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Short-term changes in phosphorus storage in an oligotrophic Everglades wetland ecosystem receiving experimental nutrient enrichment

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Abstract. Natural, unenriched Everglades wetlands are known to be limited by phosphorus (P) and responsive to P enrichment. However, whole-ecosystem evaluations of experimental P additions are rare in Everglades or other wetlands. We tested the response of the Everglades wetland ecosystem to continuous, low-level additions of P (0, 5, 15, and 30 μg L^{-1} above ambient) in replicate, 100 m flow-through flumes located in unenriched Everglades National Park. After the first six months of dosing, the concentration and standing stock of phosphorus increased in the surface water, periphyton, and flocculent detrital layer, but not in the soil or macrophytes. Of the ecosystem components measured, total P concentration increased the most in the floating periphyton mat (30 μg L^{-1}: mean = 1916 μg P g^{-1}, control: mean = 149 μg P g^{-1}), while the flocculent detrital layer stored most of the accumulated P (30 μg L^{-1}: mean = 1.732 g P m^{-2}, control: mean = 0.769 g P m^{-2}). Significant short-term responses of P concentration and standing stock were observed primarily in the high dose (30 μg L^{-1} above ambient) treatment. In addition, the biomass and estimated P standing stock of aquatic consumers increased in the 30 and 5 μg L^{-1} treatments. Alterations in P concentration and standing stock occurred only at the upstream ends of the flumes nearest to the point source of added nutrient. The total amount of P stored by the ecosystem within the flume increased with P dosing, although the ecosystem in the flumes retained only a small proportion of the P added over the first six months. These results indicate that oligotrophic Everglades wetlands respond rapidly to short-term, low-level P enrichment, and the initial response is most noticeable in the periphyton and flocculent detrital layer.

Abbreviations: ENP = Everglades National Park; N = Nitrogen; P = Phosphorus; SRP = Soluble reactive phosphorus; TP = Total phosphorus; WCA = Water conservation area

Introduction

Eutrophication of wetland and aquatic ecosystems by anthropogenic nutrient inputs is a common and growing global problem (Mitsch & Gosselink 1993; Carpenter et al. 1998; Pringle & Barber 2000). Nutrient enrichment frequently changes the structure and function of these ecosystems by affecting ecosystem components such as surface water, algae and periphyton, macrophytes, and consumers (Smith 1998). As a consequence, the abatement and mitigation of eutrophication in aquatic ecosystems has received considerable attention (National Research Council 1992). Additions of both nitrogen (N) and phosphorus (P) contribute to the eutrophication of aquatic ecosystems (Carpenter et al. 1998). However, P rather than N limits ecological processes in most freshwater lakes (Schindler 1977; Smith 1998) and oligotrophic lakes in particular (Downing & McCauley 1992). Phosphorus also appears to be the limiting nutrient in many freshwater wetlands (Bedford et al. 1999). However, there is much less known about the effects of P enrichment in wetlands compared to lakes. Determination of the effects of P enrichment in oligotrophic wetland ecosystems is important to the management of these systems.

Historically, the Everglades wetland ecosystem was oligotrophic and limited by P (Steward & Ornes 1983; Vymazal et al. 1994; McCormick et al. 1996; Noe et al. 2001). The natural system was extensive (1.17 million hectares), with a subtropical climate, flat limestone bedrock, and sheetflow hydrology that all limited surface water P inputs and resulted in a primarily atmospheric source of P (Davis 1994; Noe et al. 2001). Consequently, the Everglades had low concentrations of soluble reactive P (SRP) and total P (TP) and biogeochemical processes were limited by P and not N (Davis 1994; Reddy et al. 1999).

In the last several decades, P enrichment has altered the structure and function of the Everglades wetland ecosystem, mostly in proximity to canal water inputs from the Everglades Agricultural Area and urban areas. Davis (1994) estimated that annual P inputs into the Northern Everglades increased from historic levels of ~129 metric tons to contemporary inputs of ~376 metric tons as the result of increased P loading from agricultural drainage. Numerous studies have documented responses to P in: (1) surface water (e.g. Koch & Reddy 1992; McCormick et al. 1996); (2) periphyton (e.g. Grimshaw et al. 1993; Pan et al. 2000); (3) soils (e.g. Koch & Reddy 1992; Craft & Richardson 1993); (4) macrophytes (e.g. Doren et al. 1997; Miao & Sklar 1998); and (5) consumers (e.g. Rader & Richardson 1994; Turner et al. 1999). Both the TP concentration and dry mass of ecosystem components change along these nutrient gradients, increasing or decreasing depending on the variable and component. Therefore, the eutrophication process alters P

standing stocks in both individual components and in the entire ecosystem. However, only a few studies have quantified P storage in multiple ecosystem components (Davis 1991; Koch & Reddy 1992; Craft et al. 1995; Daoust 1998; McCormick et al. 1998; Miao & Sklar 1998); thus, few Everglades studies have facilitated a whole-system P budget.

Most ecological research has taken place in the northern portions of the Everglades (Water Conservation Area (WCA)-2A; Figure 1) close to the sources of P-enriched waters and where even the least-impacted marshes are enriched compared to the Southern Everglades (Stober et al. 1998). All three experiments that tested the effects of P enrichment on Everglades wetlands *in situ* occurred in the Northern Everglades [(1) Vymazal et al. 1994; Craft et al. 1995; (2) McCormick & O'Dell 1996; McCormick & Scinto 1999; and (3) Pan et al. 2000; Qualls & Richardson 2000]. Furthermore, all P-dosing experiments in the Everglades, with the exception of the study presented in Pan et al. (2000) and Qualls and Richardson (2000), and the study we present here, utilized a nutrient loading approach in which a mass of P was added to surface waters periodically (weekly to bimonthly). Interpretation of these results is complicated by the fact that oligotrophic Everglades wetlands typically receive anthropogenic P via the continuous inflow of water high in P, rather than a discontinuous pattern of P loading.

In 1998, we initiated an experiment to identify the response of Everglades wetlands to enriched P concentrations in surface water. One of the primary objectives of this study was to identify the lowest concentration of P in water flowing into the Everglades that causes 'an imbalance in the natural populations of aquatic flora or fauna' of the ecosystem (Everglades Forever Act; Florida Legislature 1994). Our study was unique in three aspects: (1) we focused on marshes in Everglades National park (ENP) rather than the much-studied and extensively-impacted Northern Everglades; (2) we used a whole-ecosystem approach; and (3) our experimental design involved continuous additions of constant P concentrations to the water column during the wet season. We used a flow-through flume technique to continuously deliver P at three different concentrations above background while maintaining natural hydrologic flow. We measured the responses of water, periphyton, flocculent detrital layer, soil, macrophytes, and aquatic consumers to P enrichment. This research is ongoing and we are continuing to quantify the response of ecosystem components to P enrichment at fine spatial and temporal scales. In this paper we synthesize and summarize the changes in ecosystem P content, storage, and retention after the first season (6 months) of dosing. Our objectives are to (1) identify short-term changes in ecosystem structure in response to P enrichment and (2) test our hypothesis that ecosystem state change occurs as a cascade of response first measur-

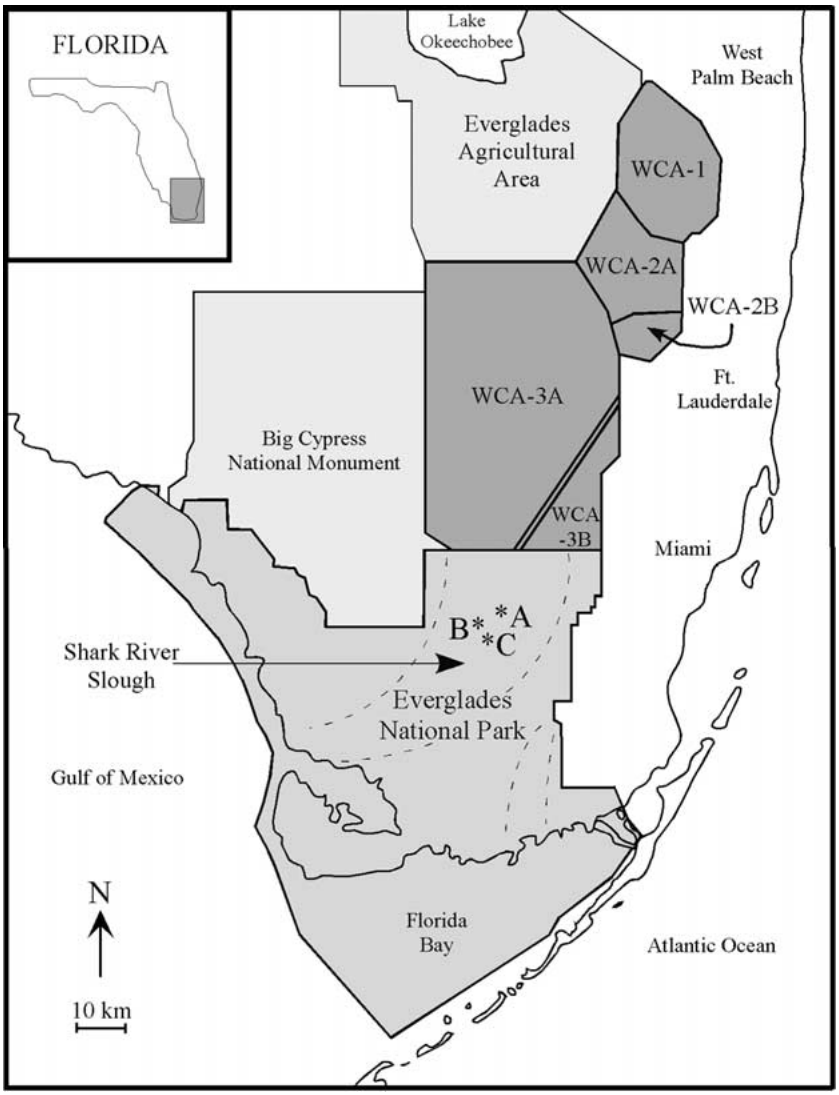

Figure 1. Map of south Florida and the Everglades. * = Flumes, A, B, and C.

able in microbial components, followed by sequential changes in periphyton, soils, microinvertebrates, emergent macrophytes, and finally macroinvertebrates (Childers et al. 2002). Analyses of ecosystem responses to elevated P in the oligotrophic Everglades will provide insight into the general effects of eutrophication on wetland and aquatic ecosystem biogeochemistry.

