	1 SE	Mean	Range	1 SE	n†
Wetland type‡										
Bogs	1.16^{b}	0.48–2.61	0.14	0.05^{b}	0.03–0.16	0.03	24.1^{a}	7.9–60.4	0.7	26
Poor fens	1.35^{b}	0.70–1.77	0.16	0.07^{b}	0.03–0.11	0.05	24.1^{a}	11.4–45.1	0.9	14
Moderate-rich fens	1.88^{a}	1.13–2.78	0.18	0.08^{ab}	0.03–0.14	0.05	26.8^{a}	11.8–55.3	0.8	15
Rich fens	1.98^{a}	0.43–3.00	0.16	0.09^{ab}	0.01–0.17	0.04	23.0^{a}	13.6–36.5	0.5	23
Marshes	1.41^{b}	0.72–1.72	0.28	0.25^{a}	0.12–0.70	0.22	8.7^{b}	2.1–13.8	1.0	5
Swamps	1.28^{b}	0.09–2.58	0.16	0.09^{a}	0.02–0.29	0.05	14.6^{ab}	4.6–25.8	0.5	26
Soil type§										
Organic soils	1.59^{c}	0.48–3.00	0.08	0.08^{d}	0.03–0.29	0.02	22.7^{c}	5.9–59.4	0.3	98
Mineral soils	0.62^{d}	0.09–1.50	0.20	0.13^{d}	0.01–0.70	0.13	8.8^{d}	2.1–30.7	0.8	11
All sites	1.50	0.09–3.00	0.08	0.09	0.01–0.70	0.03	21.3	2.1–60.4	0.3	109

† Number of observations.

‡ Among wetland types, means with the same lowercase superscript letter (a, b) are not significantly different at $P < 0.001$.

§ Between soil types, means with the same lowercase superscript letter (c, d) are not significantly different at $P < 0.004$.

a limited number of studies from North America. Other than the work by Keddy and his colleagues, we found only two data sets for freshwater wetlands of North America. A study from southeast Alaska (Pollock et al. 1998) found that species richness, which was only weakly related to an index of total aboveground productivity, declined above 300–400 g dry biomass·m^{-2}·yr^{-1}. A study from the southern United States (Gough et al. 1994) also initially suggested a very weak relationship between diversity and biomass. However, when Marrs et al. (1996) re-analyzed the data, the probability of a site being species poor decreased significantly above a threshold of 3000 g/m^2, a biomass 2–7 times greater than reported in other studies. Clearly, no single threshold can be defined.

While Keddy's model has limitations, his studies of species-rich and species-poor wetlands in Canada make two key points regarding species diversity and biomass gradients. First, uncommon and rare species are positively associated with low-to-intermediate-biomass, species-rich sites, but do not occur at high biomass values (Moore et al. 1989). Johnson and Leopold (1994) also found that rare species occurred only in species-rich New York wetlands. Second, sites with low standing crop have a greater diversity of wetland community types as determined by dominant species. The number of vegetation types declined as standing crop increased, with sites of highest biomass all being dominated by cattail, *Typha* spp. (Moore et al. 1989). If these two findings are generally true, then the overall eutrophication of the landscape (Vitousek 1994) portends the loss of both species and community types.

Species richness and pH/base cation gradients.—Until recently, almost all studies of both North American and European peatlands related vegetation characteristics to surface-water chemistry, especially pH and concentrations of Ca and Mg (e.g., Walbridge 1994). Few comparative studies of peatland vegetation also reported N and P concentrations in peat (Richardson and Marshall 1986, Vitt 1990, Vitt and Chee 1990, Walbridge 1991, Bridgham and Richardson 1993). Fewer still included any direct measure of N and P supply to plants, i.e., nutrient flux rates (Walbridge 1991).

Recent studies of Canadian (Vitt 1990, Vitt et al. 1995*a*) and North Carolina (Walbridge 1991, Bridgham and Richardson 1993) peatlands call into question the assumed concordance between acidity–alkalinity gradients, as indicated by pH and base cation concentrations, and nutrient-availability gradients. In a survey of 100 sites in Alberta (Canada), Vitt (1990) found that pH and Ca differentiated among mire vegetation types (i.e., bog, poor fen, moderate-rich fen, extreme-rich fen). However, nutrient concentrations in surface waters did not correlate with surface-water pH or Ca concentrations. He also found no significant correlation of NO^{-}_{3}, NH^{+}_{4}, total organic N, or total P in surface water with mire vegetation type. A later study (Vitt et al. 1995*a*), using both surface and subsurface water, also showed that while pH and alkalinity could be used to corroborate classifications of peatland type based on vegetation and hydrology, nutrient concentrations showed either no relationship or a slight decrease along the bog–rich fen gradient. Given their (Vitt 1990, Vitt et al. 1995*a*) use of concentrations rather than nutrient-flux measurements, the lack of correlation is not surprising. Nonetheless, the sometimes higher concentrations of inorganic forms of nutrients in bog waters than in fen waters emphasize the need to measure nutrient availability directly. European data on rates of phosphorus release and nitrogen mineralization show bogs to have higher rates than fens (Verhoeven et al. 1990).

Vitt (1990) also concluded that bryophyte productivity does not differ among bogs and fens. If the availability of N and P follows the same gradient as pH, Ca, and Mg, then, as Vitt (1990) points out, bogs should have the lowest productivity and rich fens the highest, with poor fens intermediate between the two. Thormann and Bayley (1997*c*) recently reported higher moss production in a bog than in two rich fens for one

