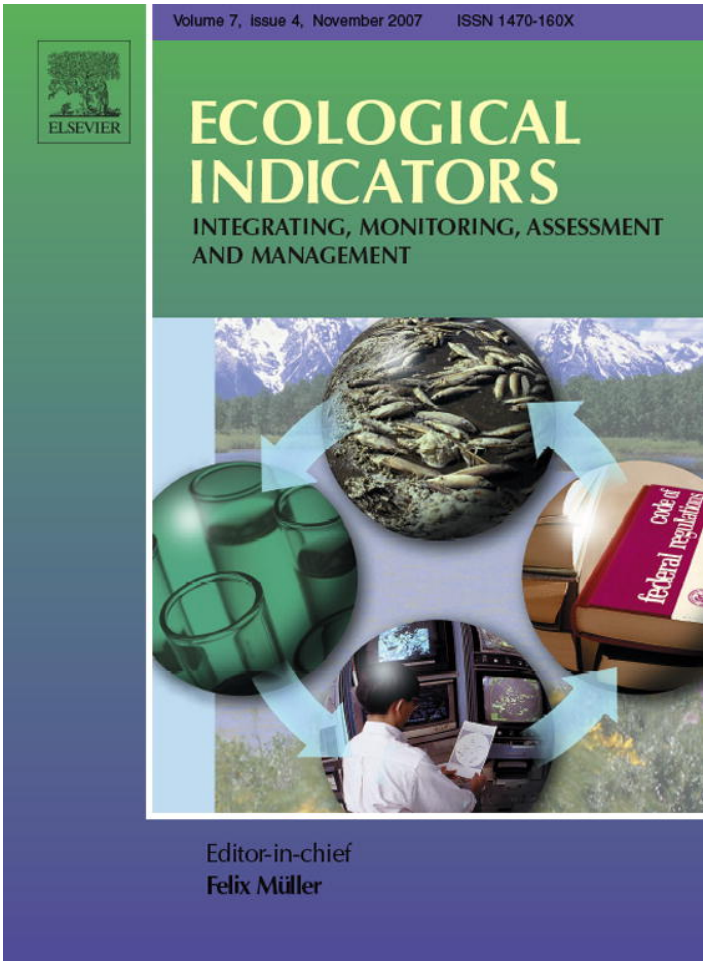
Volume 7, Issue 4, November 2007 ISSN 1470-160X
ELSEVIER
ECOLOGICAL INDICATORS
INTEGRATING, MONITORING, ASSESSMENT AND MANAGEMENT
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Editor-in-chief
Felix Müller

Ecological Indicators 7 (2007) 733–750

ECOLOGICAL INDICATORS

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Ecological indicators of nutrient enrichment, freshwater wetlands, Midwestern United States (U.S.)

Christopher Craft [*], Kandice Krull, Sean Graham

School of Public and Environmental Affairs, Indiana University, Bloomington, IN 47405, United States

Received 28 March 2006; received in revised form 7 August 2006; accepted 12 August 2006

Abstract

Vegetation and soil indicators of nutrient condition were evaluated in 30 wetlands, 10 each in 3 Nutrient Ecoregions (NE) (*VI-Corn Belt and Northern Great Plains*, *VII-Mostly Glaciated Dairy Region*, *IX-Temperate Forested Plains and Hills*) of the Midwestern United States (U.S.) to identify robust indicators for assessment of wetland nutrient enrichment and eutrophication. Nutrient condition was characterized by surface water inorganic N (NH_4-N, NO_3-N) and P (PO_4-P) concentrations measured seasonally for 1 year, plant available and total soil N and P, and aboveground biomass, leaf N and P and species composition of emergent vegetation measured at the end of the growing season. Aboveground biomass, nutrient uptake and species composition were positively related to surface water NH_4-N (N) but not to PO_4-P or NO_3-N. Aboveground biomass and biomass of aggressive species, *Typha* spp. plus *Phalaris arundinacea*, increased asymptotically with surface water N whereas leaf P, senesced leaf N and senesced leaf P increased linearly with N. And, species richness declined with surface water N. Soil total P was positively related to surface water PO_4-P but it was the only soil indicator related to wetland nutrient condition. Individual regressions for each NE generally were superior to a single regression for all NEs. In NE VI (*Corn Belt*), few indicators were related to surface water N because of the high degree of anthropogenic disturbance (85% of the landscape is cleared) as compared to NEs VII and IX (24–53% cleared). Of the indicators evaluated, stem height ($r^2 = 0.42$ for all NEs, $r^2 = 0.56$ for NE VII + IX) and percent biomass of aggressive species, *Typha* spp. plus *Phalaris*, ($r^2 = 0.46$ for all NEs, $r^2 = 0.54$ for NE VII + IX), were the best predictors of wetland nutrient enrichment. Vegetation-based indicators are a promising tool for assessment of wetland nutrient condition but they may not be effective in NEs where landscape disturbance is intense and widespread.

Keywords: Eutrophication; Water quality; Nitrogen; Phosphorus; Standards

1. Introduction

Nutrient enrichment is an increasing threat to aquatic and wetland ecosystems. The best documented example of wetland eutrophication in North America is the Florida Everglades where, near canals that convey N

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[*] Corresponding author. Tel.: +1 812 855 5971; fax: +1 812 855 7802.
E-mail address: ccraft@indiana.edu (C. Craft).

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doi:10.1016/j.ecolind.2006.08.004

and P enriched agricultural drainage stimulates P uptake and growth of emergent vegetation (Davis, 1991; Miao and Sklar, 1998), periphyton (McCormick et al., 1996) and microbial activity (Qualls and Richardson, 2000; Wright and Reddy, 2001). Soil P pools, including porewater bulk soil, are enriched relative to areas distant from the source of nutrient loading (Koch and Reddy, 1992; DeBusk et al., 1994, 2001; Qualls and Richardson, 1995). And, in P enriched areas, native sawgrass (*Cladium jamaicense*) and slough vegetation are replaced by near-monoculture stands of cattail (*Typha domingensis*) (Jensen et al., 1995; Craft and Richardson, 1997).

Like the Everglades, wetlands in other regions exhibit a similar response to nutrient enrichment. Wetland vegetation responds to nutrient dosing by increasing nutrient uptake and biomass production (Aerts and Berendse, 1988; Hayati and Proctor, 1991; Verhoeven and Schmitz, 1991; Shaver and Chapin, 1995; Bridgham et al., 1996; Shaver et al., 1998, 2001) though the response depends on whether N, P or other nutrients are limiting. A decline in plant species richness often is seen with progressive enrichment (Vermeer, 1986; Pegtel et al., 1996; Shaver et al., 2001; Gustafson and Wang, 2002) as aggressive species such as *Typha* spp., *Phalaris arundinacea* and *Phragmites australis* invade and dominate the site (Chambers et al., 1999; Galatowitsch et al., 1999; Svengsouk and Mitsch, 2001; Green and Galatowitsch, 2002; Maurer and Zedler, 2002; Woo and Zedler, 2002). Except for the Everglades, though, where tens of millions of dollars have been spent to identify the causes, effects, indicators and thresholds of P enrichment, there has been little systematic effort to identify the origins (N or P), document the effects and identify indicators of wetland nutrient enrichment in other geographic regions.

We measured surface water nutrients (N, P) and vegetation-, litter- and soils-based indicators of nutrient enrichment in 30 freshwater wetlands spanning three Nutrient Ecoregions (NEs) in the Midwestern United States to answer the following questions: (1) Do predictive relationships exist between surface water nutrient concentrations and vegetation-, litter-, or soil-based indicators, and, if so, which indicators exhibit the strongest response? (2) Is the response linked to N or P? and (3) Are the relationships robust, that is, are they applicable across NEs or do they vary among NEs? We chose these indicators because they respond similarly to nutrient enrichment in a variety of wetland types and have been suggested as potential indicators of wetland enrichment (U.S. EPA, 2002).

The Nutrient Ecoregion approach, the classification of landscape units based on geology, physiography, vegetation, climate, soils, land use and other factors was derived from Omernick (1987) by the U.S. Environmental protection Agency to develop water quality (N, P) standards for rivers, streams and lakes of the U.S. (http://www.epa.gov/waterscience/criteria/nutrient). This approach takes into account differences in environmental factors that result in differences in water quality. For example, in NE VI (*Corn Belt*) which is underlain by fertile soils and is intensively farmed, rivers and streams contain more N (2.2 mg/L) and P (76 ug/L) than rivers and streams of NE VII (*Mostly Glaciated Dairy Region*) (TN = 0.5 mg/L, TP = 33 ug/L) and NE IX (*Southeastern Temperate Forested Plains and Hills*) (TN = 0.69 mg/L, TP = 37 ug/L) where the soils are less fertile and forest cover is greater. By stratifying sample collection among NEs, we partition some of the geographic variability in wetland nutrient condition, recognizing that some NEs (e.g. NE VI) will exhibit higher baseline levels of nutrients, and so ecological indicators may respond somewhat differently to nutrients than NEs with lower baseline concentrations of N and P. One goal of this study is to identify ecological indicators that can be used as nutrient (N, P) standards for wetlands, comparable to the ecologically based nutrient standards such as chlorophyll *a* that are used for water quality assessments of rivers, streams and lakes (http://www.epa.gov/waterscience/criteria/nutrient).