Methods

Site description

Phosphate dosing is being conducted at three replicate flumes (A, B, and C) in the oligotrophic, unimpacted marshes of Shark River Slough, ENP, roughly 15 km downstream of the Tamiami Canal (Figure 1) – the only source of waterborne nutrients to this region of ENP (Walker 1999). Average non-dosed water-column TP concentrations at our ENP flumes are typically <10 μg L^{-1} (0.32 μM). The flumes are located in peat-based wet prairie marshes (sensu Gunderson 1994), characterized by a relatively long hydroperiod, abundant periphyton, and a macrophyte community dominated by a few species. Hydrology in this subtropical climate is characterized by deeper, faster flowing water in the wet season compared to shallower, slower moving water in the dry season. Water depth rarely exceeds one meter and drawdown is rare in peat-based wet prairies, although water management has increased the frequency of drying in this area of the Everglades compared to pre-drainage conditions (Fennema et al. 1994). Floating periphyton (metaphyton), associated with the floating macrophyte *Utricularia purpurea* Walter, is the dominant form of periphyton in wet prairie marshes, with small amounts of periphyton found on macrophyte stems (epiphyton) or the benthos (epipelon). *Eleocharis cellulosa* Torr. is the most widespread and abundant macrophyte species in our flumes. Other macrophytes include *Panicum hemitomon* Schult., *Sagittaria lancifolia* L., *Pontederia cordata* L., *Paspalidium geminatum* (Forssk.) Stapf, *Nymphoides aquatica* (J.F.Gmel.) Kuntze, *Nymphaea odorata* Sol., and *Eleocharis elongata* Chapm.

Flume design

Each flow-through flume (Figure 2) has four open-ended channels, including three where we added NaH_2PO_4 + Na_2HPO_4 (pH = 7) to continuously increase TP concentrations by 5, 15, and 30 μg L^{-1} above ambient ($\sim$ 0.16, 0.48, and 0.97 μM, respectively) and one control that received no P (Childers et al. 2002). Thus, the four treatments resulted in planned surface water TP concentrations of approximately 10, 15, 25, and 40 μg L^{-1} at the point of dosing. Dosing began in October 1998 and will continue through May 2001, although P dosing is halted in the dry season when water velocities decrease below 2 mm sec^{-1}. The flumes are oriented parallel to the predominant direction of water flow. Each channel is 100 m long and 3 m wide with floating walkways that separate each channel. Channel walls are constructed of heavy-gauge plastic sheeting that is attached at the top to rollers on the edge of the floating walkways and attached at the bottom to metal flanges inserted 30–40

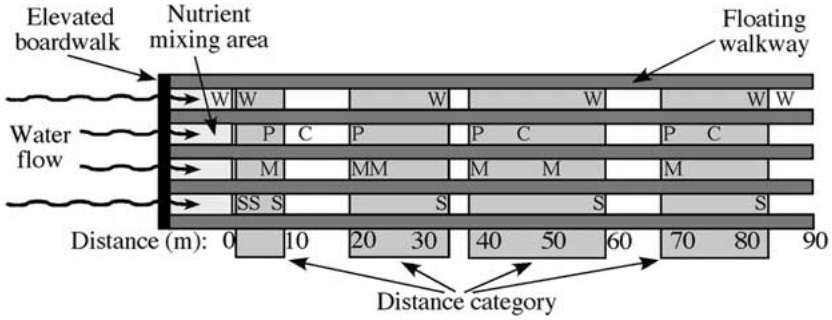

Figure 2. Aerial schematic view of a flume showing sampling locations and distance categories. W = water, P = periphyton, C = consumers, M = macrophytes, and S = soil and floc. Each component was sampled in each of the four channels.

cm into the soil. Wall effects are minimized by adjusting the height of the channel walls to the depth of water and confining most sampling to the center of the channels. The first 10 m of each flume channel is a nutrient mixing area (header box) devoid of vegetation with a solid fiberglass floor placed on top of the soil surface.

Data collection

All major ecosystem components were sampled throughout the first season of dosing. In this paper, we report on the specific methods used to characterize the ecosystem at the end of the first six months of dosing. Surface-water samples were collected within the flumes at points upstream and downstream of the marsh and different points within the marsh. The first set of water samples were taken from upstream (downstream end of the nutrient mixing area and beginning of the marsh, designated 0 m) and downstream (5 m upstream from end of channel, designated 85 m) stations in all flume channels (Figure 2) over a period from 26 March to 4 April 1999. We collected 250 mL of water at each station in each channel from the middle of the water column of both stations. Water was collected at noon and midnight with ISCO® automated water samplers for a total of 12 sampling events. The 12 samples were combined into a single, 3 L composite sample for each of the upstream and downstream stations in each channel. The second set of water samples was collected from permanent sampling sites at 3, 33, and 83 m downstream from the mixing area in each channel (Figure 2). These samples were taken at Flumes A and B on 29 March 1999 and Flume C on 30 March 1999. In order to characterize TP concentrations at distances between 33 and 83m, additional water samples were collected from plots at 58 m on 22 March 1999 at Flume A, 31 March 1999 at Flume B, and 7 April 1999 at Flume C. For

the entire second set of samples, 500 ml of water was collected at mid-depth in the water column; a 100 μm Nytex® screening excluded floating debris from the samples. Total P concentration in the water samples, and all other ecosystem components, were analyzed colorimetrically (EPA 365.1, 1983) after dry-combustion according to methods of Solorzano and Sharp (1980). Finally, water depth and velocity were measured continuously by a pressure transducer and accoustic doppler flow sensor, respectively, located at the front of the mixing area in each channel.

Periphyton, the aggregrated matrix of microalgae, microconsumers (bacteria, fungi, protists, and microinvertebrates), invertebrates, detritus, $CaCO_3$, and associated aquatic macrophytes, is a common structural feature of the Everglades wetland ecosystem (Browder et al. 1994; McCormick et al. 1998). We characterized both the biomass and concentration of P in these periphyton mats. Periphyton was sampled from Flumes A, B, and C on 22 March, 31 March, and 12 April 1999, respectively, from permanent 1-m^2 quadrats located 5, 18.5, 36.5 and 66.5 m downstream from the nutrient mixing area in each channel. To estimate biomass, 15 4.2-cm^2 diameter cores were extracted from the periphyton in each quadrat, and were then combined into one sample. Samples were stored frozen until they could be processed. We examined thawed samples under a microscope and removed *U. purpurea*, other dead plant material, and animals from the periphyton mat. The remaining periphyton was homogenized and diluted to a measured volume with distilled water. A subsample of known volume was removed, dried to constant weight at 100 °C ($\sim$2 days), and weighed. Another subsample was dried to constant weight and analyzed for tissue TP concentration. To convert biomass estimates from a cm^{-2} to m^{-2} unit, mat cover was estimated from digital photographs of the 1-m^2 quadrats taken in the field with a high-resolution (2 megapixel) digital camera. Areal cover was estimated from the images using Image Pro® 4.0 analysis software (Media Cybernetics L.P. 1993).

The flocculent detrital layer (floc) and soil were sampled from Flumes A, B, and C on 22 March, 31 March, and 7 April 1999, respectively. Cores were taken from permanent 1-m^2 quadrats located at 1, 3, 8, 33, 58, and 83 m downstream of the nutrient mixing area. Three intact cores were collected at each channel location by sliding a 2.36 cm I.D. cellulose-acetate-butyrate tube with a razor-blade edge into the upper 10 cm of soil. A rubber stopper was inserted into the top of the core to create suction and the intact core was removed. The core was dewatered by gentle decantation through a foam rubber plug. Depth of the floc was measured and the floc was decanted into sample bags. The soil was extruded into separate sample bags. The three floc and soil samples from each quadrat were combined into one composite

sample for each component. Anomalous materials (live roots, snail shells, etc.) were removed from the soil and floc samples in the lab. The samples were then dried (80 °C), weighed for field bulk density (g dry cm^{-3}), and analyzed for TP concentration.