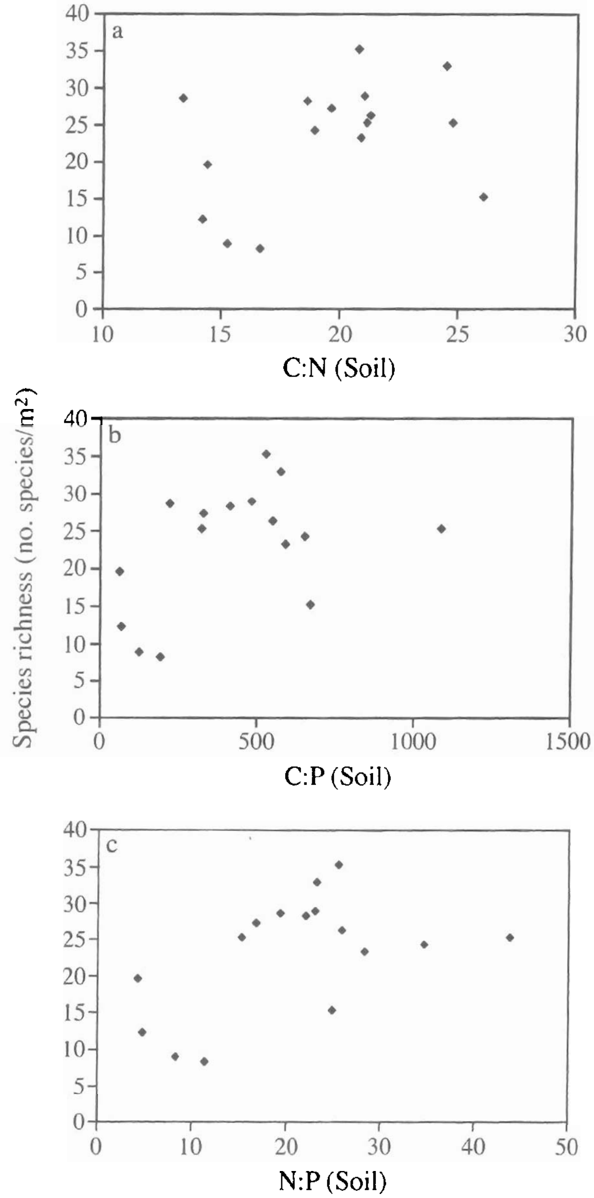

FIG. 1. The relationship between species richness and soil nutrients within a single New York (USA) rich fen. Richness is the mean number of species (vascular plants and bryophytes) per square meter for three replicate 1-m^2 plots, plotted as a function of (a) the carbon-to-nitrogen ratio (C:N), (b) the carbon-to-phosphorus ratio (C:P), and (c) the nitrogen-to-phosphorus ratio (N:P) in the soil. Soil ratios are all based on total C, N, and P.

year and no significant differences between the bog and one of the fens in another year. More significantly, Thormann and Bayley (1997*c*) found somewhat higher total aboveground production (all strata) in a bog than in two fens, and no significant difference between the bog and the mean of three fens. Furthermore, in a summary of other data on aboveground net primary production in North American peatlands, they report that the mean for bogs was somewhat higher than that for fens.

Because findings from North Carolina peatlands (Walbridge 1991, Bridgham and Richardson 1993) are based on nutrient values in soil, they provide even stronger support for Vitt's (1990, Vitt et al. 1995*a*) conclusions, which are based primarily on surface-water chemistry. The North Carolina studies also question the assumption that vegetation gradients necessarily follow gradients of pH and base-cation concentrations in all peatlands. Walbridge (1991) found that several measures of P availability increased along the gradient from short pocosin to tall pocosin to bay forest, thus linking plant community composition to nutrients rather than to pH or cation concentrations. Although his data did not include measures of water chemistry against which to check concordance with pH or cation gradients, his nutrient-flux data showed an increasing trend along the expected gradient. However, Bridgham and Richardson (1993), working in the same study area, found that: (a) pH and exchangeable base metal cations in soils did not differentiate among plant community types; (b) the lowest base saturation occurred in minerotrophic swamps; (c) pH and Ca concentrations were similar among vegetation types; and (d) soil nutrients were better predictors of community type. Thus, pH and base-cation concentrations in soils do not appear to differentiate community types in these southern peatlands in the same way that surface-water chemistry appears to differentiate among northern bogs and fens.

Bryophyte species richness.—The failure of many studies to include bryophytes precludes drawing strong conclusions about the relationship between nutrient availability and diversity in peatlands where mosses dominate the ground layer in all undisturbed types (Vitt et al. 1995*b*). Recent work in Canada suggests that the bryophyte pattern is not one of increasing species richness along the gradient from bogs to rich fens. Vitt et al. (1995*b*) examined bryophyte species richness in 96 peatlands of continental western Canada to determine if patterns in bryophyte richness paralleled the apparent increase in overall species richness typically cited for the bog-to-rich-fen gradient. They found 53 species in bogs, 44 in poor fens, 35 in moderate-rich fens, and 67 in extreme-rich fens. None of nine surface-water variables they measured (pH, conductivity, Ca, Mg, K, Na, Fe, P, and S) correlated with bryophyte species richness when all sites were considered, and no pattern in richness emerged along the bog–fen gradient at the site level. We observed only a weak correlation between moss species richness and pH in a study of 19 New York fens (Fig. 2). Species richness of vascular plants and, therefore, total species richness increased with pH but for bryophytes the pattern is less clear.

Within individual types, Vitt et al. (1995*b*) found that bryophyte species richness increased with pH in poor fens, decreased in extreme-rich fens, but did not vary with pH in bogs and moderate-rich fens. At the

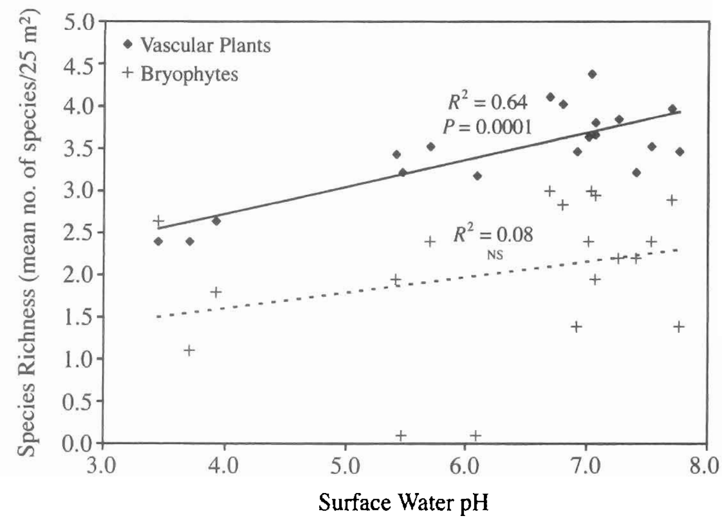

FIG. 2. Species richness of vascular plants and bryophytes plotted against the pH of surface waters in 19 New York (USA) fens. Richness data have been natural-log transformed.

site level, bryophyte species richness of bogs and poor fens ranged from 5 to 24 species while that of moderate-rich and extreme-rich fens ranged from 5 to 28 species. Thus, any individual bog might contain more species than an individual fen. Because fens were more variable in species composition, however, the gamma (landscape) diversity of fens was higher than that of bogs. Of the 110 species Vitt et al. (1995*b*) found, 62% occurred in bogs and poor fens and 71% occurred in brown moss-dominated rich fens. Habitat heterogeneity (46%) and temperature (15%) explained most of the variation in richness within these undisturbed peatlands. However, Vitt et al. (1995*b*) did not include any direct measure of nutrient availability other than total P in surface waters in their study, and their data did not include diversity of vascular species.

Forested wetlands.—For forested wetlands, patterns in species composition and richness most typically have been related to gradients of flooding frequency, hydroperiod, water source, and hydrogeomorphic setting, rather than to direct measures of nutrient availability or productivity as a proxy for nutrient availability (cf. Brinson 1990, Brinson 1993, Mitsch and Gosselink 1993). Brinson (1990) reviewed community-level aspects of riverine forests worldwide and found that, in general, tree species diversity increased as flooding frequency decreased. He attributed low diversity of understory (including shrub) species to low light availability in these closed-canopy forests, but did not rule out the effects of flooding and low soil aeration (Brinson 1990). Hall and Harcombe (1998) found that sapling distributions in a Texas floodplain forest responded primarily to flooding and light availability.

