Cascading Ecological Effects of Low-Level Phosphorus Enrichment in the Florida Everglades

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ABSTRACT

Few studies have examined long-term ecological effects of sustained low-level nutrient enhancement on wetland biota. To determine sustained effects of phosphorus (P) addition on Everglades marshes we added P at low levels (5, 15, and 30 $\mu g\ L^{-1}$ above ambient) for 5 yr to triplicate 100-m flow-through channels in pristine marsh. A cascade of ecological responses occurred in similar sequence among treatments. Although the rate of change increased with dosing level, treatments converged to similar enriched endpoints, characterized most notably by a doubling of plant biomass and elimination of native, calcareous periphyton mats. The full sequence of biological changes occurred without an increase in water total P concentration, which remained near ambient levels until Year 5. This study indicates that Everglades marshes have a near-zero assimilative capacity for P without a state change, that ecosystem responses to enrichment accumulate over time, and that downstream P transport mainly occurs through biota rather than the water column.

FLOODED GRASSLANDS are generally highly productive and thus thought to be a sink for nutrients that fuel high standing crops of vegetation (Kadlec and Knight, 1996). Particularly in warmer climates, rapid growth of vegetation and attached periphyton allow efficient removal of incoming nutrients and subsequent burial in the sediments (Vymazal, 1995). A study by Richardson and Qian (1999) compiled data from 126 wetlands and showed that the average long-term assimilative capacity of P for North American wetlands is close to 1 g m^{-2} yr^{-1}. Assimilative capacity was defined therein as the amount of P absorbed with no significant ecosystem state change and no downstream transport of P. The convention to express assimilation on an annual basis implies that marshes have the ability to continuously remove some excess P at a constant rate without incurring change, regardless of exposure duration. However, few studies have tested the assimilative capacity of wetlands over time scales greater than a few years, and no long-term experimental investigation of P assimilation has taken place in the Everglades, where one of the largest restoration projects in history is currently underway.

The Everglades is a flowing-water wetland that is historically oligotrophic (reviewed in Noe et al., 2001). Decades of P enrichment have significantly degraded portions of this wetland, prompting studies to determine the levels of P input that would afford protection to remaining federally protected marshland. Enclosure studies suggested that water column P levels in excess of 10 $\mu g\ L^{-1}$ (ppb) cause biotic change in the Everglades (McCormick and O'Dell, 1996). However, enclosure studies are designed to dose with a predetermined mass of P m^{-2} yr^{-1}, which is difficult to relate to actual marsh water column concentrations (Noe et al., 2002; Gaiser et al., 2004). While enclosure studies have provided useful biotic metrics of P enrichment in the Everglades (McCormick and Stevenson, 1998), they do not address long-term cumulative effects of nutrient influx to this flowing-water system.

One flow-through experimental dosing study was conducted in marshes of Water Conservation Area 2A (Richardson et al., 1995) upstream of protected areas, and found significant alterations in communities exposed to water total phosphorus (TP) concentrations exceeding 15 $\mu g\ L^{-1}$ (approximately 5 $\mu g\ L^{-1}$ P above background concentrations). In that study P was continuously added at quantities sufficient to raise the water column concentration throughout the channels to predetermined levels, and biological responses were related to the surrounding water column TP concentration. However, large areas of marsh near canal inputs in this and other marshes have been shown to be dramatically altered ecologically without the water column being significantly enriched (Smith and McCormick, 2001; Childers et al., 2003), indicating that biotic changes can occur *before* enhancements are measured in the water column. In P-limited systems, excess P is rapidly and efficiently sequestered by biota and mainly transported downstream through biota rather than the water column (Gaiser et al., 2004). Experimental manipulations aimed at elevating marsh water P concentration to a certain level therefore rely on loading rates that exceed the naturally high rate of assimilation, creating an enrichment design that is different from the mode of P transport downstream of most canal inputs.