Macrophyte quadrats were located at 5, 18.5, 21.5, 36.5, 49, and 66.5 m downstream of the nutrient mixing area. The aboveground biomass of each macrophyte species in each plot was estimated using non-destructive morphometric measurements made from 11 to 25 January 1999. The ability of plant morphometry to accurately predict biomass in Everglades marshes has been demonstrated previously (Daoust & Childers 1998). Species measured for biomass estimation included *E. cellulosa* (EC), *N. aquatica* (NA), *N. odorata* (NO), *P. geminatum* (PG), *P. hemitimon* (PH), and *S. lancifolia* (SL). *E. elongata* and *P. cordata* were present but did not occur in sufficient quantities to contribute appreciably to the biomass of any plots. For emergent species, shoot heights were measured from the water surface to the tallest node (PG and PH) or growing tip (EC and SL). These measurements were then added to an average plot water depth to obtain total shoot heights. Emergent shoot diameters were measured approximately halfway between the water surface and the tallest node or growing tip for EC, PG, PH, and SL. We counted the number of live leaves for PG and PH. The shoot volume of EC, using a cylindrical model, was included in its regression. For the floating-leaved species, NA and NO, the length (parallel to the leaf notch) and width (perpendicular to the leaf notch) of the leaf blades were measured. The relationships between these morphometric measurements and dry weight biomass were modeled using species- and flume-specific regressions developed from macrophyte samples collected immediately adjacent to the flumes. The regressions had high r^2 values for each species, ranging from 0.86 to 0.99 (Edwards and Noe, unpublished data). Shoots of each species were counted in each plot, and average shoot mass was multiplied by these counts to estimate quadrat biomass (g m^{-2}). Macrophyte tissue samples were collected for TP analysis on 20 January 1999 at Flume A and 22 January 1999 at Flumes B and C. Whole shoots were collected from plants growing within 0.5 m of each permanent sampling plot. In all cases, we selected unblemished, fully developed shoots of each abundant species for sampling of tissue TP.

Aquatic consumers were sampled in each channel with two throw-trap samples placed adjacent to the channel walls at 11 m, 45 m, and 74 m. The throw trap was a square cage, 1 m on each side, open at the top and bottom, and enclosed with 2-mm mesh on the sides (Jordan et al. 1997). Fish, aquatic invertebrates, and amphibians were removed by systematic sweeping of the trap with a 2-mm mesh bar seine and 1.2-mm mesh dip nets. Throw traps effectively sample the fish and large macroinvertebrates that comprise the

majority of consumer biomass in the Everglades (Turner & Trexler 1997) but do not collect large fish efficiently (Jordan et al. 1997). The wet mass of consumers was measured and converted to dry-mass estimates using the average water content of Everglades fish species (Kushlan et al. 1986). The average of the two samples at each location was used in our analyses. Flumes A, B, and C were sampled from 19 to 26, 22 to 30, and 29 to 30 March 1999, respectively. The TP concentration of consumers was not measured. Consequently, estimates of P standing stock were calculated using the average TP content of three dominant Everglades fish species (38.461 mg g^{-1}; C. Stevenson, FIU, unpublished data) applied to the four dosing treatments. Previous research found that the concentration of P in fish is constant across lakes (Sterner & George 2000), and presumably constant with respect to nutrient availability. Estimates of TP concentrations in invertebrates were not available; we apply the estimate of fish TP concentration to invertebrates for the purposes of estimating total consumer P standing stock.

We sought to minimize disturbance resulting from spatial overlap among research groups working on different ecosystem components. Thus, rather than have all research groups sampling at the same locations in the flume channels, different components were often sampled at different locations. This precluded the use of distance as a consistent variable. As an alternative, we used four distance categories (1–8 m, 19–33 m, 37–58 m, and 67–83 m downstream from the nutrient mixing area), such that each distance category included all measured components, excluding consumers (Figure 2). This enabled integration of the components into a spatially explicit whole-ecosystem analysis. Other distance category combinations were clearly possible; however, the categories we used here maximize the number of distance intervals while also covering most of the channel length. If a component was sampled at multiple locations within a distance category, then an average of those samples was used.

P standing stocks and retention

Standing stocks of P (g m^{-2}) in the different ecosystem components were calculated as the product of TP concentration (g g^{-1} or g L^{-1}) and the mass (g m^{-2}) or volume (L m^{-2}) of the component. Total ecosystem P standing stock was calculated by summing the standing stock of individual ecosystem components, assuming that all important components were sampled. Aquatic consumer P standing stock was not included in the calculation of total ecosystem P because of the mobility of consumers and the possibility of an 'oasis effect,' where animals move from nearby oligotrophic areas into enriched areas of the flumes. The theoretical load of P to each dosing channel from the start of dosing in October 1998 to the end of dosing in March

1999 was calculated by summing the quantity of P added into the mixing areas at the front of each channel. The standing stock of P in the marsh of each channel (g channel^{-1}), dosed and control, was calculated by integrating estimates of P standing stock at each distance category over the entire surface area of each distance category. Standing stocks in those sections of the channels not included in the distance categories were calculated as an average of adjacent distance segments. Percent retention by each dosed channel was estimated by comparing the amount of accumulated P (g channel^{-1}; standing stock of dosed channel – control channel of same flume) to the theoretical P load (g channel^{-1}) for that dosed channel. Data from the control channel of Flume A were not used due to a tear in the channel wall that separated the control channel from an adjacent dosed channel. Thus, P standing stocks in the control channel at Flume A were estimated as an average of the control channels at Flumes B and C.

Statistical analysis

Differences in the TP concentration and standing stock of each ecosystem component, total ecosystem P standing stock, and channel P retention were each tested for significance with ANCOVAs. Dosing treatment was the main factor and P load was included as a covariate to account for variation in the response variables that could be explained by differences in P loading rates within each dosing treatment. However, loading rate was highly correlated with dosing treatment and violated the assumption of ANCOVA that the covariate is independent of the treatment (Mead 1994). Instead, variation in cumulative load within treatments was used as the covariate. This load residual was calculated as the difference between channel loading rate and the average loading rate of that dosing treatment (n = 3). When the main factor (dosing) was significant, differences between treatments were evaluated with Tukey's Honestly Significant Difference post-hoc tests. All statistical analyses were performed with SYSTAT (SYSTAT, Inc. 1992) on log-transformed data, with the exception of an arcsine-squareroot transformation of percent retention. Data from the control channel at Flume A were not included in the statistical analyses. A α level of 0.10 was used for all statistical analyses. This α value was chosen to balance Type I and II error rates because of the importance of minimizing Type II error rates in Everglades management and restoration (i.e. failure to detect a change in the ecosystem in response to phosphorus enrichment when one occurs; e.g. Peterman 1990).

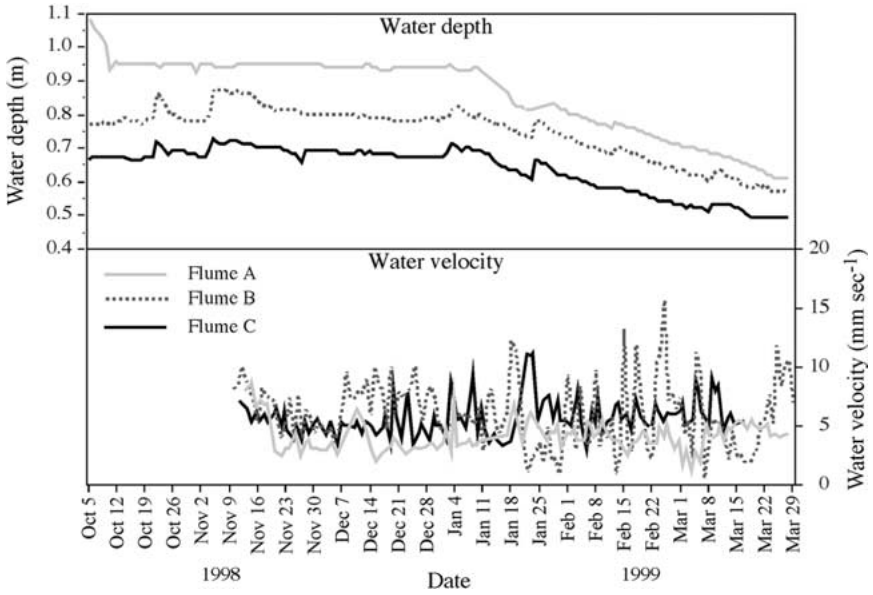

Figure 3. Water depth and velocity at each of the three flumes during the first season of dosing.

Results

Surface-water levels declined over the first six months of dosing, October 1998 to March 1999, ranging from about 1.0 m to 0.5 m deep (Figure 3). The three flumes differed consistently in water depth; water at Flume A was roughly 20 cm deeper than at Flume B, which was 10 cm deeper than at Flume C. Water typically flowed at a rate of about 5 mm sec^{-1}, although Flume B usually had higher velocities than the other flumes (Figure 3).

Phosphorus concentration and standing stock

Water that had passed through the nutrient mixing area, but had not yet entered the marsh (upstream station), did not differ in TP concentration among treatments (Figure 4, Table 1). After water flowed into the first 1–8 m of the channel, a spike of increased TP concentration was observed in the 30 μg L^{-1} treatment compared to the control (Figure 4). However, high variability among replicates in the 30 μg L^{-1} treatment resulted in a statistically insignificant difference among treatments (Table 1). There were no treatment effects on water TP concentration at 19–33, 37–58, and 67–83 m (Figure 4, Table 1). Water leaving the flumes (downstream) had elevated concentrations of TP in the 15 μg L^{-1} channels relative to the control channels; the 30 μg L^{-1} treatment average was greater than the control, although the difference

Table 1. *P*-values of ANCOVAs testing for the effect of treatment concentration (Conc.; category, df = 3) and P load (covariate, df = 1) on the TP concentration of ecosystem components at different distances down-flume (n = 3). Significant p-values (α = 0.10) are highlighted in bold

Ecosystem component	Factor	Upstream	1–8 m	19–33 m	37–58 m	67–83 m	Downstream
Water	Conc.	0.294	0.104	0.540	0.540	0.554	**0.046**
	Load	0.106	0.601	0.614	0.581	0.180	**0.021**
Periphyton	Conc.		**0.094**	0.382	0.315	0.656	
	Load		0.229	0.424	0.214	0.401	
Floc	Conc.		**0.003**	0.438	0.430	0.904	
	Load		**0.047**	0.406	0.289	0.290	
Soil	Conc.		0.531	0.873	0.934	0.973	
	Load		0.592	0.270	0.342	0.330	
Eleocharis	Conc.		0.665	0.409	0.927	**0.099**	
cellulosa	Load		0.767	0.893	0.252	**0.091**	

between the means was not statistically significant. However, the magnitude of differences in TP concentration between treatments was small at the downstream end of the flumes (Figure 4). The 5 μg L^{-1} treatment was similar to all other treatments at all distances. Water flowing out of the channels receiving P loading greater than the treatment average also had higher TP concentration (Table 1). Differences in mean surface-water P standing stock, a product of TP concentration and water depth, also were large but not statistically significant in the 30 μg L^{-1} treatment compared to the control at 1–8 m (Figure 5, Table 2). The pool of P in the water also did not differ among treatments at the upstream and downstream stations, or at 19–33, 37–58, and 67–83 m (Figure 5, Table 2). Variation in water-column P standing stock at the downstream end of the flumes was explained by differences in P loading (Table 2).