Compositional differences in southeastern swamps are commonly observed along red- vs. blackwater rivers, whose waters arise in the Piedmont or Coastal Plain, respectively. The former are considered more nutrient rich because their waters carry higher sediment and nutrient loads; the latter are considered more oligotrophic, with waters dominated by dissolved organic acids (cf. Lockaby and Walbridge 1998). We found no studies that directly addressed the relationship between nutrient availability and species diversity in forested wetlands of the southeastern United States. However, Marks and Harcombe's (1981) study of forests in southern Texas included species richness and unpublished data on total P and C in soils for wet forests (Peter Marks and Paul Harcombe, *personal communication*). Our analysis of their data (not shown) showed no clear relationship between total species richness and total P or C:P ratio in the soils.

Thus, the relationship between species composition or diversity and nutrient availability is largely one that is assumed through the relationship of nutrient availability to productivity or, more often, the limited surrogate of aboveground biomass. Few studies of either herbaceous or forested wetlands from North America include direct measures of both nutrient availability and species diversity of bryophytes and vascular species. Changes in the acidity/alkalinity of surface waters along the gradient from bog to rich fen have been used to infer that increases in total species diversity along this gradient are linked to increases in nutrient availability. The link between surface-water acidity/alkalinity and nutrient availability to plants is yet to be established.

C:N:P stoichiometry in plants and soils—relation to nutrient availability and limitation

Well-controlled and well-replicated nutrient-addition experiments are the only way to determine unequivocally what resource limits either an individual plant population or a community type. Even under these circumstances, lack of response does not necessarily mean that a particular nutrient is not limiting (Chapin et al. 1986). In the absence of such experiments, nutrient limitation has been inferred from element ratios in live plants, their litter, or from element ratios in the soil or water in which plants grow (Vitousek and Howarth 1991). The fundamental basis for the use of these ratios is the functional relationship between C, N, and P in living organisms (Redfield 1958, Reiners 1986). The empirical basis is a large number of observations showing that N:P ratios in plant tissues and soil are highly correlated with each other and reflect the relative scarcity or abundance of these elements in their environment, though several studies have questioned this correlation (see Wassen et al. 1995). Experimental data from European wetlands, however, are largely consistent with theory. Nitrogen : phosphorus ratios in plant tissues increased when N was added to mesotrophic fens in The Netherlands (Verhoeven and Schmitz 1991) and to bogs in Sweden (Aerts et al. 1992).

Nutrients limiting plant growth in fertilization studies from North America.—Bridgham et al. (1996) recently reviewed fertilization studies from northern wetlands. Only 11 of the 33 studies were from temperate North America. Species and community types were limited; none of the studies examined community responses. Four of the studies were from pocosins in North Carolina, and only one study dealt with more than one species. The species examined included only three species of *Sphagnum*, seven species of trees and shrubs, one carnivorous herb, and two graminoid species plus unidentified *Carex* species. Only two of the studies were conducted on mineral soils.

Unlike studies from Europe, the temperate North American studies suggest that the question of which nutrient(s) are limiting in wetlands is unresolved and that multiple gradients are more likely to be limiting (Bridgham et al. 1996). Most of the European studies clearly demonstrate either N or P limitation (Bridgham et al. 1996, Verhoeven et al. 1996). Only two of the North American studies show a single nutrient to be limiting. More recent fertilization studies (Li and Vitt 1997, Thormann and Bayley 1997*a*) have not resolved the issue. Li and Vitt (1997) found that N additions increased production of the mosses *Sphagnum fuscum* in a bog and *Tomenthypnum nitens* in a rich fen, but not of the shrubs *Ledum groenlandicum* in the fen nor *Betula pumila* in the fen. In contrast, production of *Sphagnum fuscum* decreased after one year when Thormann and Bayley (1997*a*) added N and water or P and water, but increased with water only. Interestingly, other responses to nutrient additions were species specific and neither N nor P seemed to limit total aboveground production in fens or marshes.

Nutrient concentrations in plants of North American wetlands.—The range of concentrations found in live biomass and litter varied among wetland types and by growth form (Table 1). Nitrogen concentrations in all samples ranged from 0.08 through 4.2% in live tissues and from 0.10 through 2.08% in litter, while P concentrations ranged from 0.004–0.64% in live tissues and from 0.002 through 0.68% in litter. When segregated by wetland type, N and P concentrations (means ± 1 SE) in live tissues were lowest in poor fens (0.80 ± 0.11%; 0.06 ± 0.01%; respectively) and highest in marshes (1.97 ± 0.11%, 0.29 ± 0.03%, respectively). For intermediate values, the rank orders of N and P concentrations were similar: bogs < rich fens < moderate-rich fens ≤ swamps (Table 1). The single value we found for bog litter had the lowest mean N concentration for litter (0.66%). Marshes and moderate-rich fens had the highest litter N concentrations (1.22 ± 0.36%, and 1.21 ± 0.20%, respectively), with intermediate rankings of: rich fens < poor fens < swamps (Table 1). Poor fens had the lowest mean P concentrations for litter (0.06 for only two clusters), followed by: rich fens < moderate-rich fens < marshes = swamps.

Among growth forms, bryophytes had the lowest N concentrations (means ± 1 SE) in live tissues (0.65 ± 0.06%), and vascular herbs the highest (1.71 ± 0.11%), with evergreen trees and shrubs and deciduous trees and shrubs in between (Table 1). Bryophytes also had the lowest mean P concentrations in live leaves (0.04 ± 0.01%) (Table 1). The highest mean P concentration in live tissues occurred in vascular herbs (0.20 ± 0.02%). Evergreen and deciduous trees and shrubs were intermediate with nearly equal values (0.09 ± 0.01% and 0.10 ± 0.01%, respectively). For litter, bryophytes had the lowest mean N concentration (0.60 ± 0.05%) and evergreen species had the highest (1.31 ± 0.24%). The rank order for mean litter N concentrations was: bryophytes < vascular herbs < deciduous trees and shrubs < evergreen trees and shrubs. For mean litter P, the order was: bryophytes < evergreen trees and shrubs < vascular herbs < deciduous trees and shrubs (Table 1). If grouped on the basis of soil type, plants growing in peat had lower N and P concentrations in live plant tissues (1.14 ± 0.08% and 0.09 ± 0.01%, respectively) and litter (1.05 ± 0.07% and 0.09 ± 0.01%, respectively) than plants growing in mineral soils (1.89 ± 0.08% and 0.25 ± 0.03%, respectively, for live tissue; 1.06 ± 0.16% and 0.17 ± 0.08%, respectively, for litter) (Table 1).