In flowing-water systems subject to elevated nutrient inputs, it is particularly important to document the sequence of changes taking place during the eutrophication process before the attainment of an enriched endpoint. Detecting the onset of state change is imperative to calculate the assimilative capacity of the system for the added nutrient, and knowing the progressive sequence of alterations can provide a model to predict

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Abbreviations: TP, total phosphorus.

patterns of ecosystem change downstream when that capacity is exceeded and the nutrient is exported. Because the rate and sequence of changes are affected not only by the magnitude of input but also by exposure duration, it is important to observe the eutrophication process over a period sufficient to evaluate whether cumulative effects of magnitude and duration of enrichment lead systems to converge to a common enriched endpoint.

To determine the cumulative responses of Everglades marsh communities to continuous low-level supplies of excess P, we designed a study that mimics the manner of natural P delivery to flowing wetlands by enriching upstream water to a measured level and recording responses at various locations downstream of that input. The range of input concentrations included levels barely above instrumental detection limits ($5 \mu g L^{-1}$) delivered over a time frame long enough to determine cumulative effects and spatial dynamics of responses to continuous low-level dosing at constant concentrations. Our central hypotheses were that: (i) this wetland has a low assimilative capacity for P and low-level additions cause a state change resulting in the types of disturbed ecosystems found in impacted areas of the Everglades; (ii) the sequence of biotic imbalances cascade from one trophic level to the next in the ecosystem; (iii) the rate of this cascade is determined by dose level and flow rate; and (iv) a similar imbalanced ecological endpoint is attained regardless of treatment level.

MATERIALS AND METHODS

Experimental Design

Three flumes were constructed approximately 2 km apart in pristine, wet-prairie marshes of Shark River Slough in Everglades National Park [see Childers et al. (2001) and Noe et al. (2002) for details on the experimental setup; Fig. 1]. Wet-prairie marshes in the Everglades have been characterized as
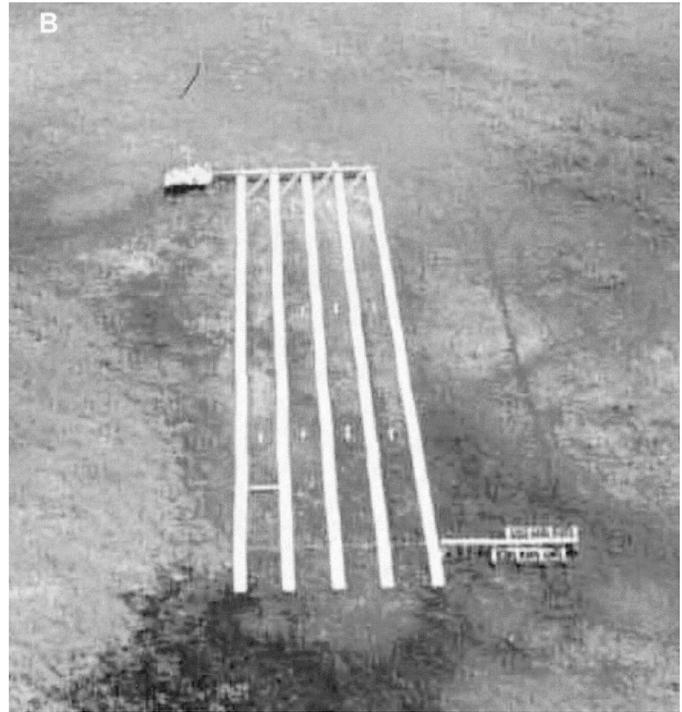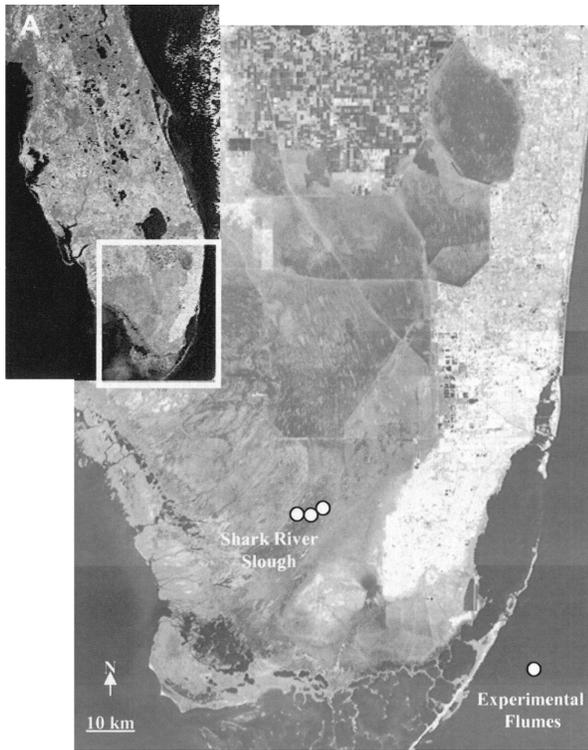

