Ecosystems (2001) 4: 603–624
DOI: 10.1007/s10021-001-0032-1

ECOSYSTEMS

MINIREVIEWS

Phosphorus Biogeochemistry and the Impact of Phosphorus Enrichment: Why Is the Everglades so Unique?

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ABSTRACT

The Florida Everglades is extremely oligotrophic and sensitive to small increases in phosphorus (P) concentrations. P enrichment is one of the dominant anthropogenic impacts on the ecosystem and is therefore a main focus of restoration efforts. In this review, we synthesize research on P biogeochemistry and the impact of P enrichment on ecosystem structure and function in the Florida Everglades. There are clear patterns of increased P concentrations and altered structure and processes along nutrient-enrichment gradients in the water, periphyton, soils, macrophytes, and consumers. Periphyton, an assemblage of algae, bacteria, and associated microfauna, is abundant and has a large influence on phosphorus cycling in the Everglades. The oligotrophic Everglades is P-starved, has lower P concentrations and higher nitrogen–phosphorus (N:P) ratios, and has oxidized to only slightly reduced soil profiles compared to other freshwater wetland ecosystems. Possible general causes and indications of P limitation in the Everglades and other wetlands include geology, hydrology, and dominance of oxidative microbial nutrient cycling. The Everglades may be unique with respect to P biogeochemistry because of the multiple causes of P limitation and the resulting high degree of limitation.

Key words: Everglades; phosphorus; biogeochemistry; wetlands; ecosystem; nutrient cycling; oligotrophy; eutrophy.

INTRODUCTION

The Florida Everglades is one of the largest and most unique wetlands in the world. It is also highly-impacted by hydrologic modification, drainage, exotic species invasions, and nutrient enrichment (Davis and Ogden 1994). In particular, changes in its ecosystem structure and function are a well-documented result of phosphorus (P) enrichment due to agricultural and urban runoff (reviewed by Davis 1994). The effects of P enrichment are noteworthy because the components of the Everglades ecosystem appear to be highly responsive to small changes in P concentrations. In this review, we discuss P biogeochemistry in the Everglades and compare less impacted, oligotrophic areas with those that have undergone increased P loading. We will also attempt to identify functional analogies between the Everglades and other wetland ecosystems that are highly limited by P.

Among the dominant characteristics of the Everglades are habitat heterogeneity, large spatial extent, and a distinctive hydrologic regime (McCally

Received 23 August 2000; Accepted 23 March 2001.
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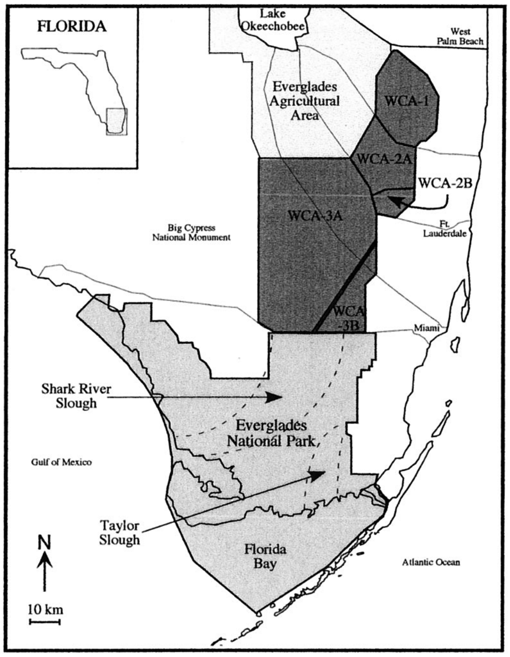

Figure 1. Map of the current Everglades and south Florida.

1999). We will demonstrate that oligotrophy is also characteristic of the Everglades. For the purpose of this review, we limit our definition of the Everglades to the freshwater wetland ecosystem. The predrainage Everglades landscape consisted of a habitat mosaic comprised predominantly of plains and patches of *Cladium jamaicense* (sawgrass), wet prairies, sloughs, tree islands, marl-forming marshes, and short-hydroperiod peripheral marshes (Davis and others 1994). Prior to efforts to drain the landscape, the freshwater Everglades were hydrologically continuous and covered 1.17 million ha of south Florida (Davis and others 1994). The Everglades ranged from Lake Okeechobee in the north to mangrove forest and Florida Bay in the south, the Gulf of Mexico and cypress forest (including Big Cypress National Monument) in the west, and the Atlantic coastal ridge in the east (Figure 1). Its hydrology was dominated by seasonal patterns of rainfall. The subtropical climate of south Florida is characterized by a dry season (December to May) and a wet season (June to November) with copious amounts of rainfall (mean, 1.4 m y^{-1}) (Duever and others 1994). This resulted in pulsed sheet flow so that water levels in the Northern Everglades were controlled by overflow from Lake Okeechobee and rainfall, whereas in the Southern Everglades hydrology was determined solely by rainfall (Parker 1974). Finally, the Everglades was noted for its abundance of wildlife, particularly the large numbers of breeding wading birds.