N:P ratios in plants of North American wetlands.—When nutrient ratios are examined among broad categories of wetland types, the data do not show a continuously decreasing trend of plant N:P along a bog–swamp gradient for either live material or litter (Fig. 3). In fact, the only significant difference among types is for live-tissue N:P in marshes, which is much lower than for all other wetland types. Swamps, which predominate on mineral soils as do marshes, have only somewhat lower N:P ratios in live tissues than do bogs, poor fens, and moderate-rich fens, which predominate on peat soils. Mean N:P in live tissues in swamps, however, is not lower than that in rich fens. Marshes also have the lowest mean N:P ratio for litter, although differences in mean litter N:P ratios among wetland types are not significantly different. N:P ratios (means ± 1 SE) of live tissues in all wetland types are between

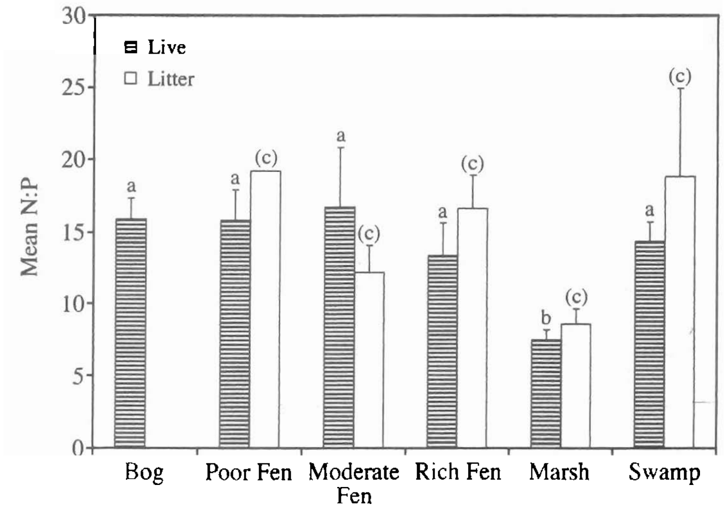

FIG. 3. Nitrogen-to-phosphorus ratio (N:P) of live tissues and litter of plants in different wetland types. Bars show means + 1 SE. Bars for live tissue with the same lowercase letters above are not significantly different among types ($P < 0.05$), and similarly for litter with letters in parentheses. Differences between N:P ratios in live tissue and litter were not significant for any type. The numbers of data points (n) and clusters (N) from which the means are derived are given in Table 1. Data sources are given in Appendices A and C.

13.4 (±2.25) and 16.7 (±4.11) except marshes which have a mean N:P = 7.5 (±0.68). Mean N:P ratios increase in litter as compared to live tissues in all wetland types except moderate-rich fens.

When grouped by plant growth form, mean live-tissue N:P ratios were significantly higher in bryophytes than other growth forms, which did not differ significantly from each other (Fig. 4). Live-tissue N:P tended to decrease in the order: bryophytes > deciduous trees and shrubs > evergreen trees and shrubs > vascular herbs (Fig. 4). Litter N:P ratios did not differ significantly among growth forms (Fig. 4), although litter N:P ratios of deciduous trees and shrubs appeared higher than those of other growth forms. Mean N:P ratios in litter increased relative to live tissues only in vascular herbs and deciduous trees and shrubs (Fig. 4).

When separated on the basis of soil type (data not shown), N:P ratios in live tissues were significantly higher ($P = 0.0001$) on peat (14.9 ± 0.85) than on mineral soils (8.7 ± 0.81) (means ± 1 SE). Litter N:P ratios, however, were higher on mineral soils (16.4 ± 5.57) than on peat (15.2 ± 1.44), though the difference was not significant. Mean litter N:P was higher than live-tissue N:P on both peat and mineral soils but not significantly so.

Data from forested wetlands in the southeastern United States show a strong relationship between N:P ratios in litterfall and forest productivity as indicated by litterfall mass (Lockaby and Walbridge 1998). For these riverine and depressional forests, as the balance between N and P in litterfall changes over a range of 5 to 21, litterfall mass first rises and then declines, approximating a normal distribution ($P < 0.05$; Lockaby and Walbridge 1998). Maximum litterfall production occurs at a litterfall N:P ratio of ~12, and declines both above and below this value. Eutrophic redwater swamps have litterfall N:P ratios below 12 (mean = 7.8) while those of oligotrophic blackwater swamps tend to lie above 12 (mean = 13.0), possibly indicating a shift from N to P limitation (Lockaby and Walbridge 1998).

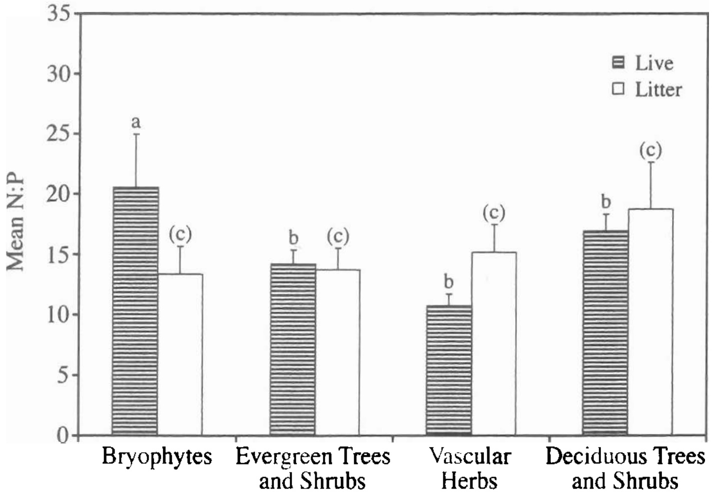

FIG. 4. Nitrogen-to-phosphorus ratio (N:P) of live tissues and litter of wetland plants of different growth form. Format is as in Fig. 3. Differences between N:P ratios in live tissue and litter were not significant for any growth form. The numbers of data points (n) and clusters (N) from which the means are derived are given in Table 1. Data sources are given in Appendices A and C.

