Long-Term Phosphorus Assimilative Capacity in Freshwater Wetlands: A New Paradigm for Sustaining Ecosystem Structure and Function

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Statistical analysis of a North American Wetland Database (NAWDB) allowed us to develop a mass loading model that was used to separate P assimilative capacity (defined as P absorption with no significant ecosystem change and no elevated P output) from storage capacity (maximum storage) in wetlands. Our analysis indicates that, given ample supplies of other nutrients, average P assimilative capacity (PAC) in North American wetlands is near 1 g m^{-2} yr^{-1}. From this analysis, we proposed a "One Gram Assimilative Capacity Rule" for P loadings within natural freshwater wetlands if long-term storage of P, maintenance of community structure and function, and low P effluent concentrations are required. An Everglades test site supports our hypothesis that natural wetlands will lose native species, become P saturated in a few years, and export unacceptable amounts of phosphate when phosphorus loading exceeds PAC. Moreover, our findings clearly demonstrate that even P-limited wetlands have the capacity to assimilate low levels of P loadings without significant changes in ecosystem structure and function.

Introduction

Determining the nutrient assimilative capacity for ecosystems has proven elusive because of the difficulty in quantifying N and P storage and cycling and in determining the nutrient thresholds needed to maintain natural ecosystem structure and function (*1−3*). Moreover, the high storage capacity of wetlands for some ions as well as their ability to efficiently transform nutrients like N and P has resulted in their selection mainly as a cost-effective means of treating runoff on the landscape (*4−9*). Nutrient storage capacity (often a design feature of constructed wetlands) is defined as the total mass per unit area that can be retained permanently by the system. However, these levels may result in significant ecosystem changes (e.g., altered community structure and diversity as well as increased productivity) and increases in downstream P and N output concentrations. By contrast, we define the nutrient assimilative capacity of a wetland as the long-term mass removal capacity per unit area that is transformed and absorbed into the system with no significant ecosystem changes in internal structure or function and in downstream output of the nutrient. This removal capacity is in addition to the nutrients received from rainfall. In this paper, we improve the predictive ability and provide new ecological response data to support our concept of P (total phosphorus) assimilative capacity in wetlands subjected to increased phosphorus loadings. A statistical analysis of the North American Wetland Database (NAWDB) as well as a site-specific test of the P assimilative capacity of wetlands is presented for the Everglades.

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Methods

We analyzed data from a large number of wetlands throughout the United States to assess the effects of different P loadings on long-term storage rates and effluent concentration patterns. The North American Wetlands for Water Quality Treatment Database (NAWDB) is a United States Environmental Protection Agency effort to collect and summarize the effectiveness of using wetlands, both constructed and natural, as a low-cost alternative for removing pollutants (*10*).

Cross-sectional data sets are appealing because they include a range of responses to nutrient inputs. This means that empirical evidence discovered from these data is likely to have a relatively broad inference base. The NAWDB includes input and output phosphorus concentrations (P_{in} and P_{out}, in mg/L), hydraulic loading rate (qs, in cm/day), treatment area (in ha), and areal input and output P mass loading rates (L_{in} and L_{out}, in g m^{-2} yr^{-1}). A piecewise linear model proposed earlier by Reckhow and Qian was used to do exploratory analysis and to prepare a nonparametric regression model fit with the data (*11*). A Bayesian change point detection method (*12*) was applied to a piecewise linear model of the data, and we developed a procedure for estimating assimilative capacity when site-specific data are available (*13*). This method was applied to data from the northern Everglades to develop a single-wetland "change point" curve. The probability of overloading the Everglades at a given P loading rate was calculated, and a nonparametrically fitted model of P outflow concentration as a function of P loading rate was developed (*14*, *15*). To further assess the relationship of P loading to assimilative capacity, we collected and analyzed data on water quality, developed indices for P availability, assessed populations of macrophytes and macroinvertebrates, and measured P storage in soils for 6 yr along a P gradient in an area of the Northern Everglades (*16−20*).

Results

The existence of wetland P assimilative capacity (PAC) became evident by analysis of a cross-sectional data set for 126 natural and constructed wetlands throughout the United States (U.S. EPA NAWDB) (*10−12*) (Figure 1a). Piecewise linear regression modeling (*11*, *14*) suggests that a significant increase in total phosphorus (P) effluent concentrations will occur from wetlands receiving a mass loading of P much above 1 g m^{-2} yr^{-1}.