2. Materials and methods

2.1. Site description

Thirty freshwater wetlands, 10 from each NE (NE VI, *Corn Belt and Northern Great Plains*, NE VII, *Mostly Glaciated Dairy Region*, and NE IX, *Southeastern Temperate Forested Plains and Hills*) were selected for sampling (Fig. 1). Nutrient Ecoregions were derived from Omernick (1987) who classified broad landscape units based on geology, physiography, vegetation, climate, soils, land use and other

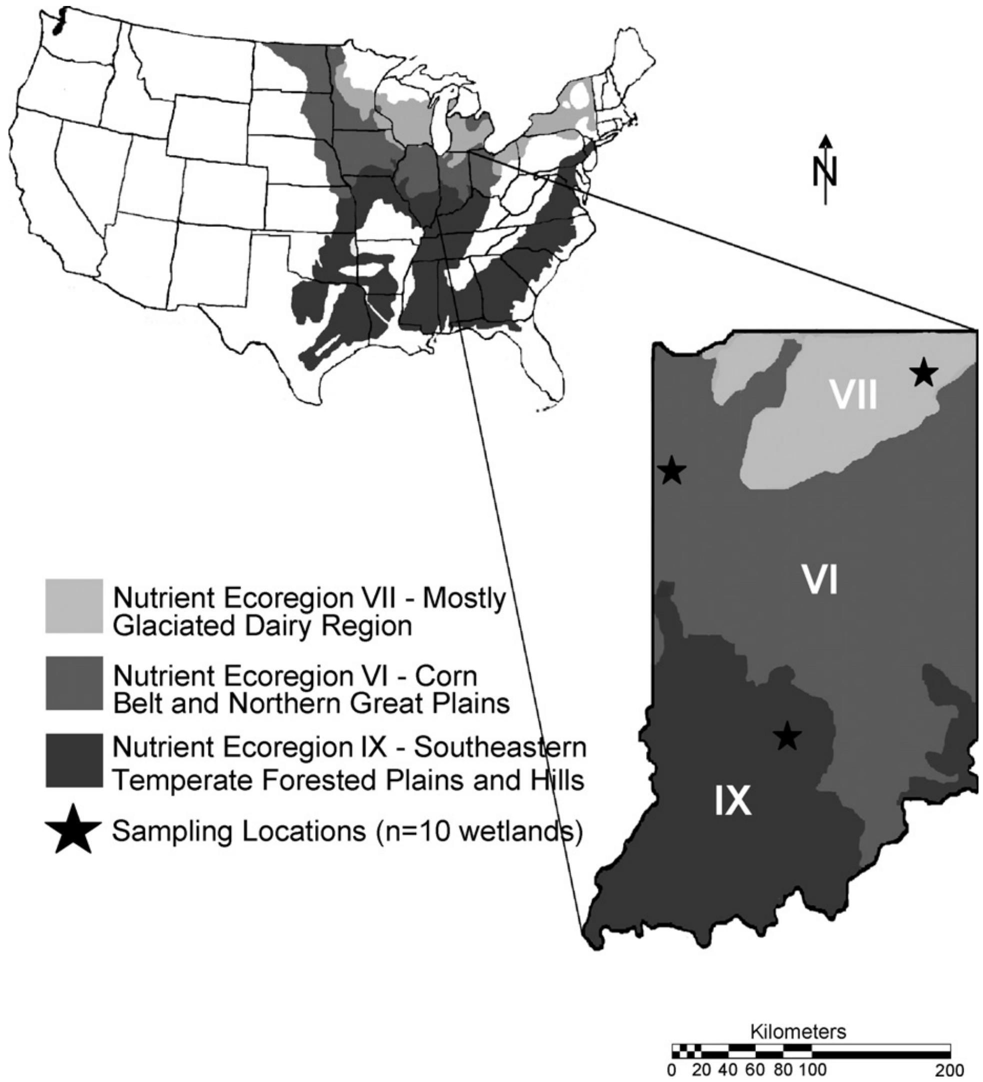

Fig. 1. Map of study area showing the three Nutrient Ecoregions (NE) and approximate sampling locations within each NE.

factors that determine nutrient concentrations in surface waters (http://www.epa.gov/waterscience/criteria/nutrient). Sandy-textured Mollisols and Entisols were common in NE VI (sandy, mixed, mesic Typic Haplaquolls and mixed, mesic Aquic Udipsamments) (USDA, 1998). Soils of NE VII consisted mainly of Mollisols (fine-loamy, mixed, mesic Typic Argiaquolls) and Histosols—organic soils (euic, mesic Typic Medisaprists) (USDA, 1981a,b). Nutrient Ecoregion IX was hillier than NEs VI and VII. It also had finer (silty-clayey) textured soils that were mostly Entisols (loamy-skeletal, mixed, acid, mesic Typic Udifluvents and fine-silty, mixed, acid, mesic Aeric Fluvaquents) (USDA, 1981a,b).

Within each NE, wetlands were chosen to encompass a range of nutrient enrichment. Wetlands containing high surface water nutrients were located in agricultural and urban catchments and included wetlands receiving treated wastewater from municipal wastewater treatment facilities. Low nutrient wetlands were situated in catchments that were mostly forested or open prairie and were located within nature preserves, protected areas and state owned wildlife management areas. To minimize differences in wetland age that may affect plant species composition (e.g. presence of pioneer species in young wetlands), we used topographic maps from the 1950s and 1960s to select wetlands that were at least 40–50 years old when we sampled in 2003.

2.2. Sample collection and analysis

2.2.1. Surface water N and P

Surface water inorganic N (NH_4-N, NO_3-N) and P (PO_4-P) were measured seasonally over 1 year (2003). On each sampling date, three water samples were collected from each wetland. Samples were filtered through 0.45 μm filter paper in the field and transported to the lab on ice. Ammonium-N and NO_3-N were determined by the phenate and cadmium reduction methods, respectively (APHA, 1998). Phosphate-P was determined using the ascorbic acid method (APHA, 1998).

2.2.2. Vegetation

Vegetation was sampled by clipping aboveground biomass from ten 0.25 m^2 quadrats in each wetland at the end of the growing season. Sampling was stratified to sample the two to three dominant zones in each wetland and, within each zone, samples were randomly collected. Height of the five tallest stems of the two to three dominant species was measured in the field. Plant material was transported to the lab where it was separated by species, then by live versus dead biomass. Vegetation was classified taxonomically based on Fassett (1957), Gleason and Cronquist (1991), and Voss (1996). Species lists for each site are presented in Appendices A–C.

Clipped material was dried at 70 °C to a constant weight. Because some species senesced earlier in the growing season (e.g. *Schoenoplectus* spp.) than others (e.g. *Typha*), aboveground live and standing dead biomass were combined for statistical analysis. Green and senesced leaves from the two to three dominant species in each quadrat were ground using a Wiley mill and analyzed for N, P and organic C. Nitrogen and organic C were measured using a Perkin-Elmer 2400 CHN analyzer. Total P was determined using the ascorbic acid method (APHA, 1998) after digestion in nitric-perchloric acid (Sommers and Nelson, 1972).

2.2.3. Litter and soil

Litter was collected from each 0.25 m^2 quadrat, dried at 70 °C to a constant weight, ground with a Wiley mill and analyzed for organic C, N and P. One soil core was collected from each quadrat using an 8.5 cm diameter by 10 cm deep stainless steel corer. Bulk density was measured by drying the soil at 70 °C, then dividing the dry mass by the volume of the corer. Plant available NH_4-N was extracted from field-moist soils with 2N KCl and analyzed using the phenate method (Mulvaney, 1996). Plant available PO_4-P of field-moist soils was extracted with sodium bicarbonate (Kuo, 1996) and analyzed by the ascorbic acid method (APHA, 1998). Total organic C and N of litter and soil were measured using a Perkin-Elmer 2400 CHN analyzer. Soils containing carbonates were pretreated with 0.1N HCl prior to CHN analysis to remove inorganic C. Total P was determined by the ascorbic acid method after digestion in nitric-perchloric acid (Sommers and Nelson, 1972). Soils data were expressed on a dry mass (g) and volume (cm^3) basis after correcting for water content determined by drying a 1 g field moist subsample at 105 °C.