Fig. 1. (a) Satellite image showing location of the three experimental flumes in Shark River Slough in Everglades National Park, Florida. (b) Aerial photograph of one of the experimental flumes, showing the four treatment channels before the initiation of dosing in 1997. (c) Downstream view of one flume, showing initial 10-m header box where P is added and flow measurements are taken.

having peat-based soils, abundant periphyton, and a macrophyte community dominated by eastern purple bladderwort (*Utricularia purpurea* Walt.), Gulf Coast spikerush (*Eleocharis cellulosa* Torr.), maidencane (*Panicum hemitomon* Schult.), and bulltongue arrowhead (*Sagittaria lancifolia* L.) (Gunderson, 1994). Each flume contained four, 100-m-long × 3-m-wide channels enclosing areas of natural marsh and were open at both ends and to the sediments. Channels were positioned parallel to water flow and for 5 yr an automated system delivered $NaH_2PO_4 + Na_2HPO_4$ (pH = 7) to achieve concentrations of 0, 5, 15, and 30 μg L^{-1} TP (approximately 0.00, 0.16, 0.48, and 0.97 μM, respectively) above ambient in a 10-m-long mixing area at the head of each channel. Concentrations were kept constant by continuously adjusting P delivery according to velocity and stage measured by a pressure transducer and acoustic doppler flow sensor capable of measuring very low velocity flow (>2 mm s^{-1}) at the head of each channel.

Critical to the interpretation of results of this study is understanding that the goal of this experimental design was not to raise water column TP in the experimental channels to a predetermined level. Rather, TP concentrations were kept constant in the upstream mixing area by continuous mechanical adjustment of P input based on the volume of water in the mixing area (3 m wide × 10 m long × water depth). When added in an inorganic form, P would be microbially incorporated in the header box so that most P transported downstream to the marsh is already in organic form, as it would be in the natural setting. Loading of P depends on water velocity; when velocities are low, only a small mass of P is delivered to the channels so that loading pulses with water flow (load is effectively 0 during the dry season, January–May, when flows are minimal). This manner of dosing mimics input water control structures on canals that feed into the marsh in that loading is low during low-flow periods and high during the wet season, although inflow concentrations at control structures may vary more than in this experiment. Importantly, water delivery to the flume structures was dependent on operations of control structures approximately 16 km upstream on the Tamiami Canal that regulate water flow into Shark River Slough. Therefore, P loading to the flumes was tightly linked to delivery from the peripheral canal into Everglades National Park.

Sample Collection and Processing

Pre-dose conditions were assessed in October 1998, immediately before initiation of P addition, and subsequently, samples were taken biweekly to bimonthly, depending on parameter response time. Each year a synoptic sampling event occurred at the end of the wet season, when water velocity dropped below 2 mm s^{-1}, and all parameters were sampled simultaneously. Synoptic events for all parameters occurred during a 2-wk period in March 1999, February 2000, January 2001, and January 2002 and a final sampling event for all parameters except macrophytes and fish in January 2003. Sampling stations for each parameter were deliberately staggered at select distances to minimize disturbance to the many parameters that were measured during the five years of study (8, 33, 58, and 83 m for water, floc, and soil; 5, 19, 37, and 67 m for periphyton and macrophytes; 11, 45, and 74 m for fish).