Analysis of the NAWDB effluent trends reveals that when P loadings to wetlands are kept below 1 g m^{-2} yr^{-1}, P output concentrations remain fairly constant and low (mean of 42.8 $\pm$ 7.3 μg/L P) (Figure 1b). On the basis of an analysis of residual sums of squares, the optimal value for the change point (see change point zone between regions 1 and 2 in Figure 1a) lies

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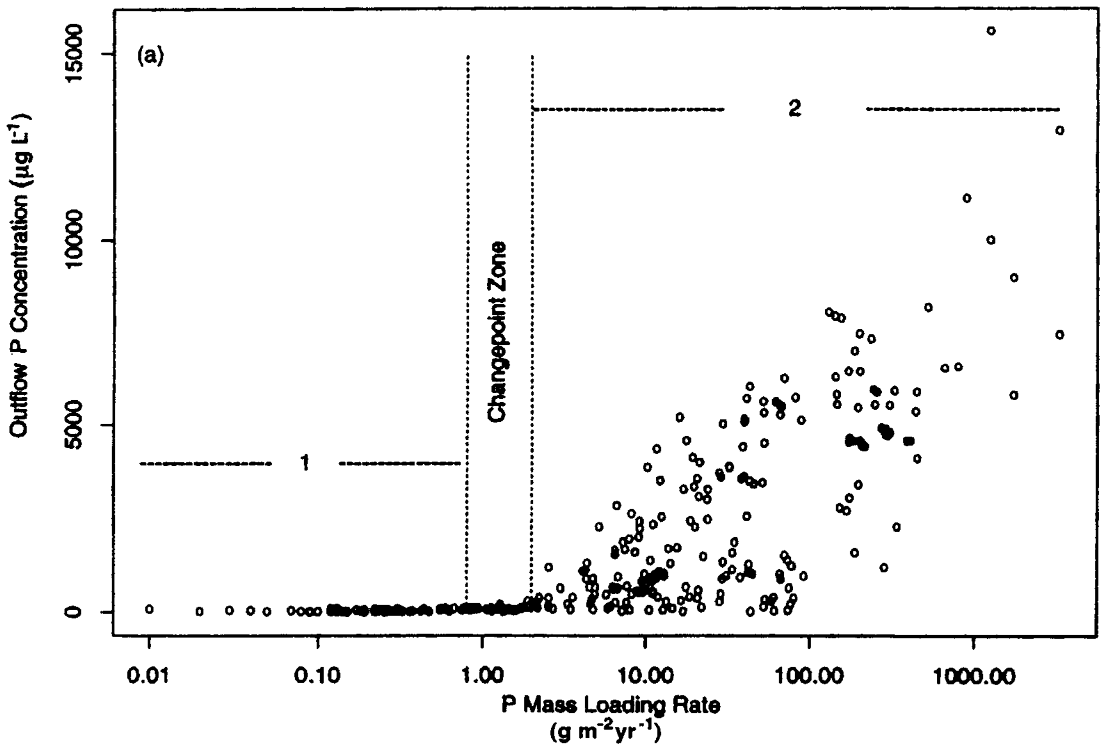