2.3. Statistical analysis

Analysis of variance (ANOVA) was employed to test for differences in surface water nutrients, vegetation, litter and soils among the three NEs (SAS, 2002). Because no one plant species was present in all wetlands, leaf nutrient (N, P) concentrations for the two to three dominant species from a given site were pooled for statistical analysis. Aboveground biomass of aggressive species, reed canarygrass (*P. arundinacea*) and cattail (*Typha* spp.), also were combined for statistical analysis because the two species seldom were present together in the same wetland but it was common to find wetlands that were dominated by one species or the other. Means were separated using the Ryan-Einot-Gabriel-Welsch multiple range test (SAS, 2002). All test of significance were made at $\alpha = 0.05$.

Correlation analysis was used to investigate associations between surface water nutrients, vegetation indicators and soil indicators of nutrient enrichment. Regression analysis was used to explore relationships between surface water nutrient concentrations and vegetation, litter, and soil indicators for all NEs and for individual NEs. Linear, quadratic and asymptotic curve were evaluated and the best fit model was selected based on the maximum r^2 obtained (SYSTAT Software, 2004). Canonical correlation analysis (CCA) was used to identify trends of species abundance with wetland nutrient condition, surface water and soil nutrients (SAS, 2002). We dropped one site (MOR in NE VI) from the correlation, regression and CCA analyses because of its high NH_4-N (1.5 mg/L) and PO_4-P (0.92 mg/L) concentrations relative to other wetlands made it an influential data point (Rawlings et al., 2001). It should be noted that this site was dominated by a near monoculture of *Typha* (see Appendix A).

3. Results

3.1. Comparisons among NEs

Surface water inorganic N and P did not differ among the three NEs though NH_4-N and PO_4-P were somewhat greater in NE VI, *Corn Belt*, than in the other NEs (Table 1). In NE VI, one wetland (MOR) had high NH_4-N (1.5 mg/L) and PO_4-P (0.92 mg/L) relative to all other wetlands sampled (Table 1). If MOR is excluded, wetlands of NE VI still contain the most surface water NH_4-N (0.11 mg/L) though PO_4-P declines to 0.02 mg/L. Wetlands of NE VII exhibited high surface water NO_3-N relative to NEs VI and IX (Table 1) that was attributed to two fens, where average NO_3-N was 7.60 mg/L and 11.10 mg/L, respectively. Fens are groundwater-fed and the high NO_3-N concentrations likely are due to deep leaching of fertilizer nitrogen from agricultural fields in the region that discharges into these wetlands (Amon et al., 2002). In NE IX, the groundwater-fed Leonard Springs wetland also exhibited high NO_3-N (1.67 mg/L) as compared to other wetlands in this NE (0.01–1.11 mg/L).

Table 1
Nutrient-related properties of surface waters, vegetation and soils of freshwater wetlands of three Nutrient Ecoregions (NEs) of the Midwestern U.S.

	NE VI (*Corn Belt*)	NE VII (*Dairy Region*)	NE IX (*Forested Hills*)
Surface water			
NH_4-N (ug/L)	0.25 ± 0.14 (0.11 ± 0.03)[a]	0.09 ± 0.03	0.07 ± 0.01
NO_3-N (ug/L)	0.03 ± 0.01	2.0 ± 1.2	0.36 ± 0.18
PO_4-P (ug/L)	0.11 ± 0.09 (0.02 ± 0.01)[a]	0.06 ± 0.02	0.07 ± 0.04
Vegetation			
Stem height (cm)	161 ± 7 a	131 ± 6 b	134 ± 7 b
Aboveground biomass (g/m^2)	780 ± 90	630 ±60	890 ± 100
Species richness (#/site)	5.2 ± 0.9 a	10.1 ± 1.4 b	8.8 ± 0.9 b
Leaf P (ug/g)	1480 ± 60 a	1210 ± 60 b	1140 ± 70 b
Senesced leaf P (ug/g)	750 ± 60 a	530 ± 50 b	780 ± 50 a
Leaf N (%)	1.3 ± 0.1 b	1.5 ± 0.1 a	0.8 ± 0.04 c
Senesced leaf N (%)	0.8 ± 0.05	0.8 ± 0.04	0.7 ± 0.03
Leaf N:P (mol)	21.2 ± 1.1 b	34.8 ± 1.3 a	18.5 ± 0.8 b
Senesced leaf N:P (mol)	30.3 ± 4.5 b	48.4 ± 3.8 a	21.9 ± 1.0 b
Aggressive species (g/m^2)[b]	620 ± 100	400 ± 60	700 ± 140
Aggressive species (%)[b]	62 ±6	50 ± 5	49 ± 6
Litter			
Dry mass (g/m^2)	190 ± 50	131 ± 17	125 ± 20
Litter P (ug/g)	840 ± 100 b	570 ± 50 c	1080 ± 80 a
Litter N (%)	1.25 ± 0.28	0.87 ± 0.12	1.19 ± 0.11
Litter N:P (mol)	39 ± 3 a,b	48 ± 4 a	28 ± 2 b
Soils			
Available P (ug/cm^3)	9.3 ± 2 b	0.9 ± 0.1 c	13.5 ± 2.2 a
Total P (ug/cm^3)	170 ± 13 b	340 ± 20 b	410 ± 20 a
Available NH_4-N (ug/cm^3)	3.5 ± 0.5 b	5.2 ± 0.4 a	3.4 ± 0.3 b
Total N (mg/cm^3)	2.1 ± 0.2 b	4.2 ± 0.2 a	2.2 ± 0.1 b
Organic C (mg/cm^3)	28 ± 2 b	58 ± 2 a	27 ± 1.4 b

Means ($n = 10$) plus/minus one standard error are presented. Means separated by the same letter are not significantly different ($p = 0.05$) according to the Ryan-Einot-Gabriel-Welsch multiple range test.

[a] Minus site MOR.

[b] *Typha* spp. plus *Phalaris arundinacea*.

Stem height was greater and species richness was less in NE VI (*Corn Belt*) than in NEs VII and IX (Table 1). Aboveground biomass did not differ among NEs, ranging from 630 g/m^2 (NE VII) to 890 g/m^2 (NE IX). Nutrient Ecoregion IX, the southernmost NE, had the greatest biomass, perhaps due to the longer growing season, and it also contained the most biomass (700 g/m^2) of aggressive species. Proportionally though, biomass of aggressive species was greater in NE VI where they accounted for 62% of total biomass as compared to 49–50% for NE IX and VII (Table 1).

Leaf P was significantly greater in NE VI, where greater surface water N but not P concentrations were measured, than in the NE IX and NE VII (Table 1). And, senesced leaf P was greater in NEs VI and IX than in NE VII. Leaf N, C:N (data not shown) and N:P did not vary consistently with surface water N among the three NEs (Table 1). There also were no clear trends in litter mass, N or P among NEs that could be ascribed to differences in nutrient condition (Table 1).

Plant available P and total P were greater in NE IX than in NEs VI and VII (Table 1) and this difference was attributed to the fine textured (clayey) soils of NE IX (USDA, 1981a,b), that have high P sorption and, hence, high available and total P relative to the sandy soils of NE VI (USDA, 1998) and the organic soils of NE VII (USDA, 1981a,b). Nutrient Ecoregion VII, which had the lowest plant available P, also had the highest leaf, senesced and litter N:P of the three NEs (Table 1). Plant available NH_4-N and total N were significantly greater in NE VII that was attributed to the high organic carbon content of the soils of NE VII (Table 1). Across all NEs, soil total N ($r = 0.89$) and available N ($r = 0.55$) were positively correlated with organic C on a volume basis.

Correlation analysis revealed that vegetation indicators were more strongly associated with surface water nutrients, in particular NH_4-N, than with soil nutrients. Aboveground biomass ($r = 0.46$, $p < 0.01$), stem height ($r = 0.41$, $p < 0.05$), species richness ($r = -0.40$, $p < 0.05$) and biomass of aggressive species, *Typha* plus *Phalaris*, ($r = 0.46$, $p < 0.05$) were correlated with surface water NH_4-N but not PO_4-P or NO_3-N or with soil N or P. Leaf P ($r = 0.46$, $p < 0.01$), senesced leaf P ($r = 0.57$, $p < 0.01$) and senesced leaf N ($r = 0.48$, $p < 0.01$) also were positively correlated with surface water N. And, senesced leaf P was positively correlated with surface water PO_4-P ($r = 0.43$, $p < 0.05$) as well as soil extractable P on a mass ($r = 0.47$, $p < 0.01$) and a volume basis ($r = 0.46$, $p < 0.05$).