Now, the geographic extent of the Everglades has been reduced, the spatial and temporal patterns of environmental forcing factors (for instance, hydrology and fire) have been altered, and wildlife populations have declined (Davis and Ogden 1994). Construction of an extensive network of nearly 2400 km of canals and dikes was started in the 1880s to drain and compartmentalize the landscape into multiple, discontinuous hydrologic units: the Everglades Agricultural Area (EAA), the Water Conservation Areas (WCAs; WCA-1, -2A, -2B, -3A, and -3B) and Everglades National Park (ENP) (SFWMD 1999) (Figure 1). Wetlands have been drained for agriculture and urbanization. Today, only 0.62 million ha of the Everglades remain—a roughly 50% loss in spatial extent (Davis and others 1994). Short-hydroperiod wetlands have been preferentially drained, reducing landscape complexity. Animal populations have declined and several species—for example, snail kite (*Rostrhamus sociabilis*), Florida panther (*Felis concolor coryi*), wood stork (*Mycteria americana*), and Cape Sable seaside sparrow (*Ammospiza maritima mirabilis*)—are now endangered. In addition, the number of nesting wading birds is thought to have decreased 90% since the 1930s (Ogden 1994). Another outcome of ecosystem perturbation has been the successful invasion of many exotic plant and animal species.

Nutrient enrichment, by P in particular, has also had a large impact on the Everglades. Historically, the dominant source of P was rainfall (Davis 1994). Agricultural activities in the EAA (predominantly sugarcane production) and urbanization have increased nutrient concentrations (both nitrogen [N] and P) in waters entering the Everglades. This increase in nutrient loading has been most pronounced in areas that receive water directly from the EAA, such as WCA-2A. Davis (1994) estimated that annual P inputs into the WCAs increased from historic levels of approximately 129 metric tons to current inputs of approximately 376 metric tons as the result of increased P loading from drained agricultural lands. This increase in nutrient loading above natural levels has led to the dramatic expansion of *Typha* species in areas that receive water from the EAA, *Typha* species are native to the Everglades but are found only in small stands in oligotrophic areas (Davis and others 1994). Even a small increase in the concentration of total phosphorus (TP) in the water column, from less than 7 to 10–20 $\mu g\ L^{-1}$, leads to replacement of the extensive cyanobacterial-diatom periphyton mats that characterize the oligotrophic Everglades with filamentous green algae (McCormick and O'Dell 1996; McCormick and Stevenson 1998). We will demonstrate that the oligotrophic Everglades ecosystem is strongly limited by P, as evidenced by the low concentrations of P in the water, soil, periphyton, and macrophytes; highly oxidized soil profiles; adaptations to low P levels; and biotic responses to additions of P.

Everglades Restoration

The Everglades Forever Act, passed by the Florida legislature in 1994, requires the development of a numeric water-quality standard for P that will "prevent an imbalance in the natural populations of aquatic flora or fauna . . . and . . . provide a net improvement in the areas already impacted." In addition, the Central and Southern Florida Project Comprehensive Review Study (The Restudy) was authorized by the US Congress in 1992 to study the feasibility of modifying water-control structures and operations to restore the south Florida ecosystem and provide for other water-related needs of the region. The Water Resources Development Act of 2000 authorized the creation of the Comprehensive Everglades Restoration Plan (CERP) as a framework for implementing this hydrologic restoration. The Everglades Forever Act, The Restudy, CERP, and other legislation, regulations, and lawsuits have fostered a new great interest in understanding P biogeochemistry and the impacts of P enrichment on the Everglades. Intrinsic to this understanding is an acknowledgment of the Everglades as a unique wetland ecosystem.

Our Approach

Efforts to protect and restore the Everglades are contingent upon an understanding of why the Everglades are so highly limited by P and how increases in P affect the structure and function of the ecosystem and trigger ecosystem state changes. In this paper, we reviewed the literature on the biogeochemical cycling of P and changes in P cycling in response to enrichment in the Everglades. In addition, we synthesized the published data on P concentrations in the Everglades and identified patterns among ecosystem components and hydrologic units and along nutrient-enrichment gradients. We then utilized this meta-analysis, as well as a summary of the qualitative conclusions from the literature, to develop hypotheses that explain the high degree of P limitation in the oligotrophic Everglades compared to other wetlands. Finally, we developed functional analogies between the Everglades and other P-limited wetlands in an attempt to identify causes and indications of P limitation in wetlands.

Published peer-reviewed literature was surveyed to obtain data on P concentration in water, soils, periphyton, macrophytes, and consumers. Only publications that presented original data and described the methods utilized were included. The South Florida Water Management District (SFWMD) undertakes an extensive sampling regime and regularly publishes reports on this data. SFWMD data were not included in this synthesis unless these data were presented in the primary literature. Data from the literature were categorized by (a) hydrologic unit (WCA-1, WCA-2A, WCA-2B, WCA-3A, WCA-3B, ENP–Shark River Slough, and ENP–Taylor Slough) (Figure 1), (b) habitat and position along the nutrient-enrichment gradient (*Typha*, mixed *Typha/Cladium*, *Cladium*, enriched slough, and slough/wet prairie), and (c) ecosystem component (water, soil, periphyton, macrophytes, and fish). Plant community composition is often used as an indicator of nutrient-enrichment gradients in the Everglades. Finally, unpublished studies were included in the nonquantitative review if they reported understudied topics.

Published P concentrations, N:P ratios, and soil P-loading rates were analyzed by meta-analysis. P concentrations and N:P ratios were often estimated from graphs and are reported as ranges if the published values do not include averages. For studies that reported separate data for *Typha* and *Cladium* plots in the *Typha/Cladium* mixed community, data were reported as the range of the monotypic plots. Macrophyte data were weighted by the relative biomass of each species, when reported, in the slough/wet prairie community. Further details on the interpretation of each publication are listed in the Appendix. In cases where a range of concentrations was reported, the midpoint of the range was used in the meta-analysis. The use of range midpoints is susceptible to skewing by outliers and is most likely in *Cladium* habitat, where several studies report high soil TP concentrations relative to other *Cladium* habitat samples within and among studies. These high soil TP plots may be areas of *Cladium* that have received nutrient-enriched water but have not yet been invaded by *Typha*.