Periphyton TP concentration increased in the 30 μg L^{-1} treatment relative to the control, but only at the most upstream distance category, 1–8 m (Figure 4, Table 1). Periphyton TP concentration did not differ among the control, 5 μg L^{-1}, or 15 μg L^{-1} treatments at any distance (Figure 4, Table 1). In contrast, the P standing stock of periphyton was affected by experimental dosing concentrations at 19–33 m, where the 30 μg L^{-1} treatment was greater than the control and 5 μg L^{-1} treatments, but not at 1–8 m (Figure 5, Table 2). The lack of a significant response of periphyton P standing stock at 1–8 m was due to a concomitant reduction in periphyton biomass that was not as severe at 19–33 m (Table 3). Variation in periphyton P standing stock was explained

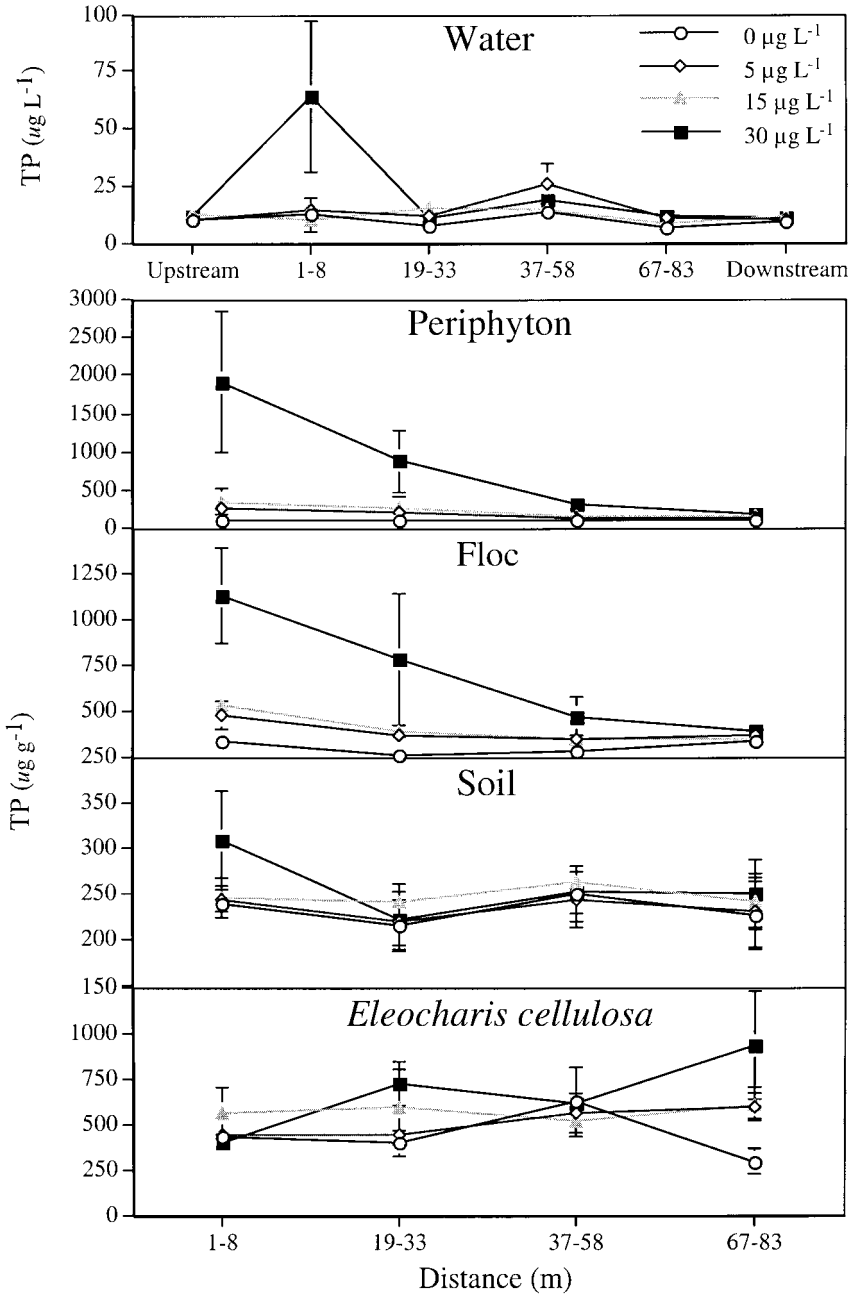

Figure 4. Total P concentrations (mean ± one s.e.) in different ecosystem components at different distances down-flume in response to P enrichment.

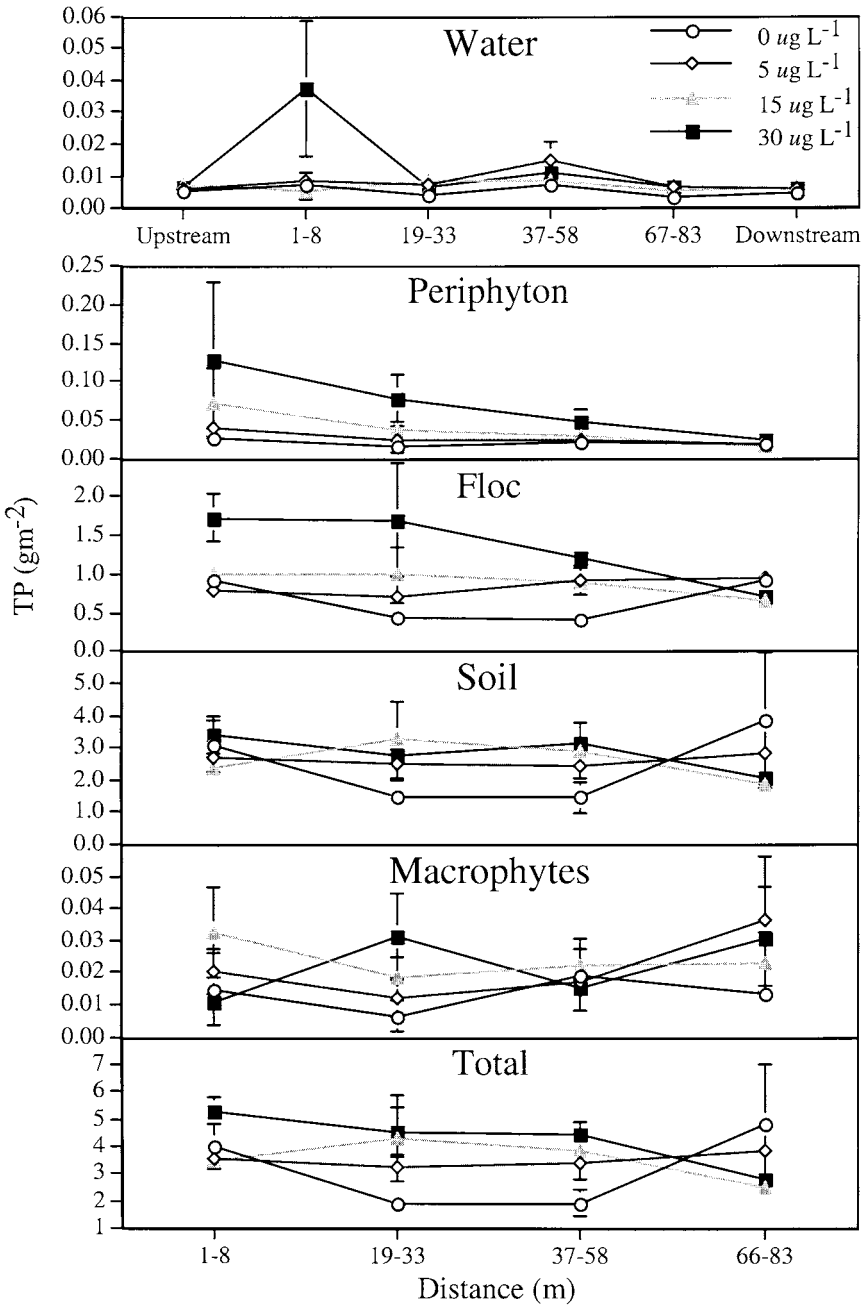

Figure 5. Phosphorus standing stocks (mean ± one s.e.) in different ecosystem components at different distances down-flume in response to P enrichment.