Water column TP was measured in triplicate 500-mL water samples that were first filtered through 100-μm screening to exclude floating debris. Sediments were sampled using a coring device that effectively separated the floc (upper loose detrital layer) from soil. Triplicate floc and soil samples were combined into one composite sample for each component. Cover of the floating periphyton mat was estimated using digital photographs and image analysis. Periphyton was collected

from 15 separate locations in each plot using a 4.2-cm-diameter, 10-cm-long coring device. Replicates were combined and, in the lab, picked free of animals, plant matter, and debris. A measured subsample was dried to constant weight at 100°C (approximately 2 d). A subsample of dried material was then analyzed for TP. A second subsample of fresh material was oxidized for diatom analysis and permanent slide mounts were prepared on which at least 500 frustules were counted and identified. To estimate macrophyte stem density, living and senescent plant stems and leaves were counted and identified in 1-m^2 quadrats. Macrophyte TP was measured in each plot using 6 to 20 dried shoots of Gulf Coast spikerush, a dominant macrophyte at all flume sites. Fish biomass assessments were made using two throw-trap samples placed adjacent to the channel walls. The throw trap was a 1-m^2 cage, enclosed with 2-mm mesh on the sides from which fish were removed by systematic dip-net sweeping. The wet mass of fish was measured and converted to dry-mass estimates using the average of the two samples at each location. All samples analyzed for P were dry-combusted before colorimetric analysis (Soloranzo and Sharp, 1980).

Statistical Analyses

For each parameter at each downstream location, we calculated the difference between each treatment–control pair and between all control plots and compared mean differences (of treatment–control, control–control pairs) among flumes (sites) using a one-way ANOVA. Among-site and -year variance in controls were used to calculate the 95% confidence interval for plotting. Differences were by subtraction except for diatom species composition, where we used analysis of similarity (ANOSIM) (PRIMER-E software; Plymouth Marine Laboratory, 2004) employing the Bray–Curtis dissimilarity metric to determine the difference between relative abundances of diatom taxa among paired control and treatment plots.

Daily P assimilation rate (in g m^{-2} d^{-1}) was calculated by determining the cumulative days of P addition at the bimonthly sampling date immediately before the first detection of significant departure from control channel values (n = 3 flumes). The distance of the upstream-most location where the first significant alteration was detected was multiplied by channel width (3 m) to determine the area over which P was transported. The mass of P delivered to that area by that date was calculated as the among-channel mean cumulative P delivery. Downstream effect rates were calculated using the same values, dividing the area of channel where a significant departure was detected by time to first detection and the 3-m channel width.

RESULTS

All levels of P addition caused significant change in all measured parameters in a time-dependent sequence that was consistent among treatments (Table 1). While effect rates were dose dependent, all treatments converged to a similar enriched endpoint. The TP concentrations in periphyton and floc were significantly elevated by the end of the first year of P dosing in all treatments, and remained elevated throughout the experiment (Fig. 2a, 2b). Changes in periphyton tissue P content were followed by alterations in diatom species composition within the periphyton mats and the eventual loss of floating periphyton in all treatments by Year 4 (Fig. 2c, 2d). Soil TP increased steadily in all treatments throughout the study (Fig. 2e) while fish biomass showed

Table 1. Time to significant change for nine categories of responses at locations 15 m downstream of 5, 15, and 30 $\mu g\ L^{-1}$ P inputs. The sequence of responses is similar among dose levels but the rate of progression of significant responses is dose dependent.

	Dose level		
	30 $\mu g\ L^{-1}$	15 $\mu g\ L^{-1}$	5 $\mu g\ L^{-1}$
Response parameter	Time to change		
		yr	
Periphyton TP†	1	1	1
Floc TP	1	1	1
Diatom species	1	1	2
Periphyton cover	1	3	4
Soil TP	2	3	3
Macrophyte TP	3	4	4
Fish biomass	1	5	?
Macrophyte density	5	5	5
Water TP	5	5	?