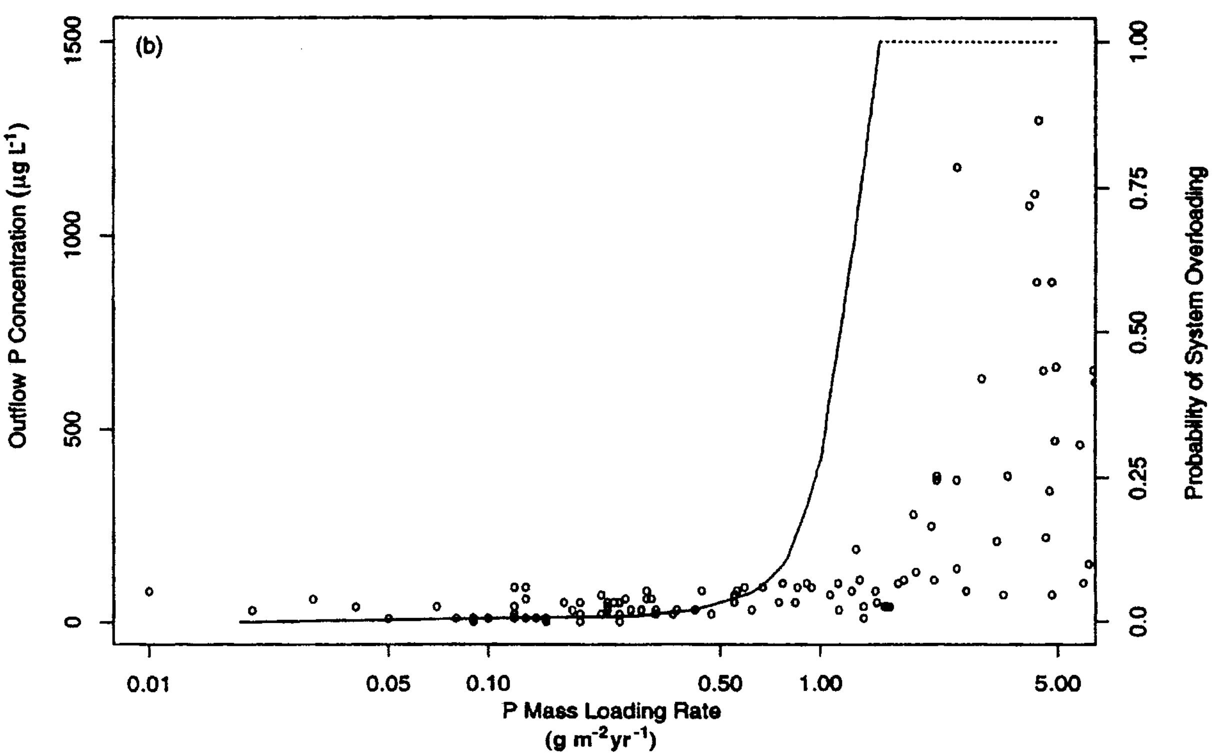


FIGURE 1. (a) Input total phosphorus (P) loading effects on P output concentrations for the North American Wetland Database (NAWDB) (*10*). Total sites are 126 with data collected over several years, $n = 317$. In region 1 where loading rate is less than 1 g m^{-2} yr^{-1}, uniform P output concentrations are found (i.e., baseline P output), and output concentration is not a function of the loading rate; while in region 2 the P loading rate is larger than 1 g m^{-2} yr^{-1}, and output concentrations increase significantly as the loading rate increases. The variation in the output concentrations is large and nonuniform. The change point in loading rate is defined as the loading rate value that divides output P concentrations into uniform and nonuniform regions. (b) An expanded scale of the NAWDB better displays the increase in outflow variation that occurs at P loadings between 0 and 5 g m^{-2} yr^{-1}. The curved line indicates the relationship between the P loading rate and the probability (or risk) of the system being overloaded. The risk-loading relationship was developed for an Everglades data set using a Bayesian change point estimation method (*12, 14*). The dashed line is extended across the NAWDB since the probability of exceeding baseline P output is equal to 1 at loadings above 1.5 g m^{-2} yr^{-1}.

between 0.4 and 1.4 g m^{-2} yr^{-1}, which is compatible with the long-term P accumulation rate reported for wetland ecosystems (*6, 16*). The variations in P effluent output around the change point suggest that PAC is a site-specific quantity. This assimilative capacity has a 95% confidence interval of 1.4–0.4 g m^{-2} yr^{-1} since this region of the model (region 1