Table 2. *P*-values of ANCOVAs testing for the effect of treatment concentration (Conc.; category, df = 3) and P load (covariate, df = 1) on the TP standing stock (g m^{-2}) of ecosystem components at different distances down-flume (n = 3). Significant p-values (α = 0.10) are highlighted in bold

Ecosystem component	Factor	Upstream	1–8 m	19–33 m	37–58 m	67–83 m	Downstream
Water	Conc.	0.450	0.112	0.378	0.554	0.616	0.394
	Load	0.507	0.378	0.537	0.588	0.270	**0.082**
Periphyton	Conc.		0.681	**0.080**	0.346	0.926	
	Load		0.127	**0.029**	**0.030**	0.155	
Floc	Conc.		**0.091**	0.241	**0.039**	0.325	
	Load		0.229	0.871	0.385	0.997	
Soil	Conc.		0.507	0.312	0.195	0.468	
	Load		0.566	0.306	0.573	0.687	
Macrophytes	Conc.		0.799	0.361	0.794	0.804	
	Load		0.907	0.494	0.523	0.683	
Total	Conc.		0.116	0.238	0.102	0.315	
	Load		0.901	0.517	0.503	0.683	

by inter-flume variation in P loading rates at the two mid-channel distances (Table 2).

The concentration of TP in floc responded to enrichment in the first two upstream distance categories, but not at the downstream end (Table 1). Floc TP concentrations in the 1–8 m category were significantly greater in the 30 μg L^{-1} treatment compared to the control, 5 μg L^{-1}, and 15 μg L^{-1} treatments (Figure 4). The 15 μg L^{-1}, 5 μg L^{-1}, and control treatments did not differ from each other at any distance. Variation in cumulative load (the covariate) also explained a significant portion of the variation in floc TP concentration at the most upstream end of the flume (Table 1). In contrast, dosing treatment, but not P load, affected the P standing stock in floc in the 1–8 and 37–58 m distance categories (Table 2). At 1–8 m, floc P standing stock was greater in the 30 μg L^{-1} treatment compared to the control, 5 μg L^{-1}, and 15 μg L^{-1} treatments (Figure 5; Table 2). The amount of P stored in the floc was also greater in the 30 μg L^{-1} treatment compared to the control at 37–58 m, whereas dosing concentration did not significantly influence floc P standing stock at 19–33 m (Figure 5; Table 2). No significant differences in P standing stock were observed between the 15 μg L^{-1}, 5 μg L^{-1}, and control treatments at any distance.

Table 3. Biomass (g dw m^{-2}; ± one s.e.) of ecosystem components at different distances down-flume and in different treatments of P enrichment above ambient (n = 3)

Ecosystem component	Treatment (μg L^{-1})	Distance category			
		1–8 m	19–33 m	37–58 m	67–83 m
Periphyton	0	237 ± 83	163 ± 55	213 ± 94	152 ± 11
	5	184 ± 57	109 ± 57	183 ± 56	138 ± 54
	15	185 ± 36	187 ± 45	204 ± 73	109 ± 39
	30	62 ± 23	120 ± 41	144 ± 13	113 ± 35
Floc	0	2760 ± 217	1631 ± 255	1478 ± 101	2811 ± 640
	5	1746 ± 320	2113 ± 601	2731 ± 733	2574 ± 329
	15	1824 ± 106	2445 ± 811	2518 ± 295	1961 ± 632
	30	1672 ± 273	2378 ± 395	2896 ± 760	1865 ± 257
Soil	0	13055 ± 4086	6732 ± 543	5696 ± 1214	18841 ± 12401
	5	11028 ± 1152	11613 ± 2473	10263 ± 1047	13729 ± 4438
	15	9584 ± 773	14229 ± 6329	27506 ± 20121	7489 ± 872
	30	11081 ± 732	13022 ± 2812	30892 ± 20519	8391 ± 1032
Eleocharis	0	15 ± 6	4 ± 1	15 ± 2	33 ± 1
cellulosa	5	23 ± 7	13 ± 4	26 ± 3	37 ± 12
	15	19 ± 6	22 ± 8	31 ± 10	24 ± 11
	30	27 ± 5	22 ± 3	15 ± 4	19 ± 13

In contrast, surface (0–10 cm) soil TP concentration and standing stock did not vary among dosing treatments or loading rates (Figure 4, 5; Table 1, 2). The mean soil TP concentration at the most upstream section of the flumes (1–8 m) tended to be higher in the 30 μg L^{-1} channels compared to the control channels (Figure 4). However, this pattern was largely due to the influence of an extremely high concentration of P in the soil in Flume A, and the difference was not statistically significant (Table 1).

The concentration of P in *E. cellulosa*, the most widespread macrophyte species, had non-intuitive responses to P enrichment. Total P concentrations in aboveground tissues were significantly higher in the 30 μg L^{-1} treatment compared to the control at the downstream end of the flumes (67–83 m), most distant from the source of dosed P (Figure 4, Table 1). Variation in P loading rate also explained TP concentrations in *E. cellulosa* at the downstream end of the flumes (Table 1). No other significant differences in *E. cellulosa* TP concentrations were observed at any distance. The other macrophyte species were too patchily distributed to warrant statistical tests of their response to P enrichment. Average TP concentrations in the control chan-

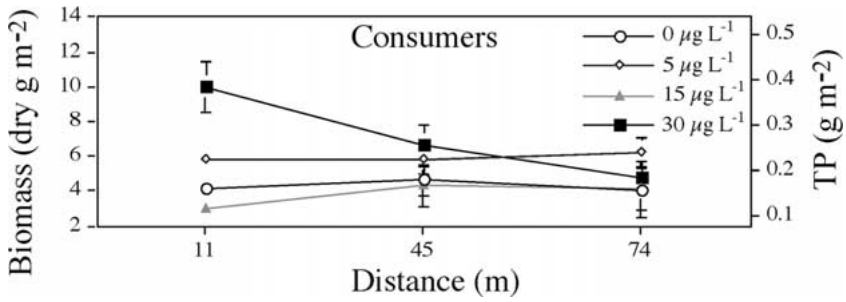

Figure 6. Biomass and estimated P standing stock (mean ± one s.e.) of aquatic consumers at different distances down-flume in response to P enrichment.

Table 4. *P*-values of ANCOVAs testing for the effect of treatment concentration (Conc.; category) and P load (covariate) on the biomass (dry g m^{-2}) of aquatic consumers at different distances down-flume ($n = 3$). Significant *p*-values ($\alpha = 0.10$) are highlighted in bold

Factor	11 m	45 m	74 m
Conc.	<**0.001**	0.403	0.509
Load	0.221	0.262	0.843

nels were 448 μg g^{-1} in *E. elongata*, 474 μg g^{-1} in *P. hemitomon*, 731 μg g^{-1} in *N. odorata*, and 914 μg g^{-1} in *S. lancifolia*. The aboveground mass of P collectively stored by all of the macrophytes did not differ among P dosing treatments or vary in relation to P loading rates (Figure 5, Table 2). The discordance between the response of *E. cellulosa* TP concentration and total macrophyte standing stock to dosing is due to the high variation in the biomass of other species among plots.

The biomass of aquatic consumers increased as a result of P dosing. Consumer biomass at 11 m was greatest in the 30 μg L^{-1} treatment, intermediate in the 5 μg L^{-1} treatment, and lowest in the control and 15 μg L^{-1} treatments (Figure 6, Table 4). Phosphorus dosing treatments had no effect on consumer biomass at 45 or 74 m, and P loading rates did not affect consumer biomass at any distance (Table 4). The estimated P standing stock of aquatic consumers at 11 m ranged from 0.383 g m^{-2} in 30 μg L^{-1}, 0.223 g m^{-2} in 5 μg L^{-1}, 0.159 g m^{-2} in the control, to 0.117 g m^{-2} in the 15 μg L^{-1} treatment.

After the first season of P additions, we could not detect any statistically significant changes in ecosystem P storage in response to either dosing treatment or loading rate. However, there was a pattern of increased total ecosystem P storage in the 30 μg L^{-1} treatment compared to the control in the

first three upstream distance categories (Figure 5). This trend was marginally statistically significant at 1–8 and 37–58 m (Table 2).

In addition to changes in the amount of P stored by ecosystem components, P enrichment altered the relative importance of the different components to total ecosystem P storage. Under non-dosed conditions, surface soils (0–10 cm) stored about 75% of the P in the ecosystem, the floc accounted for 20%, and the floating periphyton mat, macrophytes, and surface water each held 1% or less (Figure 7). Under the high dosing regime (30 μg L^{-1}), the floc compartment became the dominant store of added P, holding about 35% of total ecosystem P at the two upstream distances, while the surface soils stored roughly 60% (Figure 7). In addition, periphyton storage of P doubled from about 1% in the control to 2% of the ecosystem P standing stock in the two upstream distance categories of the 30 μg L^{-1} treatment. The pattern of P storage at the two most downstream distance categories in the 30 μg L^{-1} treatment was similar to the control channels (Figure 7). Finally, aquatic consumers stored 4% of total ecosystem P in the control and 7% in the 30 μg L^{-1} treatment when estimated consumer P standing stock at 11 m was included in the calculation of total ecosystem P storage in the first distance category.

Phosphorus retention

The amount of added P that was retained by the ecosystem within the flumes varied widely among channels. Phosphorus accumulation in the dosed channels ranged from –34 g $channel^{-1}$, or a net export of dosed P, to 516 g $channel^{-1}$. In general, whole ecosystem P standing stocks increased with increasing dosing concentration (Table 5). However, the retention of the P load was less than 40% in all channels (Table 5) and did not differ among dosing treatments ($P = 0.340$, ANCOVA) or loading rates ($P = 0.749$, ANCOVA).