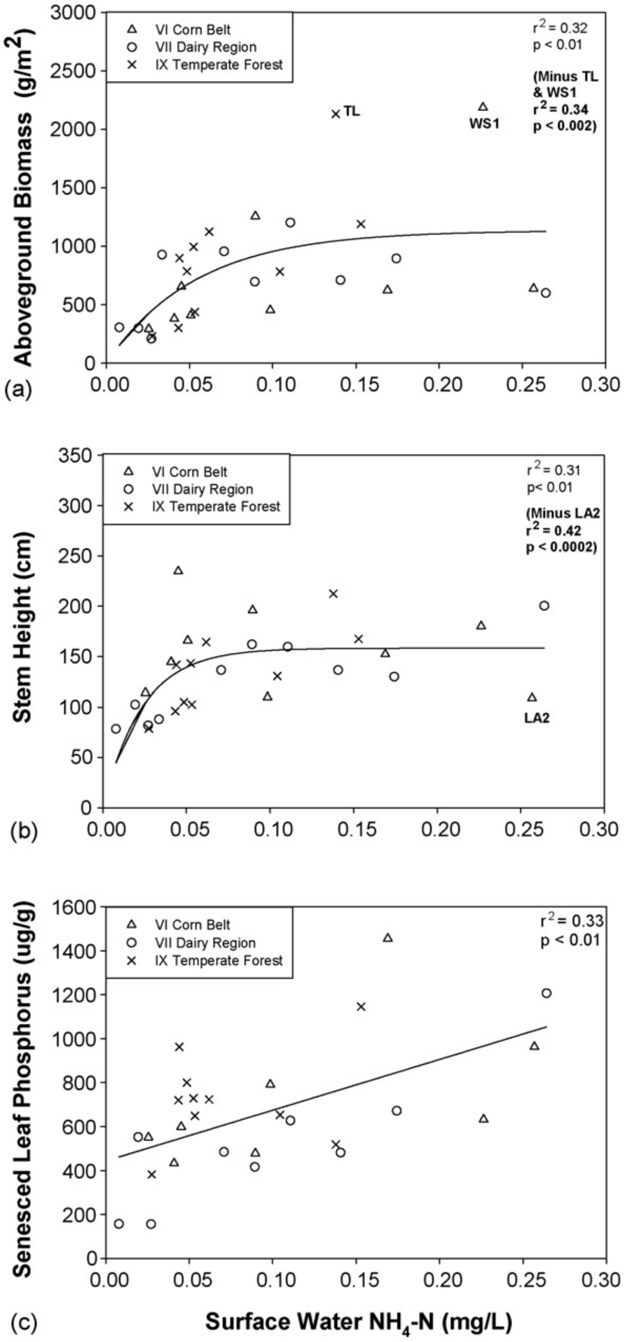

Fig. 2. (a) Aboveground biomass, (b) stem height and (c) senesced leaf P vs. mean surface water NH_4-N of 29 wetlands of NEs VI, VII and IX.

3.2. Indicators of nutrient enrichment: all NEs

Aboveground biomass and stem height increased asymptotically with NH_4-N (Figs. 2a and b). Senesced leaf P (Fig. 2c), leaf P ($r^2 = 0.21$, $p < 0.05$) and senesced leaf N ($r^2 = 0.24$, $p < 0.01$) also increased with surface water N. One would expect leaf and senesced leaf P to be related to surface water P rather than N though, in our wetlands, surface water NH_4-N and PO_4-P were positively correlated with each other ($r = 0.90$, $p < 0.0001$; minus site MOR, $r = 0.42$, $p < 0.05$). Species richness declined with surface water NH_4-N (Fig. 3a) while aggressive species, *Typha* spp. plus *P. arundinacea*, increased with surface water NH_4-N. Aboveground biomass of *Phalaris* plus *Typha* increased asymptotically with surface water NH_4-N (Fig. 3b). Of the vegetation indicators surveyed, percent biomass of aggressive species exhibited the strongest relationship with surface water N ($r^2 = 0.46$, $p < 0.0001$) (Fig. 3c).

Litter and soil indicators were not strongly related to wetland nutrient condition relative to vegetation. Litter P increased asymptotically with surface water NH_4-N ($r^2 = 0.26$, $p < 0.05$) but not with PO_4-P and soil total P (ug/g) increased asymptotically with surface water P ($r^2 = 0.26$, $p < 0.01$). There were no relationships between soil available P, available N and total N, and surface water nutrients.

3.3. Indicators of nutrient enrichment: individual NEs

We observed significant relationships between ecological indicators and surface water nutrients for NEs VII and IX but generally not for NE VI, *Corn Belt*. In NEs VII and IX, aboveground biomass increased with surface water NH_4-N and an asymptotic curve best fit the data for both NEs (Fig. 4a). Stem height also increased asymptotically and species richness declined linearly with surface water NH_4-N in the two NEs (Fig. 4b and c). Biomass of aggressive species (*Typha* plus *Phalaris*) increased asymptotically with surface water NH_4-N in NE VII and linearly with NH_4-N in NEs VI and IX (Fig. 5a). When expressed as the percentage of total biomass, aggressive species increased with surface water N in NEs VII and IX but not in NE VI (Fig. 5b). Green leaf P and senesced leaf P were positively related to surface water NH_4-N in NE VII but not in the other NEs (Table 2). Except for NE VII where litter P which was positively related to surface water NH_4-N (Table 2), we observed no relationships between litter and soil nutrients and surface water N and P for individual NEs.

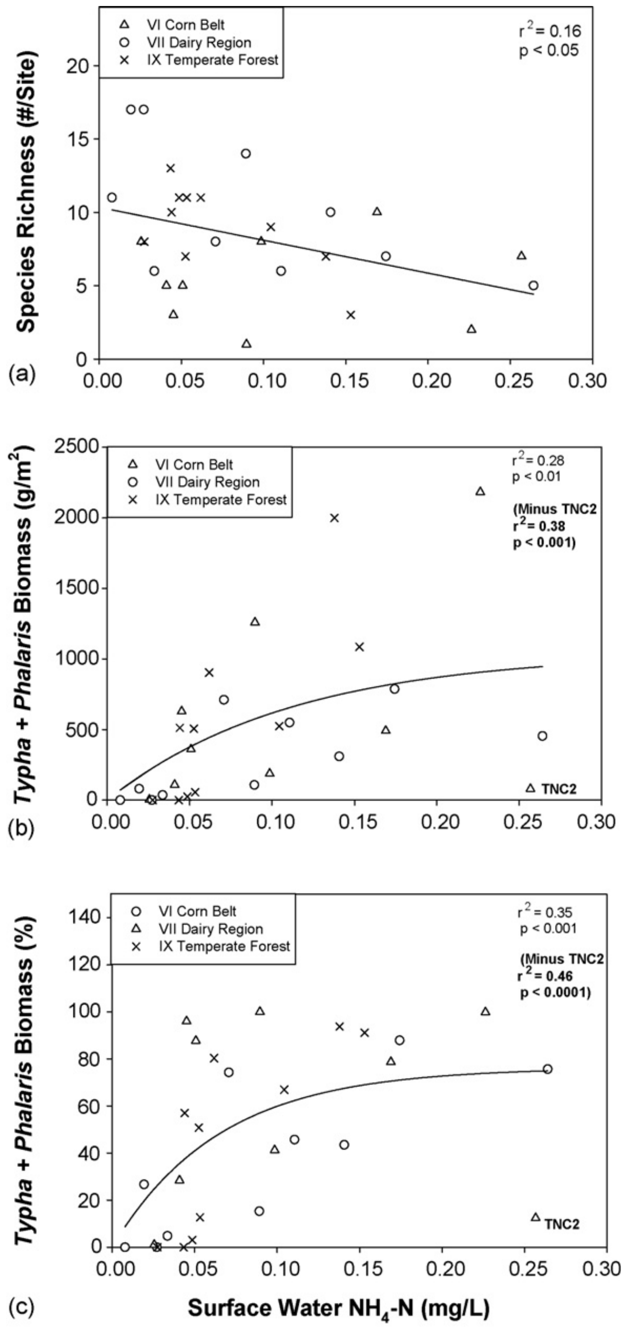

Fig. 3. (a) Species richness and biomass of aggressive species expressed as (b) g/m^2 and (c) percent of total community biomass vs. surface water NH_4-N of 29 wetlands of NEs VI, VII and IX.