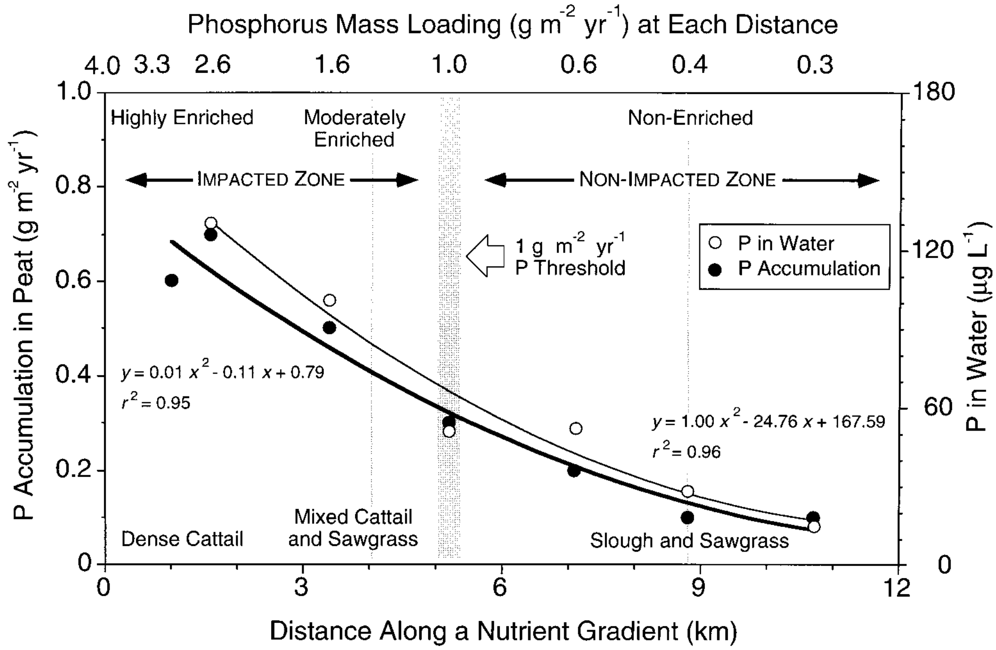


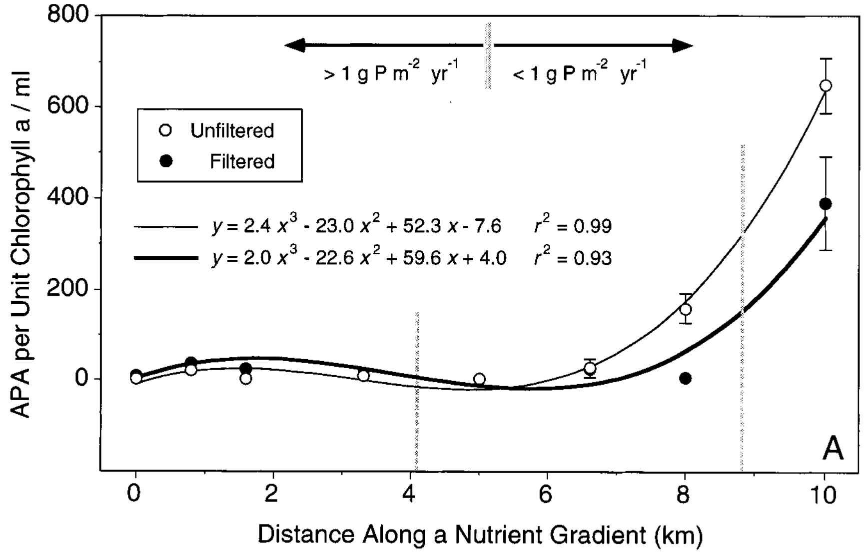
FIGURE 2. Relationship between surface water total phosphorus and mean soil P accumulations along an eutrophication gradient (transect C) in WCA-2A in the Northern Everglades of Florida. Estimated phosphorus mass loadings over the past 26 yr are shown for set distances from the Hillsboro Canal and are calculated following a P retention model developed for the Everglades wetland (*17*). The model was run successively to calculate the amount of P stored in each zone, and the remaining P was used as the load to the downstream zone. The degree of enrichment and amount of impact are shown for each zone and are based on the amount of P loadings, elevated water column P concentrations, and changes in macroinvertebrate and plant community structure (*18*–*20*). Vertical dashed lines show the 95% confidence intervals (1.4–0.4 g m^{-2} yr^{-1}) around the 1 g m^{-2} yr^{-1} P threshold.

in Figure 1a) maintains stable outflow P concentrations (see expanded scale, Figure 1b). Therefore, we postulate that the long-term PAC for wetlandsdoes not exceed 1 g m^{-2} yr^{-1} P. The 1-g level, however, represents an overall North American average against which site-specific assimilative capacity should be estimated when appropriate data are available. Moreover, the 1-g level should be considered an upper conservative P loading value for assimilative capacity that sustains natural structure and functions in the wetland.

Kadlec suggested that the central tendency of the cross-sectional data set of the NAWDB cannot be used to draw general conclusions about general ecosystem behavior (*21*). This is true if it is only used as the final model to estimate particular parameters for specific sites. The exact change point is a case of such a parameter. We suggest that the Bayesian change point method can be used with a piecewise linear model to develop specific parameters for each wetland type. We used this change point detecting method utilizing both NAWDB and an independent data set from the Everglades to estimate PAC, i.e., the probability of overloading Everglades ecosystem processes and increasing P effluent above background outputs. The probability analysis suggests a 90% chance of overloading at 1.4 g m^{-2} yr^{-1}, a 40% chance at 1.0 g m^{-2} yr^{-1}, and a 10% chance at 0.7 g m^{-2} yr^{-1} (see solid line, Figure 1b). These results suggest that the Everglades data support the 1-g P assimilative capacity rule.