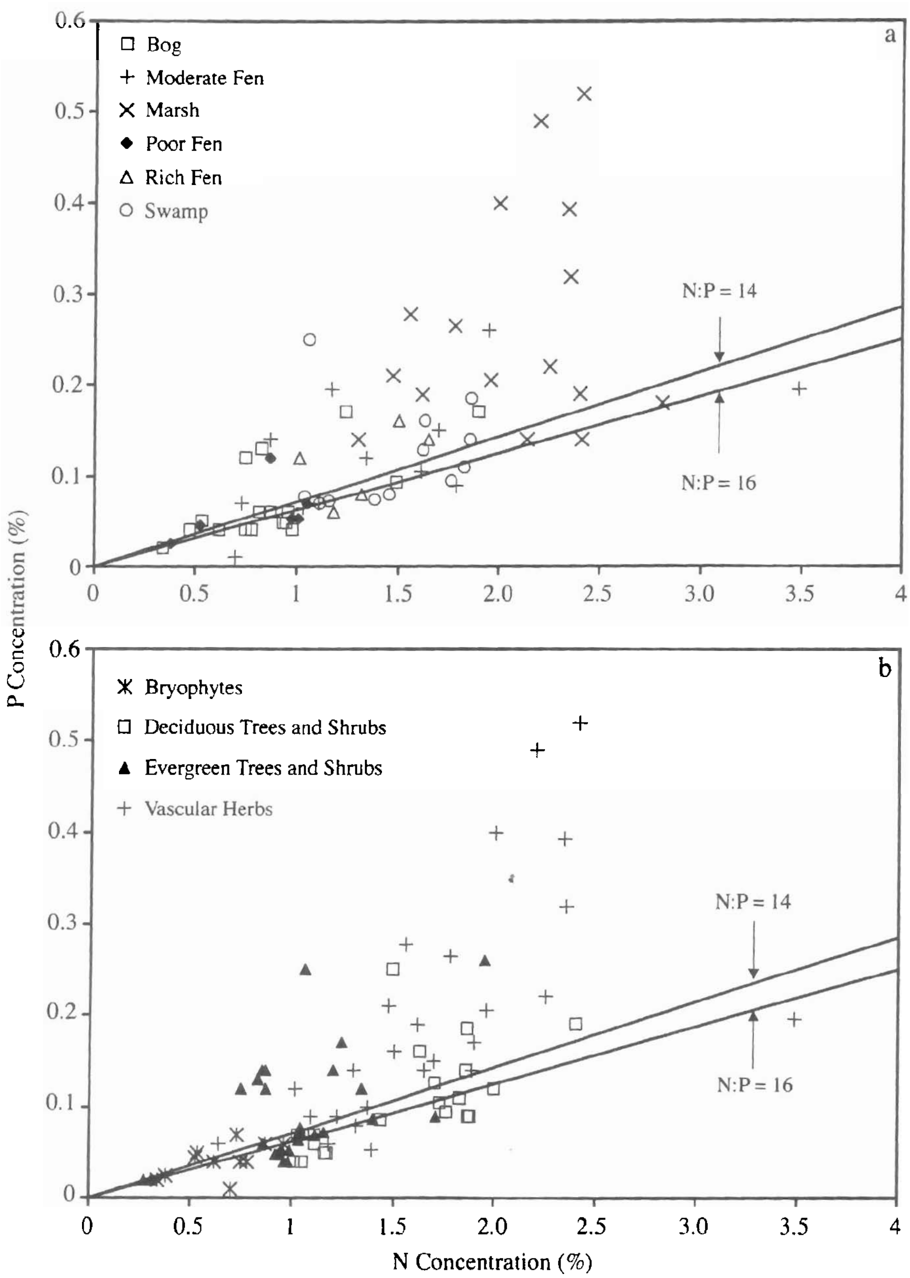

FIG. 5. Phosphorus (P) and nitrogen (N) concentrations in live tissues of wetland plants: (a) data plotted by different wetland types; (b) data plotted by different plant growth forms. Data sources are given in Appendices A and C.

Relationships between nutrient concentrations and N:P ratios, and among types and growth forms, can be examined by plotting P concentrations against N concentrations for all wetland types and all growth forms (Fig. 5a and b). For wetland types (Fig. 5a), the strongest pattern that emerges is that plants growing in marshes almost always have live-tissue N:P < 14, suggesting N limitation (Verhoeven et al. 1996). Marsh plants also tend to have higher N and P concentrations than other wetland types. All other types have some cluster means with live-tissue N:P < 14 and some with N:P > 16, suggesting P limitation (Verhoeven et al. 1996). Bogs, poor fens, and moderate-rich fens also have clusters lying between N:P = 14 and N:P = 16, suggesting colimitation by N and P (Verhoeven et al. 1996). Bogs and fens tend to have lower N and P concentrations than swamps or marshes.

Neither N nor P limitation is consistently indicated for any plant growth form (Fig. 5b). The most consistent pattern is seen in vascular herbs; almost all clusters have N:P < 14. Vascular herbs also show the highest mean N and P concentrations. Bryophytes group at the

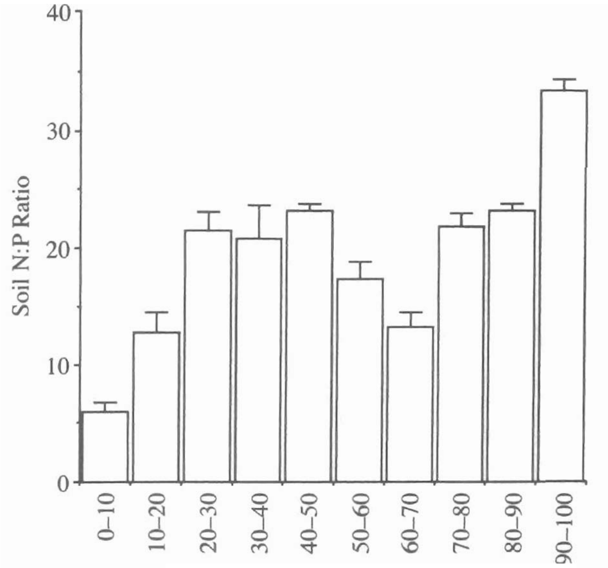

FIG. 6. Surface-soil N:P ratios in temperate North American freshwater wetlands averaged over 10% intervals of soil organic-matter content. Values are means + 1 SE. Data sources are given in Appendices B and C.

low ends of both the N and P concentration gradients but are not consistently either N or P limited. However, like deciduous and evergreen trees and shrubs, bryophytes have more clusters with N:P > 16 or between 14 and 16 than with N:P < 14. About 70% of clusters for deciduous species and 60% of those for evergreen species have N:P > 16 or between 14 and 16. Evergreen trees and shrubs show a wide range of P concentrations but usually have N concentrations <1.4%. Deciduous species generally have higher N concentrations but a similar range of P concentrations.

Nutrient concentrations and N:P ratios in surface soils of North American wetlands.—We found 24 studies that reported both N and P concentrations in surface soils (Appendix B). Average N concentrations were significantly higher in moderate- and extreme-rich fens than in other wetland types; average P concentrations were significantly lower in bogs and poor fens than in marshes and swamps (Table 2). Soil N:P ratios ranged from 2 to 60 (Table 2), with most values between 5 and 40 (Appendix B). Marshes (8.7 ± 1.0) and swamps (14.6 ± 0.5) (means ± 1 SE) had lower average soil N:P ratios than bogs and all types of fens (Table 2). Average N:P ratios of bogs (24.1 ± 0.7) and poor fens (24.1 ± 0.9) were identical, although poor fens had slightly higher average concentrations of both N and P in soil (Table 2). Moderate-rich fens (26.8 ± 0.8) had slightly higher average N:P ratios than bogs (Table 2), reflecting significantly higher soil N concentrations (Table 2). Rich fens (23.0 ± 0.5) had slightly lower average soil N:P ratios than bogs and poor fens (Table 2).