The matrix of published data was summarized by calculating arithmetic means of nutrient concentrations and geometric means of nutrient ratios and their associated 95% confidence intervals (CI). Published nutrient data in any given hydrologic unit, community, and ecosystem component vary in part due to different analytical techniques and differences in the timing and location of sampling. Consequently, analysis of the published values serves to summarize coarse patterns of P in the Everglades and contrast oligotrophic and enriched areas.

Analysis of variance (ANOVA) was used to test for differences in published nutrient concentration, ratio, and loading data among the four macrophyte communities (*Typha, Typha/Cladium, Cladium*, and slough/wet prairie), where each datum was a single literature value. All ANOVAs were assessed for violations of assumptions with scatterplots; water TP concentration was log-transformed to achieve homoscedasticity and normality of residuals. Differences among habitats for each significant test were assessed with Tukey's HSD multiple comparisons.

Geology of the Everglades

The Everglades began to form about 5000 years BP in a basin underlain by limestone bedrock (Jones 1948; Gleason and Stone 1994). The bedrock is very flat, sloping gently from a high at Lake Okeechobee to a low southward at Florida Bay. The very low relief of the bedrock has variously been estimated to be 2.4 m (Jones 1948), 2.9 m (Light and Dineen 1994), or 4.6 m (Parker 1974) in the 160 km from Lake Okeechobee to Florida Bay. The slope is somewhat exaggerated by deeper soils near Lake Okeechobee. In 1940; the depth of peat ranged from about 2.1 m near the lake to 0.3 m in the Southern Everglades; however, by 1940, significant subsidence of the peat, by roughly 1.5 m, had already occurred in agricultural areas near Lake Okeechobee (Jones 1948). Therefore, the soil surface likely decreased about 6 m in elevation from the shore of Lake Okeechobee to Florida Bay before drainage began. There is very little exposed rock and no terrigenous-clastic sediment input to the Everglades wetlands, although limestone is exposed in some areas of the Southern Everglades. Therefore, P made available from the weathering of mineral rock—the ultimate source of P to ecosystems—is not available to the Everglades.

The Water Component

The hydrology of the Everglades was historically controlled by the subtropical pattern of rainfall, the low relief, and dense vegetation. As a result, historic Everglades hydrology was seasonal in response to rainfall patterns and characterized by a low-velocity sheet flow with a large spatial extent and long periods of inundation (Parker 1974; Fennema and others 1994). In addition, the interaction of surface water with groundwater that had passed through the limestone bedrock resulted in high pH and calcium (Ca) concentrations in surface waters. This interaction with groundwater was greatest in the southern Everglades, where the limestone bedrock is more porous and permeable and is often directly exposed to surface water (Jones 1948). As will be shown later, this carbonate-rich water chemistry has a large impact on the availability of P.

Historically, the primary source of P to the Everglades was from atmospheric deposition rather than the inflowing of surface water. Davis (1994) estimated that wet and dry deposition contributed about 90% of the total P load to the Everglades prior to anthropogenic enrichment. Dry deposition of TP is clearly important to the nutrient budget of the Everglades. However, the estimation of dryfall TP loading is prone to sampling error. In the EAA, 87% of TP deposition was due to dryfall; the remainder came from rainfall, although the rate of TP deposition via dryfall increases near agricultural areas in Florida (Hendry and others 1981). In parts of the Everglades near agriculture, the highest rates of atmospheric dry P loading are likely to occur at the end of the dry season as dust is blown off dry fields that have been fertilized for many years. Calculations of wet deposition depend on the concentration of TP in the rainfall and the amount of rainfall, both of which vary in space and time. The concentration of TP in rainfall in South Florida was estimated to be 10.6 $\mu g\ L^{-1}$ (Ahn 1999), whereas mean rainfall TP concentrations at meteorological stations within or bordering the Everglades was 7.9 $\mu g\ L^{-1}$ (data in Ahn 1999). Davis (1994) calculated total (wet and dry) TP deposition to be 0.036 $g\ m^{-2}\ y^{-1}$ using mean annual rainfall rates and an estimate of 29 $\mu g\ L^{-1}$ in rainfall (pooled wet and dry deposition), which he characterized as an overestimate. Fitz and Sklar (1999) estimated total P deposition to be 0.03 $g\ m^{-2}\ y^{-1}$, while Moustafa and others (1996) estimated 0.03 g P $m^{-2}\ y^{-1}$ in the Kissimmee River basin, approximately 100 km north of the Everglades. Finally, Hendry and others (1981) estimated total P deposition to be 0.017 g $m^{-2}\ y^{-1}$ at an isolated site in the Florida Keys and 0.096 $g\ m^{-2}\ y^{-1}$ near agriculture in the EAA.

Phosphorus in overflow from Lake Okeechobee (which was likely at low concentrations in the past) was probably removed by the custard apple forest (*Annona glabra*) once present at the southern shore of the lake or by the sawgrass plains immediately downstream prior to the draining of wetlands for the EAA and construction of the WCAs. Rudnick and others (1999) reported a high amount of P uptake over a 3-km section of Taylor Slough in the Southern Everglades; TP decreased from a flow-weighted mean of 11.6 to 6.1 $\mu g\ L^{-1}$. In addition, it is estimated that more than 90% of P in waters entering the Everglades from the EAA is removed within the WCAs and associated canals before it enters ENP (Rudnick and others 1999).