To further test our hypothesis and separate P storage capacity and PAC, we first calculated P mass loadings and related surface water P and soil P accretion rates to P availability as indexed by measurements of phosphatase activity in water (*2*) and N:P ratios in plants (*22*). Changes in plant community structure, plant productivity, and macroinvertebrate diversity were then used to estimate change in ecosystem structure and function along a 10-km P gradient in the Everglades. Phosphorus loading rates ranged from 4.0 g m^{-2} yr^{-1} in the highly enriched dense cattail zone nearest the Hillsboro discharge canal to background P loadings of 0.3 g m^{-2} yr^{-1} in the most unenriched sawgrass region 10 km downstream from the inputs (Figure 2). Surface water P concentrations and soil P accretion rates are highly correlated ($r = 0.94$, $p < 0.05$), and both decrease exponentially with distance from the input structures (Figure 2). However, the highly enriched area (zone 0–2 km) that received the highest average P loadings (2.7 g m^{-2} yr^{-1}) maintained water column concentrations >100 μg/L P (Figure 2). The region of the moderately enriched zone (2–5 km) receiving P loadings above 1 g m^{-2} yr^{-1} had water column concentrations from 60 to 100 μg/L P, well above the average P output concentrations of 43 μg/L P displayed by the NAWDB wetlands (Figure 1a,b). It was not until P loadings decreased to below 1 g m^{-2} yr^{-1} (6–8 km) in the nonimpacted zone that P concentrations reached the mean baseline output concentrations of 43 μg/L P reported for the NAWDB (Figure 1a,b). However, the Everglades ecosystem, like many freshwater wetlands, is P-limited (*16, 18*). This causes P concentrations in the water column to be further reduced to a mean background level of 10.4 ± 1.3 μg/L before water exits the wetland (*13, 14, 16*). Highest P storage capacity in the wetlands is found with increased P loading near the inputs (0–0.7 km) at decreased P removal efficiency (*13, 16*) (Figure 2). These increased loadings above the PAC for the wetland resulted in highest downstream P concentrations and ecosystem changes in the high P-loading zone.

For example, two biochemical indices of P availability, phosphatase activity (APA) in the water column and molar N:P ratios in sawgrass (*Cladium jamaicense*), revealed that P limitations only existed below the 1 g of P m^{-2} yr^{-1} loading threshold (Figure 3a,b). In the region above the 1 g of P m^{-2} yr^{-1} loading, APA enzyme activity per unit of chlorophyll was almost undetectable. By comparison, the region below the 1 g of P m^{-2} yr^{-1} loading displayed significant APA activity in both the filtered and unfiltered samples (Figure 3a). The magnitude of increase in the molar N:P ratios found in



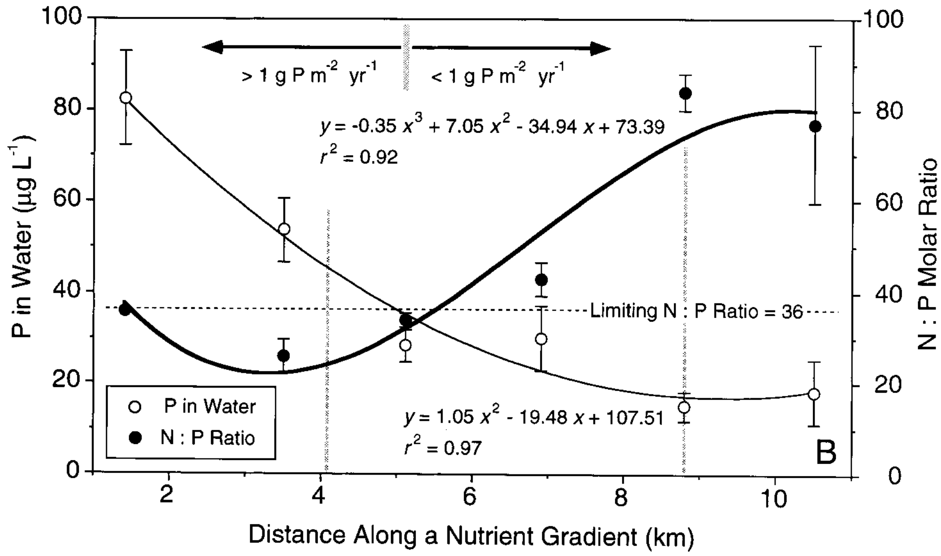


FIGURE 3. (a) Water column phosphatase activity (APA) per unit of chlorophyll along a nutrient gradient in the Northern Everglades (transect C, WCA-2A). Phosphatase was normalized over the amount of chlorophyll found per milliliter. Both filtered and unfiltered APA are shown to clarify the amount of activity due to varying densities of particles versus bacteria and algae in the water column. Methods followed the 4-methylumbelliferyl phosphate technique of Wetzel (*2*). Vertical dashed lines show the 95% confidence intervals (1.4−0.4 g m^{-2} yr^{-1}) around the 1 g m^{-2} yr^{-1} P threshold. (b) The molar N:P ratio for sawgrass leaves along a nutrient gradient in the Northern Everglades (transect C, WCA-2A). Methods of analysis for N and P followed Craft and Richardson (20) and Verhoeven et al. (*24*). Vertical dashed lines show the 95% confidence intervals (1.4−0.4 g m^{-2} yr^{-1}) around the 1 g m^{-2} yr^{-1} P threshold.

sawgrass leaves generally followed the increase in APA activity in the water column (Figure 3a,b). Interestingly, the plant N:P ratios reach their maximum values near the 0.4 g of P m^{-2} yr^{-1} loading rate, but APA activity increased until water column P concentrations reached their lowest concentrations along the gradient (Figure 3b). Both indices of ecosystem P limitations showed their highest values below the 1 g of P threshold.