Discussion

Six months of P dosing affected the TP concentration and standing stock of oligotrophic Everglades wetland ecosystem components. We detected significant responses in the water, periphyton, floc, and consumers, but not in the soil and macrophyte components. Most responses to P enrichment occurred in the 30 μg L^{-1} treatment and only at the upstream ends of the flumes, closest to the source of P. However, finer-scale temporal analyses have found significant changes in periphyton TP concentration, biomass, productivity, and species composition in the 5 and 15 μg L^{-1} treatments throughout the

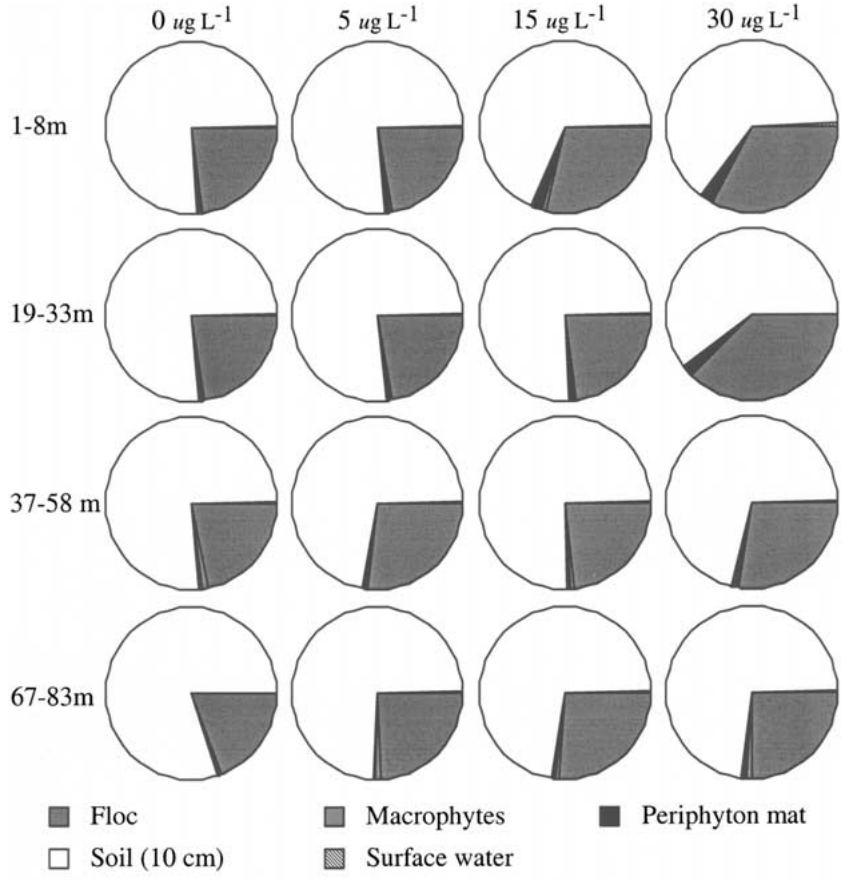

Figure 7. Proportion of whole-ecosystem P standing stocks in different ecosystem components.

length of the flumes (Gaiser et al. unpublished manuscript). The spatial extent and magnitude of increased P storage after six months of dosing suggested that the added P was taken up quickly from the water by periphyton and floc and that much of the enriched periphyton tissue was eventually deposited into the floc layer. The lack of increased water TP concentrations at the intermediate distances in the flume, where the floc was enriched with P, suggests that TP was transported downstream in particulate, organic forms, and thus indicated that P spiraling occurred (*sensu* Newbold et al. 1981). Our results are similar to patterns of P cycling in most other wetlands, where most short-term nutrient cycling and long-term nutrient retention occurs in the microflora and surface soils, while macrophytes play a minor role (Howard-Williams 1985). This analysis also supports our initial hypothesis that the effects

Table 5. Phosphorus standing stock, P load, amount of the P load accumulated, and percent retention of the P load in flume channels

Treatment (μg L^{-1})	Flume	P standing stock channel^{-1} (g)	P load channel^{-1} (g)	P load accumulation channel^{-1} (g)	P load retention (%)
0	B	628	0		
0	C	857	0		
5	A	943	505	200	39.7
5	B	721	911	93	10.3
5	C	954	457	96	21.1
15	A	709	1450	–34	–2.3
15	B	706	2695	78	2.9
15	C	1261	1682	404	24.0
30	A	1259	3407	516	15.2
30	B	911	5032	283	5.6
30	C	966	2538	108	4.3

of phosphorus enrichment will be observed first in microbially-dominated components.

P standing stock increased in the high dose channels despite a reduction in the biomass of floc and periphyton. Floating periphyton mats collapsed following P enrichment. The decrease in floc mass arose from a decrease in floc depth while floc bulk density did not change. These decreases in floc depth are most likely due to: (1) a decrease in periphyton deposition into the floc layer; (2) an increase in the mineralization of organic matter in the floc; or (3) both mechanisms simultaneously. The former hypothesis is supported by the decrease in periphyton biomass that began 60 days after the start of dosing (Gaiser et al. unpublished manuscript). Phosphorus enrichment stimulates the decomposition of macrophyte detritus (Davis 1991; DeBusk & Reddy 1998; Qualls & Richardson 2000) and respiration by soil microbes (Amador & Jones 1993) in the Everglades, supporting the latter hypothesis. We also found that P enrichment stimulated CO_2 production from the floc (Jayachandran et al. unpublished manuscript). However, long-term P enrichment in the Everglades increases organic matter accumulation in the soil (Craft & Richardson 1993; Reddy et al. 1993). Oligotrophic soils in the Everglades are oxidized (Gordon et al. 1986; Bachoon & Jones 1992), and the addition of P to these soils increases microbial respiration resulting in a shift to anaerobic conditions (Drake et al. 1996). We hypothesize that short-term

P enrichment stimulates aerobic microbial mineralization of organic matter, which together with decreased deposition of periphyton detritus results in a reduction of the floc layer. Long-term additions of P increase macrophyte productivity (Miao & Sklar 1998) and make the floc and soil anoxic, which decreases carbon mineralization (DeBusk & Reddy 1998), thus resulting in greater pools of floc and soil organic matter.

The flocculent detrital layer responded the most and stored the largest amount of added P storage component in the ecosystem after six months of P addition. Reddy et al. (1999) also found that floc was important to phosphorus cycling and storage and was responsive to P enrichment in the Northern Everglades. Similarly, White and Reddy (2000) concluded that detritus is the most microbiologically active portion of Everglades wetland soils. Similar shifts in aquatic ecosystem partitioning and cycling of P have been documented in other systems. In an oligotrophic, brackish coastal lake, 53% of the ecosystem P standing stock was found in the top one centimeter of sediment; this overlying flocculent detrital layer was a strong sink for added P (Howard-Williams & Allanson 1981). In addition, Doremus and Clesceri (1982) found that the floc in a temperate oligotrophic lake had a large potential for P uptake relative to lower sediments and was very responsive to P additions. In a temperate fen, 90% of P was in the soil and microorganisms, and fine surficial sediments controlled the uptake of P (Richardson & Marshall 1986). In wet meadow tundra, 2% or less of the total quantity of P in the ecosystem was found in vegetation (Chapin et al. 1978); this is also typical of fens (Verhoeven 1986). Finally, soil, as opposed to live macrophytes, stored most of the P that Dolan et al. (1981) added to a freshwater marsh in central Florida. These studies and our research suggest that the floc layer, and the microbial community therein, controls short-term uptake and cycling of P in the Everglades and other wetland and aquatic ecosystems.

Other Everglades studies also have documented that P enrichment results in the loss of the floating, calcareous periphyton mat (Browder et al. 1994; Vymazal et al. 1994; McCormick & O'Dell 1996; Pan et al. 2000), as well as changes in algal species composition (Grimshaw et al. 1993; Vymazal et al. 1994; McCormick & O'Dell 1996; McCormick et al. 1998; Pan et al. 2000). This often coincides with a short-term periphyton biomass increase (up to $\sim$82 days, Vymazal et al. 1994) but a long-term biomass decrease (after 5 mo, McCormick & O'Dell 1996; after decades, McCormick et al. 1998; Pan et al. 2000). The concentration of P in periphyton mats also is strongly correlated with water column P concentrations (Grimshaw et al. 1993; McCormick & O'Dell 1996; McCormick et al. 1998; Pan et al. 2000) and increases with P enrichment (McCormick & Scinto 1999; Pan et al. 2000) in other regions of the Everglades. On average, published values for

periphyton tissue P concentrations in WCA-2A and WCA-2B are about 250 μg g^{-1} in unenriched, 900 μg g^{-1} in enriched, and 2900 μg g^{-1} in highly enriched marshes (Noe et al. 2001). This range in periphyton TP concentrations is similar to patterns of periphyton concentrations we have observed in our experimental flumes. Finally, McCormick et al. (1998) determined that periphyton P standing stock decreased in areas of WCA-2A receiving long-term nutrient enrichment compared to interior, less-enriched areas. In our study, periphyton P standing stock had not decreased relative to the control channels after six months of dosing, but we anticipate that more P additions will further decrease periphyton biomass and result in changes to low-biomass green algal communities. Seasonal variation in mat biomass complicated our ability to detect changes in periphyton P standing stock; periphyton biomass at our sites is normally lowest in March and April (Gaiser et al. unpublished manuscript) and mats were senescing when samples were collected. This breakdown of P-rich periphyton at the front of the high dose channels likely contributed to the very high surface-water TP concentrations.

Phosphorus enrichment increased the biomass of aquatic consumers in this study, as has been observed along P gradients in the Everglades (Rader & Richardson 1994; Turner et al. 1999). The biomass of fish, but not macroinvertebrates, increased in enriched compared to oligotrophic areas (Turner et al. 1999) and in our experiment (Trexler et al. unpublished data). Turner et al. (1999) hypothesized that a trophic cascade was operating and that the fish (primarily carnivorous) reduced invertebrate biomass in nutrient-enriched areas. Although the oligotrophic Everglades has very low fish and aquatic invertebrate biomass relative to other freshwater wetlands (Turner et al. 1999), we estimate that aquatic consumers stored about 5% of the total ecosystem P pool. Consumers also could be very important to the active cycling of P. However, it should be noted that the close proximity of the nutrient-enriched channels to nearby oligotrophic areas could have resulted in an 'oasis effect', in which mobile consumers moved into the enriched marsh within the flumes to feed.