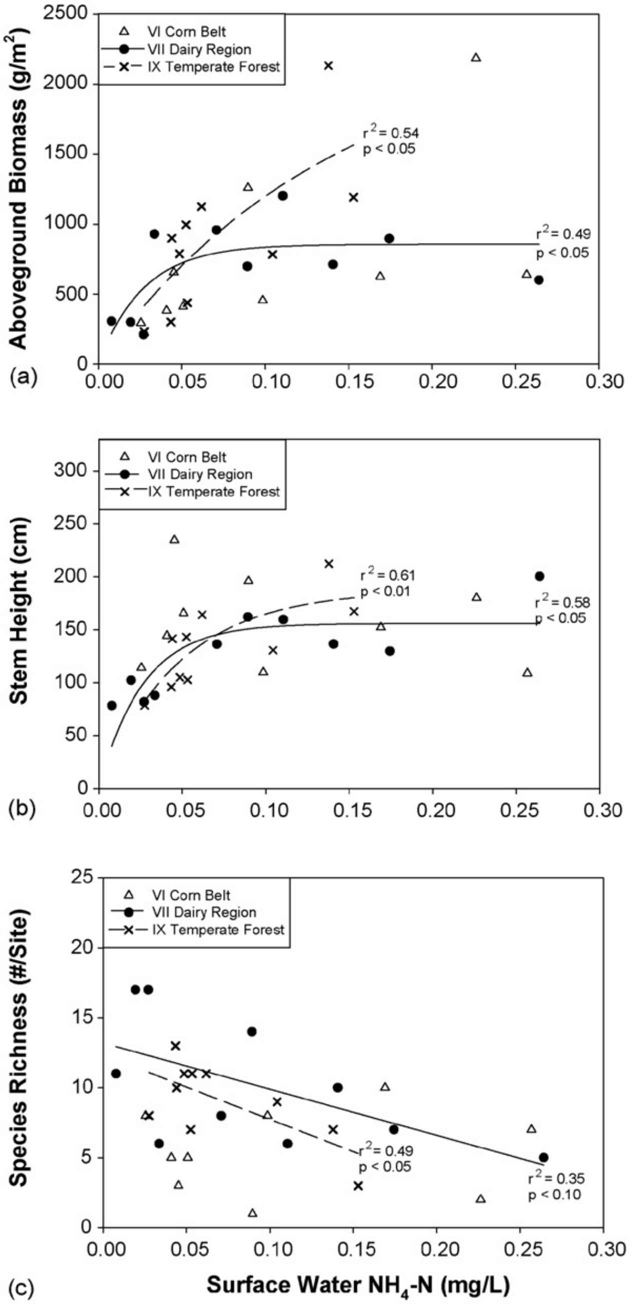

Fig. 4. Ecoregion-specific regressions of (a) aboveground biomass, (b) stem height and (c) species richness vs. surface water NH_4-N from 29 wetlands of NEs VII and IX. No significant relationships were observed for NE VI.

4. Discussion

Nutrient enrichment leads to predictable changes in wetland structure and function, including increased N and P uptake and NPP (Davis, 1991; Miao and Sklar, 1998) and dominance by aggressive species (Jensen et al., 1995; Craft and Richardson, 1997; Chambers et al., 1999; Svengsouk and Mitsch, 2001; Green and Galatowitsch, 2002; Maurer and Zedler, 2002; Woo and Zedler, 2002) that leads to a decline in species richness (Vermeer, 1986; Drexler and Bedford, 2002; Gustafson and Wang, 2002). We report similar alteration of vegetation structure and function correlated with increasing surface water NH_4-N (Figs. 2 and 3) but not PO_4-P or NO_3-N. For example, across all NEs, indicators associated with NPP (aboveground biomass, stem height), nutrient uptake (leaf N, P) and dominance by aggressive species (*Typha*, *Phalaris*) increased with surface water NH_4-N and species richness declined (Table 2). Indicators of NPP (aboveground biomass, height, biomass of aggressive species) increased asymptotically with N, suggesting that the subsidy effect of increased N is

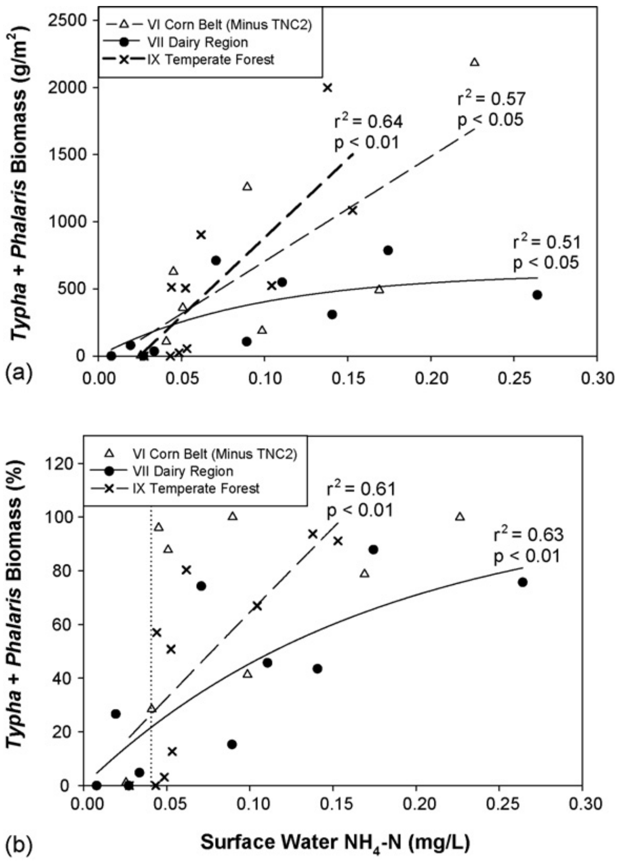

Fig. 5. Ecoregion-specific regressions of aboveground biomass of aggressive species expressed as (a) g/m^2 and (b) percent of total community biomass vs. surface water NH_4-N for 28 wetlands of NEs VI, VII and IX. Site TNC2 (NE VI) was dropped from the analysis.

Table 2
Goodness of fit (r^2) of statistically significant relationships ($p < 0.05$) between ecological indicators and wetland nutrient condition

Indicator	Nutrient	Model	Nutrient ecoregion (NE)				
			All NEs	VI	VII	IX	VII + IX
Vegetation							
Aboveground biomass (g/m^2)	NH_4-N	Asymptotic	0.32	ns	0.49	0.54	0.36
Stem height (cm)	NH_4-N	Asymptotic	0.42[a]	ns	0.58	0.61	0.56
Green leaf P (ug/g)	NH_4-N	Linear	0.21	ns	0.43	ns	–[b]
Senesced leaf P (ug/g)	NH_4-N	Linear	0.33	ns	0.77	ns	–[b]
Senesced leaf N (%)	NH_4-N	Linear	0.24	ns	ns	ns	–[b]
Species richness (#/site)	NH_4-N	Linear	0.16	ns	0.35	0.49	0.33
Aggressive species (g/m^2)	NH_4-N	Linear	0.38[c]	0.57[c]	0.51	0.64[d]	0.58[e]
Aggressive species (%)	NH_4-N	Asymptotic	0.46[c]	ns	0.63	0.61	0.54
Litter							
Phosphorus (ug/g)	NH_4-N	Asymptotic	0.26	ns	0.67	ns	–[b]
Soil							
Total P (ug/cm^3)	PO_4-P	Asymptotic	0.26[f]	ns	ns	ns	–[b]

ns, not significant.

[a] Minus site LA2.

[b] Not analyzed.

[c] Minus site TNC2.

[d] Asymptotic fit.

[e] NE VI + IX.

[f] Minus site BOT.

diminished at higher surface water NH_4-N concentrations (Gerloff and Krombholz, 1966; Odum et al., 1979) whereas indicators of nutrient uptake (leaf N, green and senesced leaf P) and species richness exhibited a linear response to N. Our findings are consistent with results from the Florida Everglades where aboveground biomass, nutrient (P) uptake and dominance by *T. domingensis* are positively correlated with P enrichment (Koch and Reddy, 1992; Craft and Richardson, 1993, 1997; Miao and Sklar, 1998; Doren et al., 1999). Drexler and Bedford (2002) report a similar response (e.g. increased stem height and dominance by *Typha latifolia*, reduced species richness) to nutrient enriched agricultural drainage for a fen wetland in upstate New York.

We observed no relationships between ecological indicators and surface water NO_3-N which is not surprising since, in the saturated soils of wetlands, most inorganic N is in reduced form as ammonium (Ponnamperuma, 1972; Craft et al., 1991). However, other studies have demonstrated that emergent vegetation responds positively to nitrate. Addition of 0, 12 and 48 g NO_3-N/m^2 year as calcium nitrate to mesocosms stimulated growth in sedge meadow vegetation (11 species) of the presence and absence of *Phalaris* (Green and Galatowitsch, 2002). In mesocosms containing *Phalaris*, biomass of reed canary grass more than doubled in the high NO_3-N treatment (1426 g/m^2) relative to the control mesocosms (619 g/m^2).