Today, drainage canals from agricultural fields in the EAA have high concentrations of TP, up to 160 $\mu g\ L^{-1}$ (Coale and others 1994). Diaz and others (1994) also measured high TP concentrations in EAA canals, 80% of which was SRP. Historically, the annual P load to the entire Everglades from inflowing waters was estimated at 21 metric tons (Davis 1994). In contrast, average annual P load to the WCAs from the EAA was approximately 175 metric tons for the period 1978–91 and 240 metric tons for 1992–96 (Walker 1999). The ENP area has seen smaller changes in total P input (Davis 1994); however, there have been recent increases in P input into areas of ENP near inflow structures. Adjusted for temporal variation in hydrology, TP inputs to Shark River Slough (ENP) increased 5.3% per year and N:P decreased 8.5% per year from 1978 to 1989 (Walker 1991). Due to the implementation of best management practices in the EAA, TP concentrations in the inflow to WCA-2A (SFWMD 2000) and ENP (Walker 1999) decreased in the late 1990s.

Although there is variability in measured TP concentrations in surface water (Table 1), the literature documents a strong trend of increasing P concentration in response to nutrient enrichment (ANOVA: $n = 23$, $P < 0.001$, multiple $R^2 = 0.77$). Mean surface-water TP concentrations across the Everglades ranges from 76 to 42 $\mu g\ L^{-1}$ in *Typha* and *Typha/Cladium* mix, which is significantly greater than in *Cladium* communities (11 $\mu g\ L^{-1}$) and unenriched sloughs (10 $\mu g\ L^{-1}$) (Table 2). The ratio of N:P is an indicator of the relative availability of the two nutrients and can be used cautiously to assess the degree of nutrient limitation by N or P. Phosphorus limitation in freshwater lakes is significantly more frequent than nitrogen limitation when molar N:P ratios are greater than 31, although there is some variation in this threshold among lakes (Downing and McCauley 1992). Molar N:P ratios in surface water change along nutrient-enrichment gradients in the Everglades (ANOVA: $n = 18$, $P = 0.001$, multiple $R^2 = 0.69$), averaging 94:1, 228:1, 542:1, and 378:1 in *Typha*, *Typha/Cladium* mix, *Cladium*, and slough, respectively (Table 2). In unenriched sloughs of WCA-2A, surface water N:P ratios are above 500:1 (Table 3). In contrast, unenriched sloughs in the southern Everglades typically have N:P ratios of about 275:1 (Table 3). Because TP concentrations are similar in unenriched areas of the northern and southern Everglades (Table 1), the higher N:P ratio in unenriched areas of the northern Everglades must be due to the higher concentrations of N in water from the EAA. The water N:P ratio in the least impacted Everglades is much higher than most oligotrophic lakes (data in Downing and McCauley 1992).

The Periphyton Component

The microflora in wetlands are productive and are often a major regulator of nutrient fluxes in freshwater ecosystems (Wetzel 1990). Microbes and algae control the short-term uptake of P in most wetlands (Howard-Williams 1985), although soil and peat accretion determine long-term storage (Richardson and others 1997). Periphyton (a community of algae, bacteria, and microfauna) occurs at the soil surface, attached to macrophytes, and at the water surface. Periphyton standing crop is much greater in the Everglades than in other wetlands (Turner and others 1999); its abundance is visually striking. Everglades periphyton often occurs in association with *Utricularia purpurea*, a submerged aquatic macrophyte common in wet prairie and slough habitats.

The abundant periphyton of the Everglades reduces water P concentrations and affects P cycling in the water and soil through biotic and abiotic immobilization. Everglades periphyton is efficient at scavenging P from the water column (Scinto 1997; McCormick and others 1998) and has higher uptake rates of P than other ecosystem components (Davis 1982). Unlike macrophytes, the algae and bacteria in periphyton are not restricted to the uptake of dissolved inorganic phosphorus (DIP) but can also utilize dissolved organic phosphorus (DOP) (McCormick and Scinto 1999). In the Everglades, periphyton use DIP and DOP in comparable amounts (Scinto 1997). Scinto (1997) estimated that benthic periphyton alone contributes about 10% of TP accretion to Everglades soils, indicating a role for periphyton in long-term P sequestration. Finally, most P enters the oligotrophic Everglades through atmospheric inputs, and the abundant mats of floating periphyton are likely the primary interceptor of atmospheric inputs of P and therefore the most important regulator of P cycling. The shift to water-column loading of P in enriched areas may have an important impact on the cycling of P.

Calcareous periphyton is characteristic of wet prairies and sloughs in the oligotrophic Everglades (Gleason and Spackman 1974). The precipitation of $CaCO_3$ by periphytic algae can immobilize P and thereby have a large impact on P availability and cycling. In waters with high Ca concentrations, decreased pCO_2 during photosynthetic activity results