The concentration of P in shoots of *E. cellulosa* increased at the most downstream end of the 30 μg L^{-1} channels. However, we view this response as an anomaly because no other ecosystem components were affected by dosing at this distal location in the flumes. The lack of macrophyte and soil responses to short-term P enrichment has been observed in other Everglades studies. Changes in soil or aboveground macrophyte tissues occur in the second year of dosing (Scheidt et al. 1989; Craft et al. 1995; Daoust 1998; McCormick & Scinto 1999; White & Reddy 2000), although Daoust (1998) found that the belowground biomass of *Cladium jamaicense* increased after the first year of dosing. The slow response of macrophytes and soils

to increased P loading in these previous studies, and the lack of a response following six months of P dosing in our study, suggests that macrophytes and soils are the last ecosystem components to respond to P enrichment. Macrophytes eventually respond to long-term enrichment with increased tissue phosphorus concentrations, increased productivity, altered biomass and nutrient allocation, and shifted species composition (Miao & DeBusk 1999). This has important implications to Everglades and other wetland water quality management issues because past analyses of water quality impacts on Everglades wetlands have focused on visible changes in the macrophyte community and measurable changes in soil P concentration. In fact, these indicators may well be documenting ecosystem state change that took place long ago.

Our accounting of ecosystem P retention suggests that the ecosystem retained little of the added P (–2% to 40%) after the first 6 months of P additions. With the exception of one treatment channel, retention ranged from –2% to 40%. Similarly, only 26–34% of added P was recovered in the macrophytes, soil, and litter of a P-loading mesocosm experiment in an *Eleocharis*-dominated habitat in the Northern Everglades (Craft et al. 1995). In contrast, a temperate fen removed 99% of added P in the first year of nutrient addition (Richardson & Marshall 1986). The low retention rates of our ENP wetlands is surprising given that P limitation and oligotrophy are characteristic of the Everglades (Noe et al. 2001). We hypothesized that the ecosystem would strongly retain and accumulate P, especially in the low dose treatments where saturation of P-uptake capacity is least likely. This pattern has been inferred by comparing long-term accumulation of P in soil to P loading rates in both relatively unenriched and enriched areas in the Northern Everglades (Craft & Richardson 1993). Our results suggest that, at the scale of our flumes, a mechanism exists for transporting P downstream at a rate fast enough to export a large proportion of added P in the initial phases of P addition. At the same time, P uptake from the water column was rapid enough that we rarely observed measurable SRP concentrations within our flume channels (Gaiser et al. unpublished manuscript). We suspect that particulate P, especially in the form of floc, was the vehicle for P transport downstream and that models of phosphorus spiraling may be the most useful mechanism of explaining P cycling in the Everglades.

We were not able to measure P standing stocks in every ecosystem component. Consequently, we underestimated whole-ecosystem P standing stocks and retention. First, the P content of consumer populations have not yet been directly quantified, although our estimate indicated that the proportion of ecosystem P stored in aquatic consumers is small. In addition, dead macrophyte tissue, macrophyte rhizomes and roots, and non-floating

periphyton were not sampled. Macrophytes also were sampled two months earlier than the other ecosystem components and may have accumulated more P in that two-month gap. However, the biomass of both epiphytic and benthic periphyton biomass were small (Childers et al. 2002). *Cladium jamaicense* roots also stored very little P in another Everglades P dosing experiment (Craft et al. 1995) and in unenriched areas of WCA-2A (data in Miao & Sklar 1998). We do not believe that we missed large pools of P in the ecosystem.

Another possible explanation for our estimation of low P-retention focused on the mixing area at the front of each flume channel that was designed to be free of anything that could potentially sequester P. However, a biofilm routinely developed on the fiberglass floor of the mixing area and was removed five times during the first season of P additions. Our estimates of the depth, bulk density, coverage, and P concentration of this biofilm suggested that it stored a maximum of about 2 g of TP over the 30 m^2 mixing area at any given time (Scinto et al. unpublished data). Thus, the biofilm in the mixing area could have retained about 10 g of TP – one to two orders of magnitude less than the mass of P that accumulated in the dosed channels (Table 4). We thus conclude that the biofilm in the mixing area did not significantly contribute to whole-ecosystem P standing stock and retention.

In addition to significant ecosystem responses to the experimental treatments of increased P concentration, the effect of the P loading rate also was evident. Our dosing protocol added constant P concentrations in dosed flume channels, such that higher water velocity at Flume B (Figure 3) resulted in a greater load of P. By design, this situation mimicked the loading of P to marshes receiving canal water enriched in P. However, it complicated our analyses because our 3 replicate flumes did not receive the same P load during the first year of P additions. For example, the theoretical cumulative loading rate in the 30 $\mu g\ L^{-1}$ treatment at Flume B was 1.5x and 2.0x greater than at Flumes A and C, respectively (Table 4). Variation in P load, the covariate, affected several ecosystem components, in one case when the dosing concentration treatment was not significant (periphyton P standing stock). Each significant P loading effect was the result of increased TP concentration or P standing stock at higher loading rates, even after we accounted for the effect of dosing concentration. Conversely, dosing concentration was also significant when loading rate was not (periphyton TP concentration, floc P standing stock, and consumer biomass). Nonetheless, the idea that oligotrophic Everglades marshes respond different to small versus large P loading has important implications for water quality management.

Total P concentrations in the control channels of the flumes averaged 10 $\mu g\ L^{-1}$ in the water, 100 $\mu g\ g^{-1}$ in the periphyton, 230 $\mu g\ g^{-1}$ in the surface (0–10 cm) soils, 340 $\mu g\ g^{-1}$ in the floc, and 460 $\mu g\ g^{-1}$ in *E. cellulosa*

(Figure 4). These values were generally lower than corresponding P concentrations published for other 'unenriched,' Northern Everglades marshes, which in turn have considerably lower P content than most other wetlands (Noe et al. 2001). Thus, our study sites are highly oligotrophic and have considerably lower concentrations of P than most wetlands. It is not yet possible to compare P biogeochemistry in different regions of the Everglades because very few process-oriented studies have been conducted in the Southern Everglades.

Conclusion

After the initial 6 months of P additions, we observed significant differences in the P content and standing stock of the flocculent detrital layer and periphyton, and biomass of aquatic consumers in our 30 μg L^{-1} above-ambient flume channels. In addition, the 15 μg L^{-1} treatment resulted in a higher concentration of P in water leaving the flumes and the 5 μg L^{-1} treatment led to more consumer biomass. The floc layer was especially important in the uptake and sequestration of added P and, consequently, in the biogeochemistry of ecosystem P cycling. Retention of added P was low, ranging from slight export to 40%. Therefore, we hypothesized that particulate P, especially in the form of floc, was the vehicle for P transport downstream and that models of phosphorus spiraling should be used to explain P cycling in the Everglades. These analyses have been used to manage our research adaptively by focusing attention on the floc layer and the cycling of P through the ecosystem. Ongoing research will permit a comparison of the short and long-term effects of P dosing – dosing of P will continue for at least two more years, followed by measurement of ecosystem recovery after P enrichment ceases.

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References

Amador JA & Jones RD (1993) Nutrient limitations on microbial respiration in peat soils with different total phosphorus content. Soil Biology and Biochemistry 25: 793–801

Bachoon D & Jones RD (1992) Potential rates of methanogenesis in sawgrass marshes with peat and marl soils in the Everglades. Soil Biology and Biochemistry 24: 21–27

Bedford BL, Walbridge MR & Aldous A (1999) Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology 80: 2151–2169

Browder JA, Gleason PJ & Swift DR (1994) Periphyton in the Everglades: Spatial variation, environmental correlates, and ecological implications. In: Davis SM & Ogden JC (Eds) Everglades: The Ecosystem and its Restoration (pp 379–418). St. Lucie Press, Delray Beach

Carpenter SR, Caraco NF, Correll DL, Howarth RW, Sharpley AN & Smith VH (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecological Applications 8: 559–568

Chapin FS III, Barsdate RJ & Barèl D (1978) Phosphorus cycling in Alaskan coastal tundra: A hypothesis for the regulation of nutrient cycling. Oikos 31: 189–199

Childers DL, Jones RD, Trexler J, Buzzelli C, Dailey S, Edwards AL, Gaiser E, Jayachandaran K, Lee D, Meeder J, Nair M, Pechmann J, Renshaw A, Richards J, Rugge M, Scinto L, Sterling P & Van Gelder W (2002) Quantifying the effects of low-level phosphorus enrichment on unimpacted Everglades wetlands with in situ flumes and phosphorus dosing. In: Porter K & Porter J (Eds) The Everglades Hydroscape (pp 127–152). St. Lucie Press, Delray Beach

Craft CB & Richardson CJ (1993) Peat accretion and N, P, and organic C accumulation in nutrient-enriched and unenriched Everglades peatlands. Ecological Applications 3: 446–458

Craft CB, Vymazal J & Richardson CJ (1995) Response of Everglades plant communities to nitrogen and phosphorous additions. Wetlands 15: 258–271

Daoust RJ (1998) Investigating how Phosphorus Controls Structure and Function in Two Everglades Wetland Plant Communities. M.S. Thesis. Florida International University, Miami

Daoust RJ & Childers DL (1998) Quantifying aboveground biomass and estimating net aboveground primary production for wetland macrophytes using a non-destructive phenometric technique. Aquatic Botany 62: 115–133