Wetlands on mineral substrates had significantly lower average soil N concentrations (0.62 ± 0.20) and N:P ratios (8.8 ± 0.8) than wetlands on peat substrates (1.59 ± 0.08 and 22.7 ± 0.3, respectively) (Table 2), possibly because peat soils store comparatively large amounts of N in organic form, while mineral soils store comparatively large amounts of inorganic P. However, significant proportions of both these pools may be relatively unavailable to plants. Surface-soil N:P ratios rose sharply at high (≥90%) soil organic-matter contents, and were generally >16 at organic concentrations above 20% (Fig. 6). If soil N:P ratios >16 indicate P limitation, then the majority (70%) of temperate North American bogs and fens are P limited (Fig. 7a); if soil N:P ratios <14 indicate N limitation, then the majority (61%) of temperate North American marshes and swamps are N limited (Fig. 7b). Of 26 swamps for which data were available (8 sites on mineral soils; 18

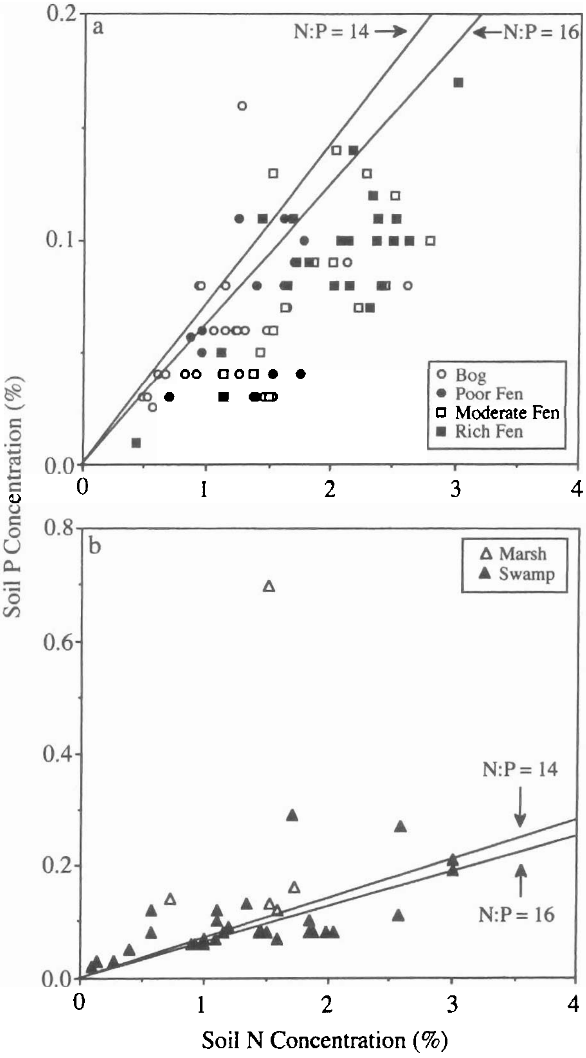

FIG. 7. Phosphorus (P) and nitrogen (N) concentrations in surface soils of temperate North American (a) bogs and fens (peatlands) and (b) marshes and swamps. Data sources are given in Appendices B and C.

sites on peat soils), all those on mineral soils had N:P ratios <11, while only 22% of those on peat soils had N:P ratios <14 (Appendix B). In bogs and fens, N:P ratios in soils were 1.5–1.7 times higher than in live plant tissues (Table 2, Fig. 3). For marshes and swamps, soil and plant-tissue N:P ratios were similar, 8.7 vs. 7.5 and 14.6 vs. 14.4, respectively. Soil N:P ratios were consistently higher than litter N:P ratios in fens, lower than litter N:P ratios in swamps, and similar to litter N:P ratios in marshes (Table 2, Fig. 3).

DISCUSSION AND CONCLUSIONS

Species richness in temperate wetlands is obviously not related solely to nutrient availability, especially for undisturbed sites where hydrologic regime and microtopography can play key roles (Pollock et al. 1998). However, given the preponderance of evidence from other systems where humans have greatly enriched nutrient loading or where fertilization experiments have been carried out, the potential for significant loss of plant species richness in North American wetlands with increasing eutrophication of the environment seems high. Do the extreme effects on plant diversity observed in Western Europe portend the response of wetlands in temperate North America to increasing nutrient enrichment? For example, Aerts and others (1992) proposed that northern Sweden (low N deposition), southern Sweden (moderately high N deposition), and parts of England (very high N deposition) could be viewed as a chronosequence in which N enrichment first causes increased productivity and N:P ratios in plants, followed by extremely high N:P ratios and a shift from N- to P-limited plant growth, and, in the extreme, to loss of plant species. In this review, we sought evidence that would allow us to evaluate the applicability of these and similar observations to temperate North American wetlands.

Four results from our review stand out as pertinent to understanding how temperate wetlands of North America may respond to nutrient enrichment: (1) the finding that plant communities at nutrient-rich sites—as indexed by elevated levels of aboveground biomass, or other presumed correlates of high nutrient supply—are consistently characterized by low species richness when compared among but not within community types; (2) the lack of concordance found in recent studies between pH–alkalinity gradients and nutrient gradients in peatlands; (3) the apparent occurrence of P-limitation in all growth forms and in all wetland types except marshes, as indicated by N:P ratios in wetland plants and soils; and (4) the indication that nutrient limitation of component species may differ from that of the community as a whole and be critical in determining effects of nutrient additions on plant diversity of wetland communities.

Species richness and nutrient availability

Though studies from temperate North America allow only limited conclusions to be drawn regarding potential response to nutrient additions, they generally confirm the picture derived from other ecosystems. When compared among communities, species richness is positively correlated with various indicators of nutrient availability (e.g., aboveground standing biomass) up to some threshold value, beyond which it declines. Low species richness characterizes all high-biomass sites and, by inference, all sites with high nutrient-supply rates. Both low and high species richness occur at intermediate biomass levels. Rare species tend to occur in low-to-intermediate biomass, species-rich sites. When examined within community types, however, these generalities do not hold, nor does the presumed positive correlation between species richness and a number of other variables related to nutrient availability, e.g., pH, soil C:N and C:P ratios.

Beyond these generalities, however, critical questions remain. If the relationship breaks down when examined within particular community types, can cross-community comparisons be used to predict response to nutrient additions within a single community type? What is the biomass threshold beyond which species richness declines for the large number of unstudied communities? What determines where that threshold lies for different communities? How might nutrient enrichment alter moss species diversity? If either high or low diversity can occur at intermediate biomass levels, and low diversity is consistently associated only with extreme biomass values, is high aboveground biomass or NPP per se the cause of species losses, or are losses related to increased nutrient supply in a more fundamental way?

pH–alkalinity gradients vs. nutrient gradients

Undisturbed peatlands typically have negligible concentrations of inorganic N and P in both surface waters (Moore and Bellamy 1974, Vitt and Chee 1990, Malmer 1993, Vitt et al. 1995*a*) and soils (Richardson and Marshall 1986, Urban and Eisenreich 1987). Peatland communities have been distinguished, therefore, largely on the basis of pH and concentrations of base cations in surface waters (Slack et al. 1980, Gorham et al. 1985), i.e., the pH–alkalinity gradient. The supply of N and P to peatlands, as well as the mosses that dominate them, received little attention from North American vegetation scientists until recently (Bayley et al. 1987, Vitt and Chee 1990, Bridgham et al. 1996). The supply of N and P to wetlands on mineral soils, e.g., marshes and swamps, on the other hand, has received attention for decades (Brinson 1977) but their plant communities have been distinguished more frequently on the basis of hydrologic regime than nutrient supply. Now that atmospheric deposition of nutrients and acidifying agents, global climate change, and land-use intensification leave no wetlands unaffected, the question of nutrient supply as a controlling factor in both peatlands and mineral-soil wetlands is receiving increased attention in North America (Morris 1991, Bridgham et al. 1996, Li and Vitt 1997, Thormann and Bayley 1997*a*).