Table 1. Total Phosphorus Concentration Data for the Everglades

		Ecosystem component			
Location	**Habitat**	**Water**	**Periphyton**	**Soil**	**Macrophyte**
EAA	Irrigation canal	100[13]			
		160[11]			
WCA-1	*Typha*			1028[21]	
				1435–2380[19]	
	Typha/Cladium			1177[19]	
	Cladium			368[21]	
				476–1017[19]	
	Slough/wet prairie			413–642[19]	
WCA-2A	*Typha*	34[20]	1900–3390[8]	1100–>1300[32]	1428[25]
		40–150[18]	2500–3750[17]	1108–1781[28]	1500[2]
		61[25]		1248[6]	1600[4]
		75[23]		1305[25]	
		101–130[32]		1338[12]	
				1401–1611[7]	
				1474[23]	
				1475–2059[19]	
				1900[4]	
	Typha/Cladium	11[25]	500–1750[17]	500–1100[32]	350–550[29]
		13–163[10]		529–1022[23]	500–900[4]
		20–30[18]		692–1538[28]	670–680[25]
		28–52[32]		720[25]	
		30–65[23]		802[12]	
				856–1793[19]	
				924–1292[7]	
				1350[4]	
	Cladium	5[25]	<100[17]	271–547[23]	150[4]
		7–20[23]	<100–640[8]	303[22]	150[29]
		8–11[18]	132–385[22]	315–786[28]	165–197[22]
		11[22]		432[6]	200[2]
		15[32]		441[25]	243[25]
				473[12]	
				495–1201[7]	
				<500[32]	
				507–1645[19]	
				600[4]	
	Enriched Slough/wet prairie			1496–1538[28]	
	Slough/wet prairie	8[20]	30–454[16]	160–435[26]	300–850[26]
		8–11[18]	<100[17]	<500[32]	
		9[26]	<100–640[8]	530[28]	
		15[32]	200[26]	586–837[19]	
			385[22]		
WCA-2B	*Typha*				
	Typha/Cladium		671[14]	321[15]	235[15]
	Cladium			317[15]	205[15]
				546[6]	
	Slough/wet prairie		160[14]	220[15]	218[15]
WCA-3A	*Typha*			1214[19]	
	Typha/Cladium				
	Cladium			351–553[19]	
				548–764[6]	
	Slough/wet prairie			349–630[19]	
WCA-3B	*Typha*				
	Typha/Cladium				
	Cladium			174–459[1]	224[1]
	Slough/wet prairie				

Table 1. (Continued).

Location	Habitat	Water	Periphyton	Soil	Macrophyte
		Ecosystem component			
ENP-SRS	*Typha*			820[31]	
				1418[19]	
				1473[5]	
	Typha/Cladium				
	Cladium			231–385[5]	
				386–1036[19]	
				611[31]	
	Slough/wet prairie	11[3]		334[31]	
		15[30]		322–1063[19]	
ENP-TS	*Typha*				
	Typha/Cladium				
	Cladium				
	Slough/wet prairie	7[3]			
		9[30]			

Data are sorted by ecosystem component, location, and macrophyte habitat.
Periphyton, soil, and macrophyte data are presented as μ*g* g^{-1} water data are presented as μg L^{-1}.
References, indicated by superscripts, are listed in the Appendix.

in high pH—as much as 1.2 higher in periphyton mats during the day (Gleason and Spackman 1974). This drop in the partial pressure of soluble CO_2 leads to the crystallization of $CaCO_3$ (Gleason and Spackman 1974) and either the precipitation of Ca-P compounds or the coprecipitation of PO_4 with $CaCO_3$ (Otsuki and Wetzel 1972; House 1990; Diaz and others 1994). A nighttime decrease in pH at the periphyton–water interface may dissolve $CaCO_3$ (Gleason and Spackman 1974), thus resulting in increased soluble P concentrations (Diaz and others 1994).

The precipitation of inorganic P bound to Ca may not only occur in association with periphyton. High concentrations of Ca-bound inorganic P have been found in the surface (0–5 cm) soils of areas of the Everglades that received P-enriched water from the EAA but had no periphyton (Qualls and Richardson 1995). Qualls and Richardson (1995) hypothesized that this increase in Ca-bound inorganic P was due to the abiotic precipitation or coprecipitation of Ca phosphates or the adsorption of P to $CaCO_3$. However, the results of Diaz and others (1994) suggest that the pH and Ca concentrations in the enriched areas that were reported by Qualls and Richardson (1995) were too low for P precipitation to occur. In addition, Ca-bound P in the soils of enriched areas could have been formed by periphyton that existed in the past and was then deposited in the flocculent detrital layer and then accreted into the soil.

Even low levels of P enrichment result in both the loss of the calcareous periphyton mat (Browder and others 1994; Vymazal and others 1994; McCormick and O'Dell 1996) and changes in algal species composition (Grimshaw and others 1993; Raschke 1993; Vymazal and others 1994; McCormick and O'Dell 1996; McCormick and others 1998). These changes often coincide with short-term increases (Vymazal and others 1994) and long-term decreases (McCormick and others 1998) in periphyton biomass and increases in mass-specific productivity (McCormick and others 1998; McCormick and Scinto 1999). P enrichment also leads to the decreased growth and loss of *Utricularia purpurea*, a common substrate for periphyton (Craft and others 1995; Vaithiyanathan and Richardson 1999). However, alterations in periphyton composition are also correlated with variations in the degree to which the water column is saturated with $CaCO_3$. The occurrence of blue-green algal calcareous periphyton is correlated with water in equilibrium with $CaCO_3$, whereas green algae, particularly desmids, are correlated with water undersaturated with $CaCO_3$ (Gleason and Spackman 1974). Hydrologic conditions can also influence the saturation and precipitation of $CaCO_3$ by periphyton (Browder and others 1994). Therefore, changes in the species composition of periphyton could be the result of altered $CaCO_3$ water chemistry and hydrology as well as increased P.