† Total phosphorus.

complex fluctuations in response to treatment and time (Fig. 2f). Macrophyte tissues were enriched in P by Year 3 (30 $\mu g\ L^{-1}$) and Year 4 (15, 5 $\mu g\ L^{-1}$ treatments), while stem density remained constant throughout the study until Year 5 when density more than doubled in all treatments (Fig. 2g). These increases were due primarily to the proliferation of dominant wet-prairie/slough taxa, Gulf Coast spikerush and maidencane, though we found three stems of cattail (*Typha domingensis* L.) at a location 15 m downstream in one 30 $\mu g\ L^{-1}$ channel in Year 5. Water column TP fluctuated between 5 and 15 $\mu g\ L^{-1}$ (ambient concentrations) until Year 5, when enrichment was detected in the 15 and 30 $\mu g\ L^{-1}$ treatments (Fig. 2h).

The spatial sequence of downstream alterations was similar to the temporal series, with rates being dependent on dose level, channel-specific velocity, and parameter response time. The mean annual P load to the head of the 5, 15, and 30 $\mu g\ L^{-1}$ channels was 513, 1406, and 2594 g P yr^{-1}, respectively, with most of this load received in the wet season (August–December) before the synoptic sampling event. Assuming no transport out of the 100-m-long channels, aerial P loading rates were 1.7, 4.7, and 8.6 g $m^{-2}\ yr^{-1}$ for the 5, 15, and 30 $\mu g\ L^{-1}$ treatments, respectively. Assimilation rates of P, calculated as the amount of P delivered into an area in a time period before significant ecological change is detected, were parameter dependent and ranged from zero (for periphyton TP in the 15 $\mu g\ L^{-1}$ treatment) to 1.5 g $m^{-2}\ d^{-1}$ (for diatom species composition in the 15 $\mu g\ L^{-1}$ treatment; Fig. 3a). The progression rates of downstream changes were also concentration dependent, although more strongly so for diatom composition, periphyton cover, and periphyton and floc TP than for soil and water TP and plant density. Daily downstream response rates were expanded to a decadal time frame for comparison with long-term monitoring data (Fig. 3b). The model shows that a decade of loading at even the lowest concentrations (5 $\mu g\ L^{-1}$) above ambient caused periphyton and floc TP to be elevated 1 to 10 km downstream of the input site. Periphyton biomass losses are also predicted 1 km downstream of decade-long 30 $\mu g\ L^{-1}$ enhancements.

DISCUSSION

Ecosystems limited by P contain microbial communities capable of rapid P assimilation (Hwang et al., 1998; Noe et al., 2003; Scinto and Reddy, 2003; Gaiser et al., 2004), such that water column P measurements are a poor reflection of P load. Efficient microbial removal and recycling of P explains the lack of correlation between downstream water column P concentration and upstream P load observed in many Everglades marshes (Smith and McCormick, 2001; Childers et al., 2003). In our experiment, we were rarely able to detect enriched water column P concentrations at any dose level until Year 5 (Fig. 2h) even at locations only 5 m from the input source, though most ecological parameters had by that time deviated from the control condition throughout the entire 100-m treatment. Our conclusion from this is that in oligotrophic, flowing-water wetlands, P moves downstream via biotic transformations between the periphyton and flocculent detrital components rather than through the water, as in streams (i.e., nutrient spiralling). Because productivity in wetlands is displaced from the water column (i.e., phytoplankton) to benthic surfaces, water column estimates of TP exclude the majority of microbially bound P.

Rapid P assimilation by periphyton and the flocculent detritus stimulated other significant biotic alterations indicative of significant ecosystem state change. By Year 2 the diatom community was altered and the calcareous periphyton mat had collapsed completely. This periphyton community, ubiquitous in the Everglades, contains an assemblage of algae, bacteria, fungi, and detritus that, in deeper sloughs, grows attached to the abundant floating macrophyte eastern purple bladderwort. These mats tend to be highly calcareous (calcite contributes 30–70% to dry mass estimates in unenriched settings) and contain a unique assemblage of oligotrophic benthic algae dominated by filamentous blue-green algae and diatoms (Gaiser et al., 2004). The replacement of the floating, calcareous mat by a non-mat-forming algal community dominated by chlorophytes has been documented by others (Pan et al., 2000), though the cause is not fully understood. As the periphyton mat collapses, eastern purple bladderwort also disappears from the system. As this assemblage dissociates and decomposes it contributes to the detrital floc, which moves downstream with water flow and is incorporated eventually into the soils.