Our review of work by Vitt and Chee (1990), Walbridge (1991), Bridgham and Richardson (1993), and Vitt et al. (1995*b*) confirms what Bridgham et al. (1996) concluded in their review of peatlands. In terms of predicting the response of plant communities to nutrient enrichment, both the pH–alkalinity and nutrient gradients must receive attention. The pH–alkalinity gradient may, but does not necessarily, parallel the gradient of increasing N and P availability, and should *not* be used as a surrogate for it. In fact, our data suggest that while nutrient availability may increase along the bog–poor fen–rich fen gradient, this gradient may also encompass shifts in nutrient limitation by N vs. P. Nitrogen or P availability rather than pH and base metal cations, and/or hydrology may control plant distribution in peatlands as well as mineral-soil wetlands. With bryophytes in peatlands responding primarily to a pH–alkalinity gradient and vascular species to a nutrient gradient (Vitt 1990, Vitt and Chee 1990, Vitt and Kuhry 1992), increased nutrient supply may lead to species losses not only through direct effects of nutrients and changing acidity on mosses but also through changes in the competitive balance between mosses and vascular species (Malmer 1993, Malmer et al. 1994).

Nutrient limitation in wetland communities and wetland plants

If we accept the N:P thresholds used by Koerselman and Meuleman (1996) and Verhoeven et al. (1996), our review suggests that either N or P can limit primary productivity in North American wetlands. Only marshes and vascular herbaceous species appear to be predominantly N limited. All other wetland types (Fig. 5a), and all growth forms (Fig. 5b), include some cases where the N:P ratio in live tissues suggests P limitation. A larger proportion of bogs and poor fens appear to be either P limited or co-limited by N and P than N limited. More bryophytes, and more evergreen and deciduous trees and shrubs, have N:P ratios suggesting P limitation or co-limitation by N and P than N limitation. Nitrogen : phosphorus in soils suggests even more strongly that P is often limiting, especially in peatlands (Fig.7a). Given the European results indicating more frequent N limitation in wetlands (Koerselman and Meuleman 1996, Verhoeven et al. 1996), and the fact that most terrestrial systems are thought to be N limited (Vitousek and Howarth 1991), these results are striking.

Our results are striking also in the wide range of N and P concentrations at which they indicated either N or P limitation (Fig. 5). Nitrogen-limited stands had plant N concentrations ranging from about 0.4 through 2.4%. Phosphorus-limited stands had P concentrations ranging from about 0.01% through 0.19%, but most were below 0.11%, the same P concentration Koerselman and Meuleman (1996) found to be the threshold above which P limitation did not occur in their sites. Thus, as Koerselman and Meuleman (1996) suggest, the relationship between plant nutrient content and nutrient limitation in wetlands is not clear. Nitrogen limitation can occur at low or quite high plant N content. Phosphorus limitation seems to have a threshold, but sites below that threshold are not necessarily P limited. In several stands with P concentrations between 0.03% and 0.19%, N:P ratios suggest N limitation. Nitrogen : phosphorus ratios seem more indicative of potential plant response to nutrient enrichment than absolute content of N or P (Shaver and Melillo 1984, Koerselman and Meuleman 1996).

More surprising perhaps, was the fact that average N:P ratios were higher in litter than in live tissue for poor fens, rich fens, and swamps, suggesting that wetland plants cycle P more conservatively than N, even when N rather than P appears to limit plant growth. In an earlier review, Walbridge (1991) found that maximum P-resorption potentials were higher on average than those reported for N (79.9 and 72.4%, respectively), despite the fact that the majority of sites examined were N limited, and suggested that P might be biochemically more retranslocatable than N. In a more recent review, Aerts (1996) reported only slightly higher mean nutrient resorption efficiency for P (52%) vs. N (50%). Several other factors might contribute to the observed increase in average litter vs. fresh-tissue N:P ratios. One factor might be a greater susceptibility of P to leaching as plant leaves begin to abscise. A second might be a greater susceptiblity of N to immobilization in freshly abscised litter. A third could be related to differences in the availabilty of soil P vs. N to plants. Phosphorus in soil is highly insoluble, and thus either a dense root system or an investment in mycorrhizae is often required by plants in order to extract significant amounts of P from soil. Even as ammonium, soil N is more soluble than P. Phosphorus resorption could be a less costly alternative than additional root or mycorrhizal biomass investments.

Several points should be considered in interpreting our results. First, the explanation for why some bogs and fens appear P limited while others appear N limited is not clear. The explanation may lie in: (a) the larger contribution of internal nutrient cycling than external inputs to peatlands, and (b) the inadequacy of traditional wetland-classification systems in capturing the factors controlling rates of nutrient cycling within wetlands. Bogs have no external source of inorganic N or P other than atmospheric deposition and N fixation; poor fens have only insignificant external sources other than the atmosphere (Malmer 1993). Rates of N mineralization and P release within sites, therefore, determine nutrient availability. These rates are controlled by factors that may not be captured in traditional classifications of wetland type, and that may vary within types. For example, seasonal variation in water-table fluctuation, which can differ among sites classified broadly as the same wetland type, exerts strong control over wetland nutrient-cycling processes through effects on redox status (Hill and Devito 1997). Bridgham et al. (1998) showed that soil bulk density, which varies within and among wetland types, was the best predictor of N and C mineralization rates within northern peatlands.

It might seem reasonable to assign the apparent frequency of P limitation to increasing atmospheric sources of N in North America (Morris 1991, Butler and Likens 1995). Wet-deposition levels comparable to parts of eastern North America shifted the primary element limiting growth of *Sphagnum* in Sweden from N to P (Aerts et al. 1992). However, this conclusion cannot be drawn from the limited data available. The most P-limited sites in our review are all peatlands, few of which are in high N-deposition areas of the northeastern United States. We located one study from a poor fen in the Adirondack region of New York State, where deposition rates are high, after we completed our analyses of the data base. This study reported very high N:P ratios in live tissues of the evergreen shrub *Chamaedaphne calyculata* (N:P = 19.8–22.25), the N-fixing shrub *Myrica gale* (N:P = 32.50–34.45), and the sedge *Carex lasiocarpa* (N:P = 23.08–26.36) (Rossell et al. 1994). In contrast, other studies have found evidence of P limitation for individual species in peatlands not subject to high levels of N deposition (Beltman et al. 1996, Thormann and Bayley 1997*b*). The N:P values reported by Beltman et al. (1996) were largely in the same range as those of Rossell et al. (1994), while those from Thormann and Bayley (1997*b*) were substantially lower.

The fundamental explanation for P limitation in rich fens and blackwater swamps is clearer. Some rich fens occur in areas where high-pH, base-rich groundwater high in calcium discharges to the surface. The continual supply of calcium in groundwater removes P from plant-available forms through precipitation of hydroxy apatite and other hydroxides of calcium. The high base status of the discharging water also maintains a high pH and precludes dissolution of Ca-P oxyhydroxides. It also creates conditions conducive to N mineralization (Verhoeven et al. 1993). Blackwater swamps occur on sandy soils that have low concentrations of mineral P, and are nourished by carbon-rich, phosphorus-poor floodwaters that arise from the same substrates.