Vymazal and others (1994) experimentally tested for N vs P limitation of epiphytic periphyton in the

Table 2. Meta-analysis of Published Data for the Everglades and Other Wetlands

Component	Bedford and Others 1999	Everglades			
		Typha	*Typha/Cladium*	*Cladium*	Slough/Wet Prairie
Water TP	—	76.1 ± 38.8 (5)[a]	42.3 ± 36.2 (5)[a]	10.8 ± 4.8 (5)[b]	10.4 ± 2.5 (8)[a]
Water N:P	—	94.1 ± 52.6 (4)[ab]	228.0 ± 221.1 (4)[bc]	542.0 ± 774.8 (3)[c]	377.6 ± 164.0 (7)[c]
Periphyton TP	—	2885.0 ± 3049.4 (2)[a]	898.0 ± 2884.3 (2)[b]	242.8 ± 337.1 (3)[c]	242.8 ± 120.1 (6)[c]
Periphyton N:P	—	—	86.0	165.0	151.7 ± 50.2 (4)
Soil TP	900 ± 590 (109)	1402.9 ± 165.6 (15)[a]	947.3 ± 230.5 (10)[b]	533.2 ± 94.0 (20)[c]	467.1 ± 116.1 (10)[c]
Soil TP load	—	0.60 ± 0.31 (4)[a]	0.38 ± 0.98 (2)[a]	0.09 ± 0.04 (10)[b]	—
Soil N:P	47.1 ± 1.3 (109)	49.0 ± 10.3 (10)[a]	**77.6 ± 20.5 (6)**[a]	**144.6 ± 30.2 (12)**[b]	**213.0 ± 80.1 (4)**[c]
Macrophyte TP	1400 ± 200 (65)	1509.3 ± 214.6 (3)[a]	**515.0 ± 346.7 (4)**[b]	**193.3 ± 32.7 (7)**[c]	396.5 ± 2268.0 (2)[bc]
Macrophyte N:P	32.9 ± 3.8 (48)	**16.7 ± 9.0 (3)**[a]	40.2 ± 21.8 (4)[b]	**76.7 ± 26.2 (7)**[c]	62.2 ± 53.3 (3)[bc]

Mean ± 95% confidence interval (CI) is presented with the sample size (number of studies) in parentheses for TP concentration (μg L^{-1} or μg g^{-1}), molar N:P ratio, and annual soil TP load (g m^{-2} y^{-1}).
Different letters indicate that a significant difference (α < 0.05) exists among Everglades habitats, as determined by Tukey's post hoc tests.
Summary statistics are calculated from the analysis by Bedford and others (1999) of nutrient concentrations in temperate North American wetlands. Macrophyte N:P data from Bedford and others (1999) only include values from peat-based wetlands.
The mean is presented when n = 1; — dashes indicate that data was not found in the literature.
Bolded cells indicate that the 95% CI of a parameter in the Everglades and in temperate North American wetlands (Bedford and others 1999) do not overlap.

Everglades. They found that epiphyton growing on macrophyte stems is predominantly limited by P, although colimitation also occurred (Vymazal and others 1994) at their relatively P-enriched sites in WCA-2B (water PO_4 = 23–30 μg L^{-1}) (Craft and others 1995). Periphyton is colimited by N and P in the littoral zone of Lake Okeechobee, which is situated at the northern edge of the Everglades and slightly enriched with phosphorus (water TP = 10–14 μg L^{-1}) (Havens and others 1999). Combined N and P fertilization results in the loss of the surface periphyton mat, a change in species composition, and increases in chlorophyll *a* concentrations, carbon uptake, and metabolism (Havens and others 1999). Although Vymazal and others (1994) and Havens and others (1999) found evidence for the colimitation of periphyton by P and N, the quick and large response of periphyton to experimental additions of P in oligotrophic areas suggests that periphyton is predominantly P-limited. The possible existence of periphyton colimitation by N and P is interesting given that the N:P ratio of the water column is much greater, and hence N-rich, than that seen in periphyton (Table 2).

The P content of periphyton mats is strongly correlated with water-column P concentrations (Grimshaw and others 1993; McCormick and O'Dell 1996; McCormick and others 1998) (Table 1) and increases with P enrichment (McCormick and Scinto 1999). TP concentrations in periphyton significantly increase along the eutrophication gradient (ANOVA: $n = 13$, $P < 0.001$, multiple $R^2 = 0.97$) from about 250 μg g^{-1} in unenriched *Cladium* and slough/wet prairie habitats, to 900 μg g^{-1} in slightly enriched sites, to 2900 μg g^{-1} in enriched sites (Table 2). Periphyton molar N:P ratios vary (Table 3), but they decrease with enrichment from an average of about 150:1 in unenriched slough and wet prairie communities (Table 2) to 86:1 in mixed *Typha* and *Cladium* habitats (Table 3).

The calcareous floating periphyton mat (metaphyton) in oligotrophic areas blocks most light (Vaithiyanathan and Richardson 1998) and therefore dominates primary productivity in the water column. Experimental removal of metaphyton greatly increases benthic dissolved oxygen (DO) concentrations, suggesting that metaphyton limits primary productivity at the water–soil interface (Vaithiyanathan and Richardson 1998). Therefore, loss of metaphyton in response to P enrichment likely stimulates periphytic and benthic periphyton growth. However, the eventual expansion of *Typha* following P enrichment is associated with the near elimination of all forms of periphyton. *Typha* shades sunlight more than *Cladium*, and the conversion of macrophyte communities to stands of *Typha* decreases the net primary productivity (NPP) of periphyton by 80% (Grimshaw and others 1997). Bacteria within periphyton mats rely on the autotrophic production of algae, and a decrease in photosynthetic productivity leads to decreased heterotrophic activity (Neely and Wetzel 1995). This reduction of both photosynthetic and heterotrophic microbial productivity in response to *Typha* invasion likely reduces the nutrient assimilation and retention capacities of periphyton and therefore of