Soils in our experimental flumes responded slowly to elevated TP, consistent with research showing that soils only become enriched after input exceeds the capacity of the biota to sequester available P from the water column or detritus (Qualls and Richardson, 2000). Once in the soil, organic detrital P, measured as P accretion (Qian and Richardson, 1997), is not lost from the system, but is rapidly remineralized through bacterial activity and made available for macrophyte uptake (Newman et al., 2003). This explains the delayed but substantial increase in tissue P content of rooted macrophytes that fuelled the spike in production seen at the end of our experiment. In addition, much of the P assimilated by periphyton and floc may have been consolidated into the soils and become more readily available to macrophytes after
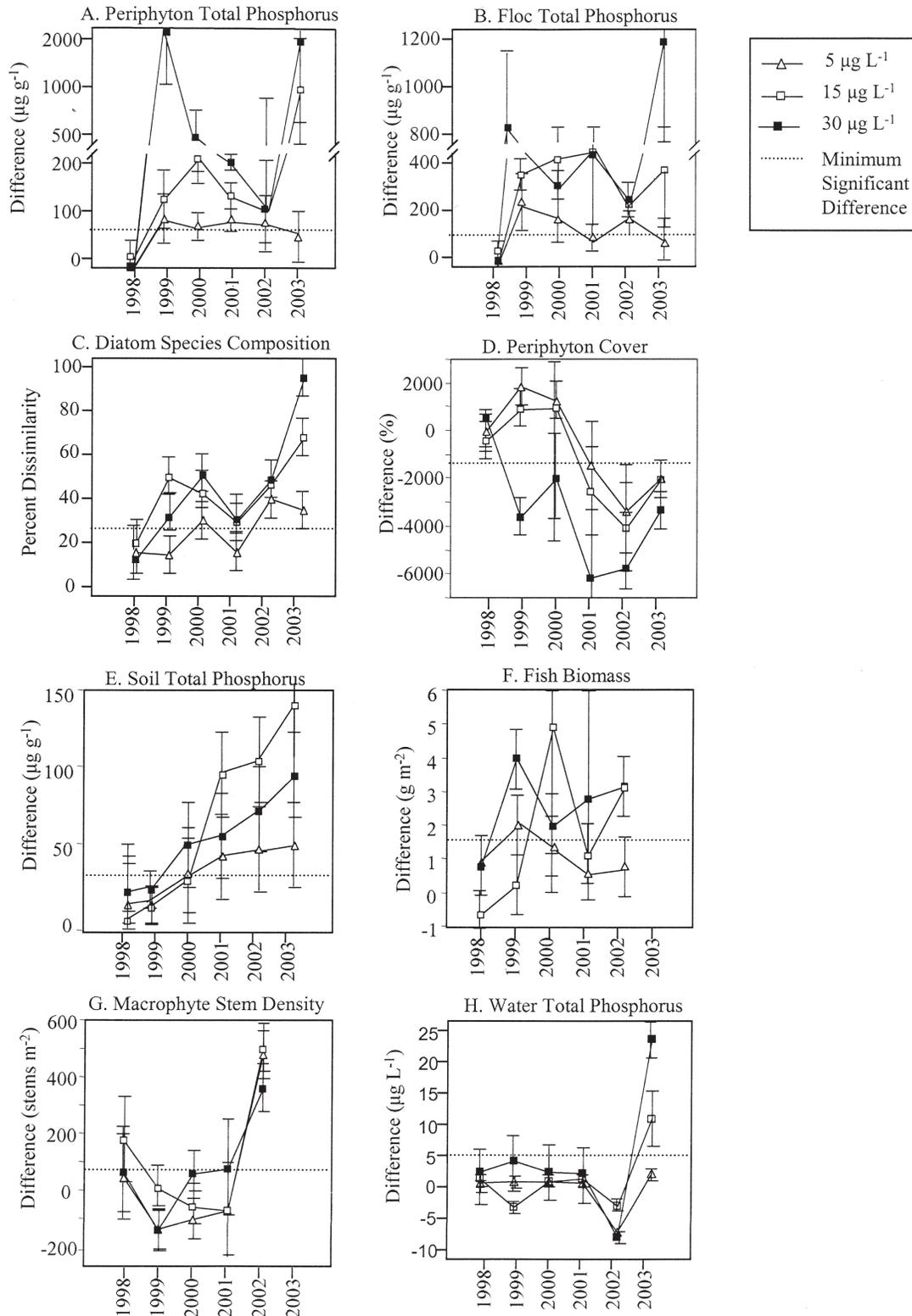
Fig. 2. Annual means for the 5-yr dosing period for the difference in measured parameters in channels receiving 5, 15, and 30 μg L⁻¹ above ambient concentrations relative to untreated control channel. The horizontal line is the minimum value representing a significant ($P < 0.05$) departure from differences expected among control channels (based on among-year variance of control channel differences).