Second, the thresholds proposed by Koerselman and Meuleman (1996) and Verhoeven et al. (1996) were based on studies of perennial herbaceous vegetation and may not apply to forested sites. Accumulation of biomass in woody structures alters element ratios in trees and shrubs relative to herbaceous species (Vitousek et al. 1988). For sites in our review, using a different threshold for N or P limitation primarily would affect interpretation of data from swamps. Data from Lockaby and Walbridge (1998), however, suggest that a litterfall N:P ratio above 12 indicates P limitation. Using this threshold would only increase the number of P-limited sites in our data set. Surface-soil N:P ratios also appear to agree fairly well with those suggested for live tissues (Klopatek 1978, Koerselman and Meulemen 1996, Verhoeven et al. 1996) and litter (Lockaby and Walbridge 1998). Walbridge (1991) reported surface-soil N:P ratios of ~19 for broad-leaved, evergreen-dominated forested wetlands in forests that are presumably P limited, while the highest soil N:P ratio for a mineral-soil wetland (11) comes from a deciduous Louisiana cypress–tupelo swamp (Kemp and Day 1981). Many of the marsh and swamp systems on mineral soils also experience significant periodic flooding. Flooding could cause both inputs and losses of soil N and P that might result in soil N:P ratios less reflective of stand nutrient availability than in peatlands and/or basin wetlands. In future studies, it will be important to assess how flooding affects surface-soil N:P ratios as nutrient-availability indices for riverine (floodplain) wetlands.

Third, the N:P ratios Verhoeven et al. (1996) used to determine their thresholds were for the plant community as a whole (i.e., bulk vegetation) rather than for individual species. The data in our review are based on element ratios in single species. In many cases, however, these species were the dominant species in the community and should reflect community nutrient limitation. Similarly, studies in which several species were included should reflect community limitation because all species from a single stand were averaged in the statistical analyses.

Fourth, differences between European and North American wetlands are considerable. For wetlands they examined, Verhoeven et al. (1996) explained N vs. P limitation in terms of successional stage of the vegetation, mowing regime, high deposition rates of N within The Netherlands, and water-management practices that influence the chemistry of water entering wetlands. Only 8 of the 45 studies in Verhoeven et al. (1996) and Koerselman and Meuleman (1996) were from areas not heavily enriched by atmospheric N deposition (J.T.A. Verhoeven, *personal communication*). They report that atmospheric deposition in The Netherlands now averages about 50 kg $N \cdot ha^{-1} \cdot yr^{-1}$, far above North American levels. As the authors point out, many sites are mown annually, which removes both N and P, but P disproportionately more than N. Thus, they did not see the expected shift from N to P limitation in as many sites as might be expected given high atmospheric N loads, and they found P limitation only in fens with a long history of mowing.

Fifth, the empirical basis for using soil N:P ratios as indicators of nutrient limitation is not as strong as that for plant-tissue N:P ratios. Soil N:P ratios have been used infrequently, though successfully, to index the nature of nutrient limitation. Walbridge (1991) found surface-soil N:P ratios declined as P availability increased along a gradient of P-limited wetlands on organic soils in North Carolina. Soil nutrient ratios offer a comparatively easy method to assess the nature of nutrient limitation in an ecosystem that deserves further attention in the literature. Future studies should focus on verifying relationships between soil N:P ratios and ecosystem response to fertilization, similar to the studies of Koerselman and Meuleman (1996) and Verhoeven et al. (1996) for N:P ratios in aboveground biomass.

Finally, differences in analytical methods, and in definitions of wetland types, may have influenced our results. Methods used to estimate total P in soils can differ in their ability to solubilize recalcitrant P (Olsen and Sommers 1982). Differences in soil bulk density among sites would affect comparisons of soil nutrient concentrations. Bulk density data are not always reported. However, analyses of nutrient ratios (e.g., N:P) are independent of bulk density differences among sites. Dates of collection for plant material could affect comparisons of both wetland types and plant growth forms because nutrient concentrations do not necessarily increase or decrease synchronously throughout the growing season in all species (Thormann and Bayley 1997*b*). Our failure to find statistically significant differences among most types of wetlands in N:P ratios could be attributable in part to a lack of consistency in how wetland scientists define wetland types (see *Methods,* above). Alternatively, the small number of clusters for some types (Table 1) could explain the lack of significant differences.

Species richness: community vs. species-specific resource limitation

Simple extension of the concept of nutrient limitation to entire plant communities is not warranted because species differ in their responsiveness to nutrient addition (Chapin et al. 1986, DiTomasso and Aarsen 1989, Bowman et al. 1995, Thormann and Bayley 1997*a*). This point is particularly important if the concern is species diversity rather than ecosystem productivity. Most species within most communities are not dominant (Whittaker 1965). If they have critical N:P ratios that differ from that of the dominant species, they could be lost from the community if nutrient-supply ratios change, even if overall community productivity does not increase. Koerselman and Meuleman (1996) presented data showing some wetland species within a particular wetland differing from the community as a whole in terms of critical-element ratios.

The data in our review for North American wetlands also highlight the importance of species-specific responses in determining the effects of nutrient enrichment on diversity. We found that the distribution of N:P ratios when plotted by growth form differed from N:P ratios plotted by community type (Fig. 5a vs. b). Far more of the data points for growth forms indicated P limitation than did the points for community types. If data for individual species are examined (Appendix A) rather than cluster means, the majority of points indicate P limitation rather than the more split pattern seen for communities (Fig. 5a). Data for different species within the same site, which we report in another manuscript (B. Bedford and A. Aldous, *unpublished manuscript*), also show differences in the proximal nutrient limiting growth. If nutrient limitation of component species differs from that of the community, effects of enrichment on diversity cannot necessarily be predicted from community limitation.

High variances in plant and soil N:P ratios suggest that understanding nutrient limitation at both the community and individual-species level is needed to predict changes in species composition and richness with nutrient enrichment. Different growth forms or individual species within the community can have different nutrient limitations than the community as a whole. Understanding effects of nutrient enrichment on ecosystem productivity may not be sufficient to predict effects on species diversity; species may be lost because they have adaptations to a particular nutrient limitation. For temperate North American wetlands, understanding how nutrient enrichment affects plant species diversity will require a greater number of fertilization studies in which both ecosystem properties and individual species responses are examined.

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APPENDIX A

A list of the studies and relevant data used in our analysis of wetland plant-tissue chemistry is available in ESA's Electronic Data Archive: *Ecological Archives* E080-012-A1.

APPENDIX B

A list of the studies and relevant data used in our analysis of wetland soil chemistry is available in ESA's Electronic Data Archive: *Ecological Archives* E080-012-A2.

APPENDIX C

Literature Cited in Appendices A and B is available in ESA's Electronic Data Archive: *Ecological Archives* E080-012-A3.