Detailed measurements of plant community structure, productivity, and macroinvertebrate diversity along this eutrophication gradient caused by nearly 30 yr of nutrient-rich agricultural runoff in the Northern Everglades revealed a shift in the dominant plant species community from open sloughs and sawgrass (*C. jamaicense*) to cattail (*Typha domingensis*) in the area near the discharge point (0−4 km, Figure 4a). The impacted zone was also the area of highest P loadings, water column TP, and maximum P accumulation (Figure 2). This region also had the highest loadings of other ions, including nitrogen, calcium, and sodium (*18, 20*). The low level of change in plant community structure from 1990 to 1996 beyond 5.1 km (Figure 4a) and the low P concentrations in the downstream water column support our hypothesis that wetlands can fully assimilate P at loadings of up to 1 g m^{-2} yr^{-1} without significant change in this ecosystem component. The nonimpacted zone (>5.1−10.5 km) has maintained the dominant native sawgrass communities (>89% frequency) and 18 out of 19 macrophyte and slough species (*23*). Moreover, sawgrass plant productivity in the impacted zones (0−5.1 km) was nearly double that of the nonimpacted area (Figure 4b). Plant frequency, however, was greatly reduced for this more desirable species above a 1 g m^{-2} yr^{-1} loading (Figure 4a).

Macroinvertebrate diversity and number of taxa were highest in the P-enriched areas (P loadings 1.6−4.0 g m^{-2} yr^{-1}) but were reduced to background levels at P inputs (<1.0 g m^{-2} yr^{-1}) (Figure 5) (*19*). The relative distribution of taxa within functional feeding groups was similar along the gradient (*19*). However, the mean annual density of benthic invertebrates was 7.4 times greater in the most enriched sites as compared to nonenriched sites (*19*).