Our regressions suggest that N as NH_4-N may limit or co-limit productivity in Midwestern wetlands. Studies from the region and elsewhere also suggest that emergent vegetation is limited by N or co-limited by N and P. In Europe, addition of N (but not P) or potassium (K) increased aboveground biomass of swale, fen and wet grasslands (Willis, 1963; Vermeer, 1986). In a fertilization study where N, P and/or K were added to 45 wetlands, N additions increased aboveground biomass in more cases (19) than any other nutrient or nutrient treatment (Verhoeven et al., 1996). Svengsouk and Mitsch (2001) added N, P and N + P to mesocosms containing *Schoenoplectus tabernaemontani* (aka *Scirpus validus*) and *T. latifolia* in Ohio. After 1 year, *Typha* produced significantly more aboveground biomass in the N + P treatment and, after 2 years, both species exhibited greater growth but only in response to N + P. Evidence to support nutrient co-limitation also comes from Wisconsin, where *Typha* × *glauca* grew more in N + P treated plots than in control plots but there was no response to N or P applied singly (Woo and Zedler, 2002).

Additional support for N limitation of Midwestern wetland vegetation comes from N:P ratios where, based on the threshold N:P of 33:1 (green leaves) suggested by Koerselman and Mueleman (1996) and Verhoeven et al. (1996), our results indicate that wetland vegetation in NEs VI and IX (N:P = 21) may be N limited. For NE VII, leaf N:P ratios of 35 and low available P in soil (Table 1) suggest co-limitation by N and P. Many western European wetlands are thought to be N limited based on N:P ratios (15–33) of fen and wet meadow vegetation (Venterink et al., 2002). In Ohio and Wisconsin, N:P ratios for *T. latifolia* (30) and *Typha* × *glauca* (<31) suggest N limitation or co-limitation by N and P (Svengsouk and Mitsch, 2001; Woo and Zedler, 2002). Some studies though caution against using biomass N:P as an index of N versus P limitation because, while it is sensitive to P limitation, it does not work as well for evaluating N limitation (Gusewell et al., 2003).

In our wetlands, species richness declined with surface water NH_4-N but the relationship was not strong (Fig. 3a). Increasing dominance by aggressive species, *Typha* and *Phalaris*, though was strongly related to surface water N (Fig. 3b and c). Reduced plant species diversity and increasing dominance by a few aggressive species has been reported in connection with nutrient enrichment of wetlands, including bogs, fens, wet meadows, riparian areas, and swamps (Vermeer, 1986; Galatowitsch et al., 1999; Drexler and Bedford, 2002; Gustafson and Wang, 2002; Childers et al., 2003). Nutrient enrichment enables aggressive species to out compete native species for light and space (Maurer and Zedler, 2002). *Typha* × *glauca*, a hybrid of *T. latifolia* and *T. angustifolia* and reed canary grass (*Phalaris arundincea*) are common invasive plants of Midwestern wetlands (Galatowitsch et al., 1999) and, in controlled experiments, both species respond positively to nutrient enrichment. In Wisconsin, additions of N + P (7:1 ratio) to greenhouse-grown *Typha* × *glauca* increased biomass production while, in a field experiment, additions of fertilizer (N, P, K) stimulated growth of *Typha* × *glauca* more than sedge meadow graminoids (Woo and Zedler, 2002). Similarly, in mesocosm and field experiments, addition of nutrients (N, P, K) promotes biomass production and dominance by *Phalaris* over other emergent species (Maurer and Zedler, 2002; Kercher and Zedler, 2004b). Our regressions suggest that, in Midwestern wetlands, expansion of *Typha* and *Phalaris*, is positively linked to nutrient enrichment, especially NH_4. It is important though to recognize that other anthropogenic disturbances (flooding, sediment, light) interact with nutrients to promote invasion by *Phalaris* and *Typha* as has been shown in greenhouse (Wetzel and van der Valk, 1998), mesocosm (Newman et al., 1996; Kercher and Zedler, 2004a,b) and field experiments (Maurer and Zedler, 2002).

In addition to the environmental factors mentioned above, wetland age and stage of succession also structures plant community composition. According to Clements (1928), succession proceeds in a predictable orderly manner as pioneer species, possibly *Typha* and *Phalaris* in wetlands, colonize the site and, over time, are replaced by succeeding assemblages of plants and leading to a stable, climax community. It is unlikely, however, that our wetlands represent the early stages of succession since they were selected using topographic maps from the 1950s and 1960s, more than 40 years prior to sampling them. Gleason (1927) suggested that succession is driven by stochastic events, fortuitous seed dispersal together with changing environmental conditions at the site that determine community composition over time. This model has been employed to describe succession in temperate freshwater wetlands such as prairie potholes (Van der Valk, 1981). Connell and Slatyer (1977) expanded Gleason's model to include inhibition – early colonizers that "hold their ground" and inhibit colonization by other species, and tolerance – early colonizers tolerate but don't inhibit colonization by other species. In Midwestern wetlands, nutrient enrichment promotes the inhibition model of succession, where aggressive species such as *Typha* and *Phalaris*, colonize and hold the site, inhibiting colonization by other species. *Typha* and *Phalaris* are competitor species according to Grime (1977) and clonal dominants according to Boutin and Keddy (1993). Both species are known to readily colonize disturbed sites such as bare soil (Grace and Harrison, 1986; Green and Galatowitsch, 2002) and once established, they rapidly spread by rhizomes, forming large clonal communities (Wetzel and van der Valk, 1998; Maurer and Zedler, 2002). As *Typha* and *Phalaris* spread, they inhibit other species from colonizing by producing a tall, dense canopy and copious litter that shades the soil and hinders seed germination and plant establishment (Apfelbaum, 1985; Maurer and Zedler, 2002). Nutrient enrichment solidifies the dominance of *Typha* and *Phalaris* as they are able to maximize growth and biomass production relative to other wetland species in response to added nutrients (Maurer and Zedler, 2002; Kercher and Zedler, 2004b).

Litter and soils-based indicators were not strongly related to surface water nutrients. Litter P increased asymptotically with surface water NH_4-N ($r^2 = 0.26$, $p < 0.05$) and total P in soil ($r^2 = 0.26$, $p < 0.01$) was positively related to surface water PO_4-P. In contrast to the Everglades (see review by Noe et al., 2001) and wetlands in Canada (Wisheu et al., 1990) where the vegetation response is linked to P, we did not see strong relationships between soils-based indicators and wetland nutrient condition in our survey of three NEs of the Midwest. The absence of strong relationships is attributed to differences in soil texture among NEs, especially clay, that promotes P sorption and precipitation (Brady and Weil, 2002), and organic matter content. Soils of NE IX contained mostly silt and clay (USDA, 1981a,b) and also had the greatest extractable P and total P concentrations of the three NEs (Table 1). Soil extractable N and total N were greater in NE VII, where soils contained more organic matter, than in NEs VI and IX (Table 1).

Regressions developed for individual NEs generally were more powerful than a single regression for all NEs which was not unexpected since environmental characteristics such as physiography, geology and soils that affect water quality vary among the three NEs. Soils of NE VI (*Corn Belt*), for example, are classified as Mollisols and Alfisols that are relatively young, having formed since the glaciers receded about 10,000 years BP, and weathered from limestone (Buol et al., 1980). These soils are fertile and richer in base cations (Ca, Mg) and P relative to the organic soils (Histosols) of NE VII and the highly weathered Ultisols of NE IX that were not glaciated and, hence, are much older and more weathered and leached (Buol et al., 1980; Cross and Schlesinger, 1995). Thus, high concentration of inorganic P in surface waters of NE VI relative to NEs VII and IX (Table 1) may be partially explained by the fertile soils that underlie this NE.

Differences in anthropogenic land use among NEs though, probably exert a greater influence on wetland nutrient condition than the above mentioned environmental factors. The impact of land use on wetland nutrient and ecological condition are most evident in NE VI (*Corn Belt*) where surface water NH_4-N and PO_4-P concentrations were highest and where few ecological indicators were related to nutrient condition (Table 2). Most land in NE VI is cleared for agriculture (85%) (NCRS, 2004; Tormoehlen et al., 2000) and conversion of native forest to agriculture involves significant disturbance such as drainage of wetlands, tillage practices as well as fertilization. In NEs VII (53% cleared) and IX (24% cleared) where of the landscape is cleared for agriculture (NCRS, 2004; Tormoehlen et al., 2000), vegetation-based indicators were related to surface water NH_4-N (Table 2).