a 6-mo drought that occurred before our 2002 sampling period. Alterations in periphyton composition and macrophyte density jointly contributed to fluctuations in fish biomass observed in the flumes. In the Everglades, fish respond with complex lags to alterations in periphy-

ton productivity and composition at the base of the food web, as well as changes in habitat complexity and macrophyte productivity (Trexler et al., 2001).

These results suggest a very low assimilative capacity for native Everglades wetlands. We found that although
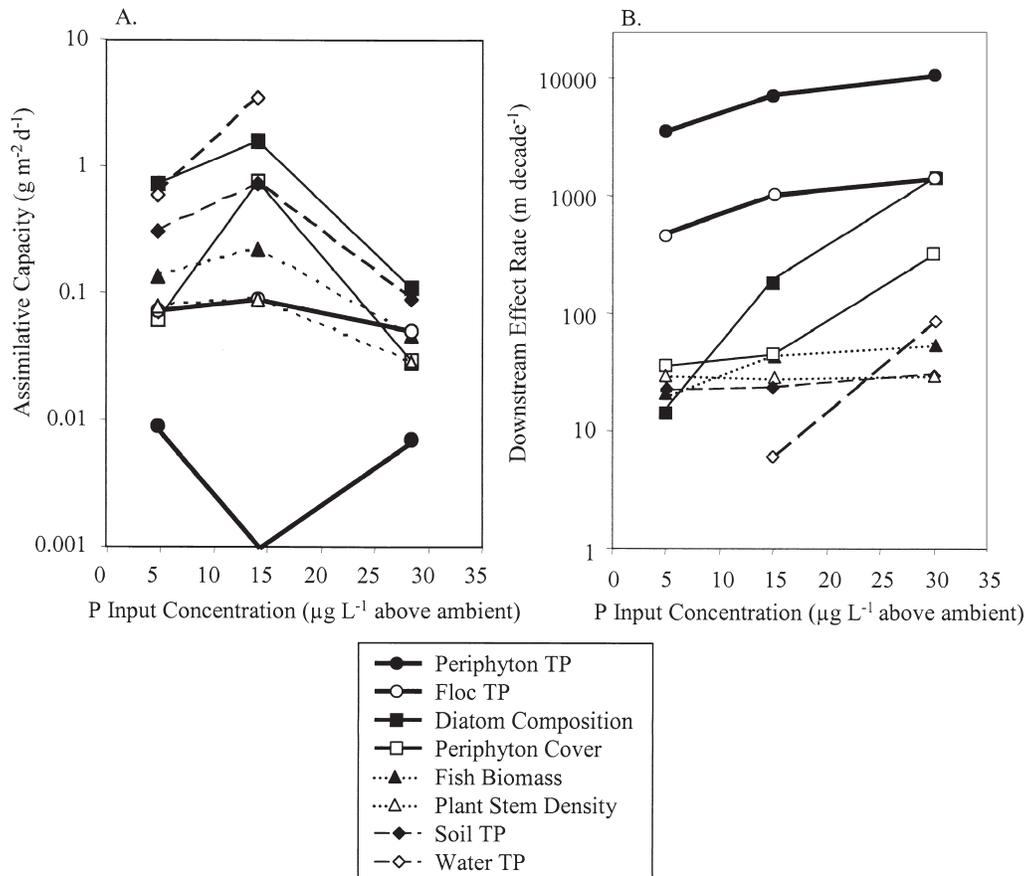
Fig. 3. (a) Parameter-specific P assimilative capacity calculated as the amount of P absorbed by an area of marsh over the time period before significant change in that parameter. (b) Dose-dependent downstream travel rates of significant alterations in measured parameters. The rates are applicable to marsh receiving P input from a control structure with a water depth of 0.5 to 1 m and input velocity of 2 to 15 mm s^{-1}.