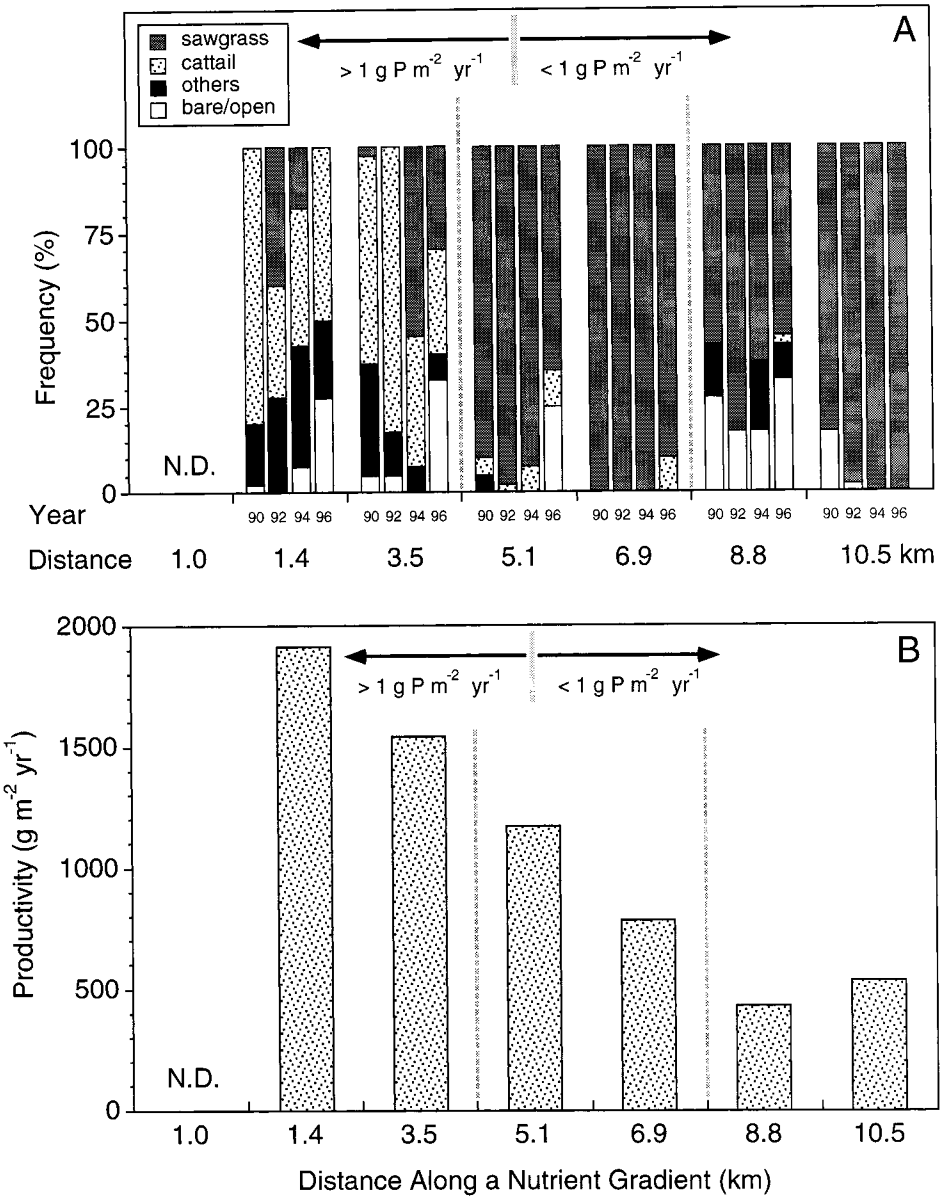


FIGURE 4. (a) Plant species composition at six locations downstream from the Hillsboro Canal in the Northern Everglades. Cattail (*Typha domingensis*) is the dominant species within the first 3.5 km. A sawgrass (*Cladium jamaicense*) monoculture has existed for 6 yr (1990–1996) at the 5.1 km location and at more distant plots even after ≅30 yr of P loadings. Plant species composition was measured in permanent plots at sampling locations in the Northern Everglades in June 1990, 1992, 1994, and 1996 to verify potential changes in cover type and to assess the changes reported in the impacted and nonimpacted zone since 1973 (*18*, *27*). Species composition was determined using the point intercept method and expressed as percent frequency of occurrence along transect C in WCA-2A (*28*). Vertical dashed lines show the 95% confidence intervals (1.4–0.4 g m^{-2} yr^{-1}) around the 1 g m^{-2} yr^{-1} P threshold. (b) Net annual primary productivity was estimated at six locations in WCA-2A. Data were recalculated from Davis (*29*). Vertical dashed lines (not scaled to distance) show the 95% confidence intervals (1.4–0.4 g m^{-2} yr^{-1}) around the 1 g m^{-2} yr^{-1} P threshold.

Discussion

Collectively, our data suggest that the Everglades ecosystem responses and water quality support the P assimilative concept that emerged from our analysis of the NAWDB. Low P loading rates and low water column P concentrations exist below the P threshold zone after 30 yr of nutrient-rich runoff with little or no significant change in ecosystem structure and function (Figures 3–5). Specifically, the long-term maintenance of the low P availability region after 3 decades of P additions has resulted in no significant changes in plant community composition, invertebrate diversity, or invertebrate taxa within functional family groups. However, the highest total number of invertebrate taxa, biomass, and density were found in the enriched areas with high plant productivity (*19*).

The nutrient limitation criteria developed by Koerselman and Meuleman (*22*) and Verhoeven (*24*) suggest that plants with molar N:P ratios >36 are P limited, while those below 31 are N limited (Figure 3b). (Note: The plant molar ratio of 36 equals an equivalent weight-base ratio of 16.) Values above 36 are only found below the 1-g loading zone, a region with elevated APA activity. Both indices suggest that P limitation, a condition found in the most undisturbed area of the Everglades, exists below the P threshold zone. Related mesocosm work on responses of the Everglades plant community to varying P dosing concentrations also indicates that annual average P concentrations must be maintained below 30 μg/L in order to prevent significant decreases in periphyton mat, macrophyte density, and algal communities (*18*). This water quality concentration is only found below