For some indicators, the trajectory or shape of the curve varied from one NE to another. For example, in NEs VII and IX, trajectories of (increasing) aboveground biomass with surface water NH_4-N were distinctly different though both curves were asymptotic (Fig. 4a). Likewise, trajectories of aggressive species biomass (g/m^2) versus surface water N differed for NE VII, where an asymptotic curve best fit the data, versus NEs VI and IX, where linear curves best described the relationship (Fig. 5a).

Vegetation-based indicators, though correlated with surface water N, were not strongly associated with nutrient availability of soils. There was no significant correlation between indices of NPP (aboveground biomass, stem height), species composition (richness, aggressive species) or most measures of nutrient uptake and soil available and total N and P. Only senesced leaf P, which was correlated surface water NH_4-N ($r = 0.57$, $p < 0.01$) and PO_4-P ($r = 0.43$, $p < 0.05$), was correlated with soil extractable P expressed on a mass basis ($r = 0.47$, $p < 0.01$) and a volume basis ($r = 0.44$, $p < 0.05$).

Canonical correlation analysis (CCA) of surface water and plant available (soil extractable) nutrients with species abundance from Appendices A–C supports the regression analysis; that plant community composition is attributed in large part to variation in surface water NH_4-N (Fig. 6). The first CCA axis was positively correlated with surface water NH_4-N ($r = 0.98$) and this axis explained 51% of the variation in the species data. The second axis (29% of the variation) was positively correlated with plant available NH_4-N ($r = 0.55$). Abundance of *Typha* was

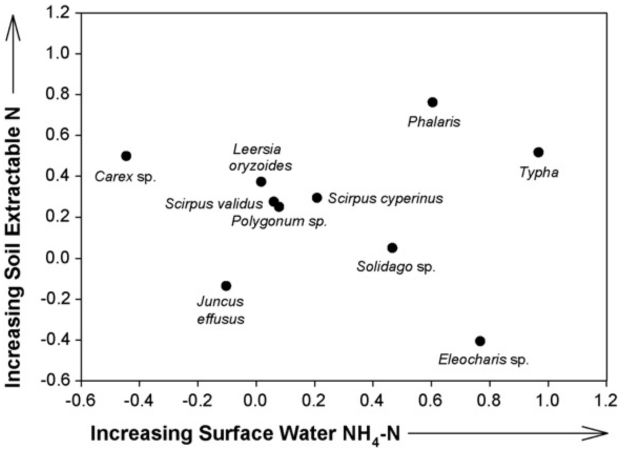

Fig. 6. Canonical correlation analysis of wetland nutrient condition with species abundance for 29 wetlands of NEs VI, VII and IX. Nutrient condition was described by surface water NH_4-N, NO_3-N and PO_4-P and plant available (soil extractable) N and P. Species abundance of the 10 most frequent species (i.e. present at five sites or more) was determined based on their fraction of the total biomass at the site.

associated with high surface water NH_4-N whereas *Phalaris* was associated with high surface water and high plant available N (Fig. 6). Abundance of *Eleocharis* sp. was correlated with high surface water N but low plant available N that was attributed to one site (TNC2) that recently was burned (C.B. Craft, personal observation). And *Carex* sp. was negatively correlated with surface water NH_4-N (Fig. 6). The results of the CCA support experimental and observational studies that link *Typha* and *Phalaris* to nutrient enrichment and *Carex* sp. to low nutrient environments (Wetzel and van der Valk, 1998; Budelsky and Galatowitsch, 2000; Maurer and Zedler, 2002; Woo and Zedler, 2002). It also supports our regression analyses that, for Midwestern wetlands, the response of vegetation is more strongly linked to N concentrations in surface water than in soil.

It is difficult to compare our findings with other NEs around the United States because, in contrast to rivers, streams and lakes, little research of this type has been published for wetlands. The lone exception is the Florida Everglades (NE XIII, Southern Florida Coastal Plain) and, here, the response of wetland vegetation to nutrient enrichment is similar that observed in the Midwest. In the Everglades, vegetation also responds to nutrient enrichment with increased biomass production, stem height and nutrient uptake (Davis, 1991; Miao and Sklar, 1998), decreased species richness and increasing dominance of aggressive species, *T. domingensis* (Jensen et al., 1995; Craft and Richardson, 1997). In contrast to Midwestern wetlands though, the response to nutrient enrichment in the Everglades differs in that (1) the primary limiting nutrient and, thus, the ‘‘problem’’ nutrient is P and (2) P enrichment of the underlying peat soils occurs. Everglades soils consist of relatively homogeneous peat that contains abundant nitrogen (2–4%) relative to P (<600 ug/g) (Craft and Richardson, 1993) and, so, strong P limitation of vegetation occurs in this wetland. Furthermore, Everglades soils become phosphorus enriched over time as P enriched detritus from the increasingly nutrient enriched emergent plant community accumulates to produce fresh peat. In contrast, soils of the Midwestern wetlands we sampled vary tremendously within and among NEs, consisting of organic soils (in NE VII only) but more commonly mineral soils, Mollisols, Ultisols, Inceptisols and Entisols, that are low in N and differ in their capacity to retain P. Thus, low soil N content and variable P sorption capacity may explain why, in Midwestern wetlands: (1) N rather than P is linked to

Table 3
Proposed ecological indicators of wetland nutrient condition for Nutrient Ecoregions (NEs) of the Midwest

Indicator	Model	NE	Goodness of fit (r^2), p value
Aboveground biomass (g/m^2)	$1096 \times (1 - e^{-23(NH_4\text{-}N)})$	VII + IX	$r^2 = 0.36$, $p < 0.01$
Stem height (cm)	$167 \times (1 - e^{-28(NH_4\text{-}N)})$	VII + IX	$r^2 = 0.56$, $p < 0.0002$
Species richness (no./site)	$12.33–33 \times (NH_4\text{-}N)$	VII + IX	$r^2 = 0.33$, $p < 0.01$
Aggressive species (g/m^2)	$620 \times (1 - e^{-11(NH_4\text{-}N)})$	VII	$r^2 = 0.51$, $p < 0.05$
	$-128 + 8920 \times (NH_4\text{-}N)$	VI + IX	$r^2 = 0.58$, $p < 0.0005$
Aggressive species (%)	$106 \times (1 - e^{-7(NH_4\text{-}N)})$	VII + IX	$r^2 = 0.54$, $p < 0.0002$

Regression models were chosen based on the significance (p value) level.

nutrient enrichment and (2) P enrichment of the soil is not evident.

For Midwestern wetlands, the best indicators and their regression models, based on the significance level (p value), are shown in Table 3. Overall, stem height and percent biomass of aggressive species were the best indicators of nutrient condition. They had high goodness of fit (0.54–0.56), low p values (<0.0002) and were applicable to NEs VII and IX. Also, in NE VII and IX, there appeared to be a threshold concentration, above which *Typha* and *Phalaris* dominate. In wetlands where surface water NH_4-N exceeded 40 ug/L, these species accounted for more than 40% of total plant biomass (see Fig. 5b). Species richness ands aboveground biomass also were robust indicators that were applicable to NEs VII and IX but the goodness of fit was not very high (0.33–0.36). Biomass (g/m^2) of aggressive species was not robust because the best models were derived for individual, not multiple NEs.

We conclude that indices of vegetation NPP and species composition are robust indicators of nutrient condition of freshwater wetlands of the Midwestern U.S., especially in NEs where other anthropogenic disturbances (e.g. land clearing, drainage) are not widespread and intense. Soils-based indicators are less effective than vegetation because properties such as texture and organic matter that affect soil nutrient enrichment vary so much among NEs. Additional work is needed to test these indicators across a range of NEs, wetland vegetation types and human disturbance regimes.

Acknowledgements

We appreciate the help of many students (Scott Struck, Kristie Overberg, Chad Washburn, Christina Pruett, Sarah Butler, Angela Vedder) who participated in field sampling and lab analyses and the land owners (Foxwood Farms, The Nature Conservancy-Kankakee Sands Preserve, Indiana Department of Natural Resources) who gave us permission to collect samples on their property. We gratefully acknowledge funding support from U.S. EPA Region 5 (Chicago) and U.S. EPA Headquarters. We appreciate the thoughtful comments of Paul McCormick, Ulo Mander and an anonymous reviewer who examined an earlier draft the manuscript.

Appendix A

Plant species collected from 10 freshwater wetlands located in Nutrient Ecoregion VI. Values in parentheses are percent of total aboveground biomass for a given site.