Table 3. N:P Molar Ratio Data for the Everglades

		Ecosystem Component			
Location	**Habitat**	**Water**	**Periphyton**	**Soil**	**Macrophyte**
EAA	Irrigation canal	55[13]			
WCA-1	*Typha*			57[21]	
	Typha/Cladium				
	Cladium			186[21]	
	Slough/wet prairie			186[21]	
WCA-2A	*Typha*	60[23]		33[4]	13[4]
		86[25]		38[24]	18[2]
		<111[18]		40[12]	20[25]
		137[20]		44–60[9]	
				44–71[29]	
				53[25]	
				57[6]	
	Typha/Cladium	70–140[23]		44[4]	27[4]
		46–422[10]		46–137[28]	34–43[29]
		166–332[18]		69–133[23]	35–49[25]
		442[25]		77[12]	
				80–82[9]	
				86[25]	
	Cladium	180–440[23]	146–184[22]	82–201[28]	46–64[22]
		>553[18]		91[4]	62[2]
		929[25]		93–124[9]	77–84[29]
				133–252[23]	82[25]
				135[12]	139[4]
				137[25]	
				177[6]	
	Enriched Slough/wet prairie			51–55[28]	
	Slough/wet prairie	517[26]	126[22]	164[28]	46–73[26]
		>553[18]	130–268[16]	268[26]	
		692[20]	177[26]		
WCA-2B	*Typha*				
	Typha/Cladium		86[14]		60[15]
	Cladium			122[6]	82[15]
	Slough/wet prairie		128[14]		88[15]
WCA-3A	*Typha*				
	Typha/Cladium				
	Cladium			93–161[6]	
	Slough/wet prairie				
WCA-3B	*Typha*				
	Typha/Cladium				
	Cladium				
	Slough/wet prairie				
ENP-SRS	*Typha*			38[5]	
				82[31]	
	Typha/Cladium				
	Cladium			124[31]	61[27]
				166–365[5]	
	Slough/wet prairie	260[30]		252[31]	46[27]
		323[3]			
ENP-TS	*Typha*				
	Typha/Cladium				
	Cladium				
	Slough/wet prairie	242[30]			
		272[3]			

Data are sorted by ecosystem component, location, and macrophyte habitat.
References, indicated by superscripts, are listed in the Appendix.

the entire wetland ecosystem (Grimshaw and others 1997).

Periphyton oxygenates the water column in oligotrophic Everglades wetlands (Browder and others 1994; McCormick and others 1997; Vaithiyanathan and Richardson 1998). However, there is conflicting evidence of the impact of P enrichment on water-column DO concentrations. Rader and Richardson (1992) concluded that DO at the soil–water and periphyton–water interface was similar between areas with and without P enrichment, but that midcolumn DO in the dry season was lower in response to P enrichment. Both Swift (unpublished in Browder and others 1994) and Belanger and others (1989) found that DO levels were lower in enriched than in unenriched sites. Finally, McCormick and others (1997) showed that nutrient enrichment was associated with reduced periphyton productivity per unit area, a shift toward increasing community heterotrophy, and protracted periods of oxygen depletion. To summarize, it is likely that P enrichment results in the depletion of water-column DO concentrations.

Finally, periphyton communities provide both food and habitat structure for higher consumers. The highly productive periphyton mats of the Everglades are probably an important base of the food web (Browder and others 1994). However, few studies have documented grazing in periphyton mats. In one of the few published studies on Everglades food webs, Hunt (1952) showed that Florida gar (*Lepisosteus platyrhincus*) in the man-made Tamiami canal consumed large quantities of mosquito fish (*Gambusia holbrooki*) and freshwater shrimp (*Palaemonetes paludosus*). In turn, the algae in the periphyton were a major part of the fish's and shrimp's diet (Hunt 1952). The loss of periphyton mats following P enrichment also has a direct effect on consumer communities.

The Soils Component

In general, phosphate loading in wetland soils is associated with adsorption to minerals, not to organic peat (Richardson 1985). The specific minerals that control P adsorption or precipitation vary depending on wetland pH (Moore and Reddy 1994). In alkaline wetlands, this soil storage is related to calcium carbonate chemistry; whereas in acidic wetlands, aluminum (Al) and iron (Fe) chemistries control P adsorption and precipitation (Richardson 1999). Therefore, P adsorption in the carbonate-rich Everglades is likely controlled by pH. In contrast, redox potential (Eh) determines the valence of Fe and Al and consequently controls P adsorption dynamics in low pH wetlands (Patrick and Khalid 1974). The paradox of pH control in the soils of the Everglades and other carbonate-rich systems is that the high carbonate concentration buffers pH changes at the same time that pH changes are responsible for most changes in P from a solid (associated with $CaCO_3$) to a dissolved state. Thus, minor changes in soil pH at the microscale, such as occurs in periphyton mats, may drive this dynamic in the Everglades.

However, other studies have found that the bulk of PO_4 flux in wetland soils is controlled by soil microbes (Chapin and others 1978; Walbridge 1991; Wetzel 1999). Microbial populations may control this flux directly, by releasing phosphatases to fix P, or indirectly, by lowering the redox potential of soils and causing the release of P from Fe complexes (Wetzel 1999). The size of microbial populations increases, in turn, in response to P additions (Reddy and others 1999). In acid organic wetland soils, 90% of added PO_4 remained available when microbial uptake was inhibited, as compared to only 10% in natural soils (Walbridge 1991). In the Everglades, PO_4 removal in the basic organic soils typical of the ecosystem is controlled by soil microbial processes rather than physical or chemical processes (Amador and others 1992), whereas TP removal is likely controlled by abiotic hydrophobic and ionic interactions with soil particles (Jones and Amador 1992). Organically bound P accounts for 71% of accreted TP in unenriched WCA-2A (Scinto 1997)—a finding that lends support to a biological model of P removal.