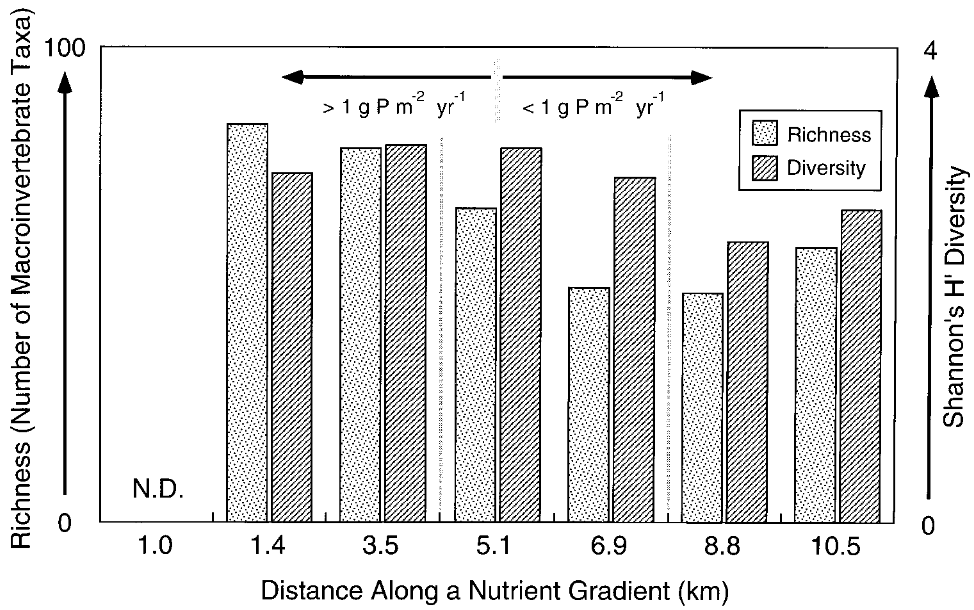


FIGURE 5. Macroinvertebrate Shannon−Wiener diversity and number of taxa were measured seasonally at six locations in WCA-2A from 1990 to 1992 using a D-frame sweep net and benthic cores (*19*). Vertical dashed lines (not scaled to distance) show the 95% confidence intervals (1.4−0.4 g m^{-2} yr^{-1}) around the 1 g m^{-2} yr^{-1} P threshold.

the 1 g m^{-2} yr^{-1} threshold (Figure 3b).

We find that once P loadings saturate short-term uptake and storage mechanisms (i.e., in the highly enriched zone), a downstream moving front of elevated P concentrations exists in the wetlands until P loadings are reduced to the PAC of the wetland (Figures 1a,b and 2). We thus propose a “One Gram Assimilative Capacity Rule” for P loadings within the Everglades and other natural freshwater wetlands if long-term storage of P, maintenance of native plant and invertebrate species, and low P effluent concentrations are the goal. This rule may not hold if high continuous loadings of Fe, Ca, Al, or P-binding sediment are added to the water entering the wetland and metal precipitation becomes the main P removal mechanism (*7, 25*).

Importantly, whether P is lost at high concentrations from a wetland depends on the size of the wetland as compared to the P loadings. Our studies suggest that all wetlands have the capacity to store some P without significant changes in downstream P concentrations or community changes. If the wetland is of sufficient acreage to decrease downstream P loadings at or below its assimilative capacity, then a high percentage of the P will be retained within the wetland and no moving P front in the water column will exist, as the system has reached an equilibrium with P additions. Long-term P removal is directly related to long-term soil P storage capacity of the ecosystem (*13*).

The goal of optimizing maximum P retention capacity for a wetland is not compatible with the PAC concept unless a large area of wetland is available and an impacted zone is acceptable within the highest load zone. For example, an impacted zone (0−5 km) is found in the region receiving 4.0 to about 1.0 g m^{-2} yr^{-1} of P loadings, and the nonimpacted area is only found below PAC (Figure 2). However, the sizing of the wetlands necessary to remove P loadings can be estimated from a model of the relationship of mass P storage inputs to water column P inputs (*13, 14*) where $A = C_iQ/Pl_i$ when A is the total storage area (m^2), C_i is the P input concentrations (μg L^{-1}), and Pl_i is the P loading inputs (g m^{-2} yr^{-1}). The equation has been further developed and tested in a paper by Lowe and Keenan (*26*).

To our knowledge, this is the first time that PAC of a wetland has been quantified at several trophic levels and separated from P storage capacity. Both the NAWDB and the Everglades show a clear pattern of low phosphorus output concentration when the total phosphorus mass loading rate was less than 1 g m^{-2} yr^{-1}, but some variation (1.4−0.4 g m^{-2} yr^{-1}) among wetland sites exists (Figure 1b). For the most sensitive P-limited wetlands, the critical loading rate may fall closer to the lower end of the P threshold zone (0.4 g m^{-2} yr^{-1}) if changes in other trophic level properties (e.g., algal mat communities) are a concern (Figure 2) (*18*). Thus, 1 g may be an upper-end P loading value for assimilative capacity in wetlands not specifically designed to treat wastewater. Importantly, our findings clearly demonstrate that even P-limited wetlands have the capacity to assimilate low levels of P loadings without significant changes in ecosystem structure and function. The PAC concept needs to be further tested in specific wetland types to verify whether the 1-g rule is a universal predictor of ecosystem change in freshwater wetlands receiving P additions.

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