LA1	LA2	MOR	TNC1	TNC2	TNC3	TNC4	WS1	WS2	WS3
Polygonum sp. (63) *Sagittaria latifolia* (1) *Scirpus validus* (8) *T. latifolia* (28) *Utricularia* spp. (<1)	*Lemma* spp. (<1) *Nymphaea odorata* (4) *T. latifolia* (96)	*Typha latifolia* (100) Unknown grass (<1)	*Eleocharis* sp. (4) *Leersia oryzoides* (2) *Mimulus ringens* (5) *Polygonum* sp. (2) *Salix* sp. (5) *S. pungens* (27) *S. validus* (54) *T. latifolia* (1) Unknown forb (<1)	*Bidens cernua* (<1) *Bidens coronata* (<1) *Eleocharis* sp. (59) *L. oryzoides* (10) *M. ringens* (4) *Schoenoplectus pungens* (3) *Scirpus fluviatilis* (5) *S. validus* (7) *T. latifolia* (12)	*T. latifolia* (100)	*Amaranthus* spp. (<1) *Brassicaceae* (<1) *Equisetum laevigatum* (20) *Lycopus* sp. (1) *Panicum* sp. (2) *S. pungens* (35) *Salix* spp. (1) *T. latifolia* (41)	*T. latifolia* (100) Unknown forb (<1)	*Acer rubra* (<1) *Boehmeria cylindrical* (1) *T. latifolia* (87) Unknown grass #1 (<1) Unknown grass #2 (12) Unknown forb (<1)	*Bidens connata* (<1) *Echinochlea muricata* (<1) *Eleocharis* sp. (<1) *L. oryzoides* (1) *Polygonum* sp. (19) *Phalaris arundinacea* (6) *S. latifolia* (1) *T. latifolia* (73) Unknown grass (<1) Unknown forb (<1)

Appendix B

Plant species collected from 10 freshwater wetlands located in Nutrient Ecoregion VII. Values in parentheses are percent of total aboveground biomass for a given site.

FM	MIT	MIT2	NF	NFS	NOT	PR	RM	TF	WOL
Bidens sp. (19)	*B. cernua* (14)	*Carex* sp. (2)	*A. rubra* (<1)	*B. cylindrica* (1)	*B. cernua* (14)	*Apios americana* (1)	*Carex* sp. (6)	*Asclepias incarnata* (<1)	*B. cernua* (<1)
Carex sp. (26)	*Cyperus esculentus* (19)	*Echinochloa crusgalli* (<1)	*Betula pumila* (4)	*C. mariscoides* (1)	*Eleocharis* sp. (3)	*Asclepias incarnata* (3)	*Eupatorium maculatum* (1)	*Cladium mariscoides* (57)	*Eleocharis* sp. (2)
L. oryzoides (<1)	*Echinochloa waltri* (20)	*Eleocharis* sp.	*C. mariscoides* (38)	*Carex* sp. (21)	*Polygonum puncatum* (<1)	*Carex* sp. (41)	*Onoclea sensibilis* (20)	*Carex* sp. (1)	*Juncus effusus* (<1)
P. arundinacea (35)	*L. oryzoides* (33)	*L. oryzoides*	*Carex* sp. (23)	*Eleocharis* sp. (2)	*S. latifolia* (2)	*E. maculatum* (9)	*P. arundinacea* (44)	*Eleocharis* sp. (3)	*L. oryzoides* (10)
Solidago sp. (6)	*P. hydropiperoides* (10)	*S. latifolia* (1)	*Drosera reutundifolia* (<1)	*Juncus effusus* (1)	*T. latifolia* (81)	*O. sensibilis* (6)	*Polygonum sagittatum* (<1)	*Equisetum* sp. (<1)	*Polygonum* sp. (<1)
Solidago uliginosa (3)	*T. latifolia* (4)	*Scirpus americanus* (22)	*Eleocharis* sp. (23)	*Juncus* sp. (<1)		*Pedicularis lanceolata* (1)	*Polygonum* sp. (<1)	*Hypericum* sp. (<1)	*P. arundinacea* (5)
T. latifolia (11)		*S. validus* (1)	*E. laevigatum*	*Lathyrus palustris* (<1)		*Phalaris arundicacea* (15)	*Rosa palustris* (<1)	*J. effusus* (1)	*T. latifolia* (83)
		T. latifolia (74)	*Juncus brachycephalus* (2)	*L. oryzoides* (<1)		*Polygonum convolvulus* (<1)	*S. americanus* (26)	*Juncus* sp. (<1)	
			Juncus sp. (<1)	*Lycopus* sp. (<1)		*P. sagittatum* (<1)	*Solidago* sp. (2)	*Potentilla fruticosa* (36)	
			L. oryzoides (<1)	*Mentha arvensis* (2)		*S. americanus* (4)	*Thelypteris palustris* (<1)	*P. lanceolata* (1)	
			Lobelia cardinalis (<1)	*P. arundinacea* (5)		*Solidago gigantea* (3)		*Setaria viridis* (<1)	
			Pedicularis lanceolate	*Rosa* sp. (<1)		*Solidago* sp. (14)		*Scirpus* sp. (<1)	
			P. fruticosa (2)	*S. americanus* (19)		*Thalictrum revolutum* (1)		*Solidago* sp. (1)	
			Rudbeckia sp. (2)	*Scirpus* sp. (1)		*T. palustris* (1)			
			Solidago sp. (<1)	*S. validus* (8)					
			S. uliginosa (<1)	*Salix nigra* (13)					
			S. validus (4)	*T. palustris* (4)					
				T. latifolia (22)					

Appendix C

Plant species collected from 10 freshwater wetlands located in Nutrient Ecoregion IX. Values in parentheses are percent of total aboveground biomass for a given site.

AR	BOT	BV	GLL	GLU	LM1	LM2	LS	SYC	TL
J. effusus (32)	*L. oryzoides* (4)	*Carex* sp. (<1)	*B. cernua* (5)	*Acer saccharinum* (2)	*B. cylindrica* (1)	*Bidens coronata* (1)	*B. cernua* (<1)	*Erigeron* spp. (3)	*B. cylindrica* (<1)
Juncus tenuis (<1)	*T. latifolia* (91)	*Juncus* sp. (<1)	*J. effusus* (3)	*B. cylindrica* (2)	*L. oryzoides* (2)	*B. connata* (11)	*B. connata* (4)	*J. effusus* (3)	*Impatiens capensis* (3)
L. oryzoides (22)	Unknown grass (5)	*J. tenuis* (1)	*L. oryzoides* (2)	*J. effusus* (3)	*P. sagittatum* (4)	*C. esculentus* (4)	*J. effusus* (17)	*L. oryzoides* (21)	*Lysimachia nummularia* (<1)
L. nummularia (<1)		*L. oryzoides* (19)	*Lamium* sp. (1)	*L. oryzoides* (1)	*Polygonum* sp. (26)	*Eleocharis* sp. (4)	*L. oryzoides* (20)	*Scirpus cyperinus* (39)	*S. cyperinus* (3)
Scirpus atrivirens (20)		*S. cyperinus* (<1)	*Scirpus atrovirens* (39)	*L. nummularia* (8)	*S. cyperinus* (32)	*Eragrostis hypnoides* (2)	*Polygonum* sp. (2)	*T. latifolia* (13)	*T. latifolia* (94)
Scirpus cyperinuns (12)		*T. latifolia* (80)	*S. cyperinus* (<1)	*P. sagittatum* (5)	Unknown forb #1 (<1)	*L. oryzoides* (37)	*P. arundinacea* (2)	Unknown forb #1 (17)	Unknown grass (<1)
T. latifolia (3)		Unknown grass (<1)	*T. latifolia* (50)	*S. atrovirens* (<1)	Unknown forb #2 (11)	*Polygonum* sp. (19)	*T. latifolia* (55)	Unknown forb #2 (1)	Unknown forb (<1)
Unknown grass (4)		Un. forb #1 (<1)	Unknown grass (<1)	*S. cyperinus* (11)	Unknown forb #3 (9)	*S. cyperinus* (17)	Unknown grass (<1)	Unknown forb #3 (1)	
Unknown forb #1 (2)		Unknown forb #2 (<1)		*T. latifolia* (67)	*Xanthium strumarium* (15)	Unknown forb (<1)	Unknown forb #1 (<1)	Unknown forb #4 (2)	
Unknown forb #2 (3)		Unknown forb #3 (<1)		Unknown forb #1 (<1)		*X. strumarium* (5)	Unkown forb #2 (<1)	Unknown forb #5 (<1)	
Unknown forb #3 (1)		Unknown forb #4 (<1)		Unknown forb #2 (<1)			Unknown forb #3 (<1)		
Unknown forb #4 (1)				Unknown forb #3 (<1)					
Unknown forb #5 (<1)									

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