Everglades marshes assimilated all added P, downstream transport in the water column was not detected until after a broad range of biotic changes had occurred (i.e., ecosystem state change). The sequence of significant biotic changes was initiated before our first sampling event (30 d) in the 15 and 30 μg L^{-1} channels and by Day 190 in the 5 μg L^{-1} channels. Using periphyton TP content as the first indication of enrichment, we found the daily assimilative capacity ranges from 0 to 0.01 g m^{-2} d^{-1} (Fig. 3a). Expanding to a yearly basis would yield an assimilative capacity ranging from 0 to 3.2 g m^{-2} yr^{-1} for this experiment, which in the higher treatments exceeds the 1 g m^{-2} yr^{-1} assimilative capacity of most wetlands (Richardson and Qian, 1999). However, for this wetland, P assimilative capacity should not be expressed on an annual basis. Even very low-level concentration enhancements (5 μg L^{-1}) result in loading rates exceeding the average assimilative capacity (1.7 g m^{-2} yr^{-1} in this study), but the downstream locations were altered well before the end of the first year. Our calculation of daily assimilative capacity may be overestimated because the effective area was taken to be the area upstream of any detected P enhancement in any parameter, and the mass P added was estimated as the total amount delivered to the head of the system immediately before detecting change. Although a P budget created by Noe et al. (2002) for this experiment suggests

some P loss occurs from the flume channels by undetected mechanisms, responses were still detected rapidly to what may have been a smaller load than we can measure, given complete retention. More importantly, the experiment shows that the system is not static: effects accumulate with time. The pristine Everglades are characterized by very high standing crops of algae and very low standing crops of aquatic consumers (Turner et al., 1999); over time, even our lowest treatment levels of P enrichment altered this distinctive pattern of community structure. The downstream and temporal progression of effects in our flumes at even the lowest dose clearly shows little resiliency of this flowing-water, oligotrophic wetland to persistent low-level P inputs.

This study shows that if P concentrations regularly exceed ambient levels, a cascade of ecological changes will be initiated and/or progress downstream in the marsh. Continuous low-level P inputs of even 5 μg L^{-1} above ambient at an average velocity of 8 mm s^{-1} would cause marshes 1 km downstream to have enhanced periphyton TP after 1 yr, floc TP after 10 yr, and a significantly altered plant and consumer community after 100 yr (Fig. 3b). Though we created this model as an exercise and realize it is projecting well beyond the spatial and temporal scope of our experiment, the predicted sequence is somewhat similar to that detected through long-term monitoring along P-gradient transects in

Water Conservation Area 2A. Between 1989 and 1999, soil TP concentrations along the transects had doubled, invading cattail had spread an additional 1 km downstream, and periphyton TP was elevated at sites as far as 14 km from the input source (Childers et al., 2003). Because this impact rate is dependent on water velocity, increased water flow through the central Everglades could accelerate P-related impacts, if input water quality does not match that of the interior marsh. At present, remediation mechanisms for P pollution in the Everglades do not achieve these low levels, and all models indicate decadal or greater time scales for elimination of excess P through biotic wetland treatment mechanisms (periphyton or macrophyte-based P removal cells upstream of protected marshes; Kadlec, 1999). Not recognizing this problem threatens the long-term success of current and future efforts to restore and manage this unique ecosystem. More generally, our study indicates that reliance on water quality standards to evaluate anthropogenic impacts on oligotrophic wetlands can lead to missing impacts in their early stages, when solutions are more easily implemented.

ACKNOWLEDGMENTS

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