Davis SM (1991) Growth, decomposition, and nutrient relation in *Cladium jamaicense* Crantz *and Typha domingensis* Pers. in the Florida Everglades. Aquatic Botany 40: 203–224

Davis SM (1994) Phosphorus inputs and vegetation sensitivity in the Everglades. In: Davis SM & Ogden JC (Eds) Everglades: The Ecosystem and its Restoration (pp 357–378). St. Lucie Press, Delray Beach

DeBusk WF & Reddy KR (1998) Turnover of detrital organic carbon in a nutrient-impacted Everglades marsh. Soil Science Society of America Journal 62: 1460–1468

Dolan TJ, Bayley SE, Zoltek J Jr & Hermann AJ (1981) Phosphorus dynamics of a Florida freshwater marsh receiving treated wastewater. Journal of Applied Ecology 18: 205–219

Doremus C & Clesceri LS (1982) Microbial metabolism in surface sediments and its role in the immobilization of phosphorus in oligotrophic lake sediments. Hydrobiologia 91: 261–268

Doren RF, Armentano TV, Whiteaker LD & Jones RD (1997) Marsh vegetation patterns and soil phosphorus gradients in the Everglades ecosystem. Aquatic Botany 56: 145–163

Downing JA & McCauley E (1992) The nitrogen:phosphorus relationship in lakes. Limnology and Oceanography 37: 936–945

Drake HL, Aumen NG, Kuhner C, Wagner C, Grießhammer A & Schmittroth M (1996) Anaerobic microflora of Everglades sediments: Effects of nutrients on population profiles and activities. Applied and Environmental Microbiology 62: 486–493

EPA (1983) Methods for Chemical Analysis of Water and Wastes. Revision March 83. United States Environmental Protection Agency, Cincinnati

Fennema RJ, Neidrauer CJ, Johnson RA, MacVicar TK & Perkins WA (1994) A computer model to simulate natural Everglades hydrology. In: Davis SM & Ogden JC (Eds) Everglades: The Ecosystem and its Restoration (pp 357–378). St. Lucie Press, Delray Beach

Gordon AS, Cooper WJ & Scheidt DJ (1986) Denitrification in marl and peat sediments in the Florida Everglades. Applied and Environmental Microbiology 52: 987–991

Grimshaw HJ, Rosen M, Swift DR, Rodberg K & Noel JM (1993) Marsh phosphorous concentrations, phosphorous content and species composition of Everglades periphyton communities. Archiv Fur Hydrobiologie 128: 257–276

Gunderson LH (1994) Vegetation of the Everglades: Determinants of community composition. In: Davis SM & Ogden JC (Eds) Everglades: The Ecosystem and its Restoration (pp 323–340). St. Lucie Press, Delray Beach

Howard-Williams C (1985) Cycling and retention of nitrogen and phosphorus in wetlands: A theoretical and applied perspective. Freshwater Biology 15: 391–431

Howard-Williams C & Allanson BR (1981) Phosphorus cycling in a dense *Potamogeton pectinatus* L. bed. Oecologia 49: 56–66

Jordan F, Coyne S & Trexler JC (1997) Sampling fishes in vegetated habitats: the effects of habitat structure on sampling characteristics of the 1-m^2 throw trap. Transactions of the American Fisheries Society 126: 1012–1020

Koch MS & Reddy KR (1992) Distribution of soil and plant nutrients along a trophic gradient in the Florida Everglades. Soil Science Society of America Journal 56: 1492–1499

Kushlan JA, Voorhees SA, Loftus WF & Frohring PC (1986) Length, mass, and calorific relationships of Everglades animals. Florida Scientist 49: 65–79

McCormick PV & O'Dell MB (1996) Quantifying periphyton responses to phosphorus in the Florida Everglades: a synoptic-experimental approach. Journal of the North American Benthological Society 15: 450–468

McCormick PV, Rawlik PS, Lurding K, Smith EP & Sklar FH (1996) Periphyton-water quality relationships along a nutrient gradient in the northern Florida Everglades. Journal of the North American Benthological Society 15: 433–449

McCormick PV & Scinto LJ (1999) Influence of phosphorus loading on wetlands periphyton assemblages: A case study from the Everglades. In: Reddy KR, O'Connor GA & Schelske CL (Eds) Phosphorous Biogeochemistry in Subtropical Ecosystems (pp 301–320). Lewis Publishers, Boca Raton

McCormick PV, Shuford RBE III, Backus JG & Kennedy WC (1998) Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, Florida, U.S.A. Hydrobiologia 362: 185–208

Mead R (1994) The Design of Experiments. University Press, Cambridge

Media Cybernetics LP (1993) Image Pro 4.0 software. Media Cybernetics, L.P., Silver Spring
Miao SL & DeBusk WF (1999) Effects of phosphorus enrichment on structure and function of sawgrass and cattail communities in the Everglades. In: Reddy KR, O'Connor GA & Schelske CL (Eds) Phosphorous Biogeochemistry in Subtropical Ecosystems (pp 275–299). Lewis Publishers, Boca Raton
Miao SL & Sklar FH (1998) Biomass and nutrient allocation of sawgrass and cattail along a nutrient gradient in the Florida Everglades. Wetlands Ecology and Management 5: 245–263
Mitsch WJ & Gosselink JG (1993) Wetlands. Van Nostrand Reinhold, New York
National Research Council (1992) Restoration of Aquatic Ecosystems. National Academy Press, Washington, D.C.
Newbold JD, Elwood JW, O'Neill RV & Van Winkle W (1981) Measuring nutrient spiralling in streams. Can. J. Fish. Aquat. Sci. 38: 860–863
Noe GB, Childers DL & Jones RD (2001) Phosphorus biogeochemistry and the impacts of phosphorus enrichment: Why is the Everglades so unique? Ecosystems 4: 603–624
Pan Y, Stevenson RJ, Vaithiyanathan P, Slate J & Richardson CJ (2000) Changes in algal assemblages along observed and experimental phosphorus gradients in a subtropical wetland, U.S.A. Freshwater Biology 44: 339–353
Peterman RM (1990) Statistical power analysis can improve fisheries research and management. Can. J. Fish. Aquat. Sci. 47: 2–15
Pringle CM & Barber M (2000) The land-water interface: Science for a sustainable biosphere. Ecological Applications 10: 939–940
Qualls RG & Richardson CJ (2000) Phosphorus enrichment affects litter decomposition, immobilization, and soil microbial phosphorus in wetland mesocosms. Soil Science Society of America Journal 64: 799–808
Rader RB & Richardson CJ (1994) Response of macroinvertebrates and small fish to nutrient enrichment in the northern Everglades. Wetlands 14: 134–146
Reddy KR, DeLaune RD, DeBusk WF & Koch MS (1993) Long-term nutrient accumulation rates in the Everglades. Soil Science Society of America Journal 57: 1147–1155
Reddy KR, White JR, Wright A & Chua T (1999) Influence of phosphorus loading on microbial processes in the soil and water column of wetlands. In: Reddy KR, O'Connor GA & Schelske CL (Eds) Phosphorus Biogeochemistry in Subtropical Ecosystems (pp 249–273). Lewis Publishers, Boca Raton
Richardson CJ & Marshall PE (1986) Processes controlling movement, storage, and export of phosphorus in a fen peatland. Ecological Monographs 56: 279–302
Scheidt DJ, Flora MD & Walker DR (1989) Water quality management for Everglades National Park. In: Fisk DW (Ed.) Wetlands: Concerns and Successes (pp 377–390). American Water Resources Association, Washington, D.C.
Schindler DW (1977) Evolution of phosphorus limitation in lakes. Science 195: 260–262
Smith VH (1998) Cultural eutrophication of inland, estuarine, and coastal waters. In: Pace ML & Groffman PM (Eds) Successes, Limitations, and Frontiers in Ecosystem Science (pp 7–49). Springer-Verlag, New York
Solorzano L & Sharp JH (1980) Determination of total dissolved P and particulate P in natural waters. Limnology & Oceanography 25: 754–758
Sterner RW & George NB (2000) Carbon, nitrogen, and phosphorus stoichiometry of cyprinid fishes. Ecology 81: 127–140
Steward KK & Ornes WH (1983) Mineral nutrition of sawgrass (*Cladium jamaicense* Crantz) in relation to nutrient supply. Aquatic Botany 16: 349–359

Stober J, Scheidt D, Jones R, Thornton K, Gandy L, Stevens D, Trexler J, & Rathbun S (1998) South Florida Ecosystem Assessment. United States Environmental Protection Agency, Athens

SYSTAT, Inc (1992) SYSTAT version 5.2.1. SYSTAT, Inc., Evanston

Turner AM & Trexler JC (1997) Sampling invertebrates from the Florida Everglades: A comparison of alternative methods. Journal of the North American Benthological Society 16: 694–709

Turner AM, Trexler JC, Jordan CF, Slack SJ, Geddes P, Chick JH & Loftus WF (1999) Targeting ecosystem features for conservation: Standing crops in the Florida Everglades. Conservation Biology 13: 898–911

Verhoeven JTA (1986) Nutrient dynamics in minerotrophic peat mires. Aquatic Botany 25: 117–137

Vymazal J, Craft CB & Richardson CJ (1994) Periphyton response to nitrogen and phosphorus additions in Florida Everglades. Algological Studies 73: 75–97

Walker WW Jr (1999) Long-term water quality trends in the Everglades. In: Reddy KR, O'Connor GA & Schelske CL (Eds) Phosphorous Biogeochemistry in Subtropical Ecosystems (pp 447–466). Lewis Publishers, Boca Raton

White JR & Reddy KR (2000) Influence of phosphorus loading on organic nitrogen mineralization of Everglades soils. Soil Science Society of America Journal 64: 1525–1534