Across the Everglades, soil TP concentrations are higher in areas receiving water enriched with nutrients and dominated by *Typha* than in unenriched areas (ANOVA: $n = 55$, $P<0.001$, multiple $R^2 = 0.72$) (Table 1). Mean soil TP concentrations are significantly higher in enriched areas with *Typha* (1403 $\mu g\ g^{-1}$) than in enriched areas with *Typha* and *Cladium* (947 $\mu g\ g^{-1}$), which, in turn, are greater than in unenriched *Cladium* and slough/wet prairie (533 and 467 $\mu g\ g^{-1}$, respectively) across the Everglades (Table 2). Surface soil TP values are even lower, sometimes less than 100 $\mu g\ g^{-1}$, in short-hydroperiod marl marshes of the southern Everglades (D. L. Childers unpublished). This pattern of changing soil P concentration along eutrophication gradients is consistent across the Everglades (Doren and others 1997) (Table 1). However, the interior areas of WCA-2A, the location for oligotrophic reference sites in this most frequently studied hydrologic unit, are enriched compared to the southern Everglades (Stober and others 1998). Changes in soil N:P also occur following P enrichment

(ANOVA: $n = 32$, $P < 0.001$, multiple $R^2 = 0.75$) (Table 3), decreasing from 213:1 in slough/wet prairie and 145:1 in *Cladium* to 78:1 in mixed *Typha* and *Cladium* and 49:1 in *Typha* habitats (Table 2).

Soil P concentrations in the oligotrophic Everglades and other subtropical/tropical carbonate-rich wetlands are far lower than those found in temperate North American wetlands. In the carbonate-rich wetlands of Belize, soil TP ranges from about 50 to 90 $\mu g\ g^{-1}$ in *Eleocharis cellulosa* marshes, 90 to 175 $\mu g\ g^{-1}$ in *Cladium* marshes, and 90 to 290 $\mu g\ g^{-1}$ in *Typha domingensis* marshes (Rejmánkova and others 1995). In comparison, the mean concentration of TP in surface soils of North American temperate wetlands is 900 ± 590 $\mu g\ g^{-1}$ (95% CI) (Bedford and others 1999) (Table 2).

Everglades soil TP in oligotrophic and enriched areas becomes lower with soil depth (Reddy and others 1998), decreasing rapidly below 5 cm (Scinto 1997). Enriched and unenriched soils in WCA-2A have similar TP at lower soil depths (Koch and Reddy 1992; Reddy and others 1993; Craft and Richardson 1993a, 1993b, 1998; Qualls and Richardson 1995; Vaithiyanathan and Richardson 1997). The depth at which TP concentration of unenriched and enriched soil profiles diverge may reflect the extent of peat accumulation following the construction of the water conservation areas and export of TP from drained agricultural land in the EAA (Vaithiyanathan and Richardson 1997; Craft and Richardson 1998). Alternatively, macrophytes are known to influence the vertical profile of TP concentration through the "mining" of P from the lower soil depths.

There is disagreement about whether there are changes in the proportion of inorganic and microbial P in soils along nutrient-enrichment gradients. In WCA-1, Newman and others (1997) and Reddy and others (1998) found that the inorganic P fraction increased in response to P enrichment. In enriched areas of WCA-2A, Vaithiyanathan and Richardson (1997) measured a large increase, Koch and Reddy (1992) found a slight increase, and Qualls and Richardson (1995) and Reddy and others (1998) observed no change in the proportion of TP that was inorganic. The conflicting results of these studies may be a result of spatial and temporal variations in soil P. Any increase in the proportion of inorganic P is most likely due to increased P loading from surface water and the mineralization of organic matter in areas that have been impacted by agricultural drainage (Reddy and others 1998). Phosphorus enrichment may also affect soil microbial P content. The concentration of soil microbial biomass P was found to increase in response to experimental PO_4 enrichment in WCA-2A (Qualls and Richardson 2000). However, a decreasing proportion of soil TP is found in soil microbial biomass in enriched areas of WCA-1 and WCA-2A (Qualls and Richardson 1995; Reddy and others 1998), suggesting that the relative importance of soil microbial mineralization to the cycling of P is greater in unimpacted oligotrophic areas. In summary, the relative importance of biologically mediated cycling and storage of P decreases in nutrient-enriched areas, where inorganic processes have increased importance.

Microbial processes may no longer be limited by P in impacted areas of the Everglades (Reddy and others 1999). Soil mineralization is limited by P (Miao and DeBusk 1999); however, N is limiting to mineralization in high-TP soils (Amador and Jones 1993, 1995). Koch-Rose and others (1994) observed seasonal variation in soil porewater soluble reactive phosphorus (SRP) at enriched sites but low and stable levels of soil SRP at oligotrophic sites, suggesting that the mineralization of organic matter by soil microbes was limited by P at oligotrophic sites and controlled by water levels and temperature at enriched sites. Increased soil microbial processing (Amador and Jones 1995) and changed soil microbial populations (Drake and others 1996) that result from P enrichment often shift soils from aerobic to anaerobic conditions. Unlike most wetlands, peat and marl soils in the unenriched oligotrophic Everglades are oxidized (>100 mV) (Bachoon and Jones 1992; Colbert 2000), with 0.7–4 mg L^{-1} dissolved oxygen in porewater (Gordon and others 1986). Furthermore, the addition of PO_4 to oligotrophic aerobic (500 mV) Everglades peat soils results in significant decreases in soil redox to anaerobic levels (−200 mV) (Colbert 2000). Drake and others (1996) also found significantly lower redox potentials in a nutrient-enriched site (–302 mV) compared to a less-enriched reference site (–94 mV). This shift to anaerobic conditions following P enrichment increases methanogenesis (Drake and others 1996; Colbert 2000) and may also increase denitrification rates (Koch and Reddy 1992). However, methanogenesis (Bachoon and Jones 1992) and denitrification (Gordon and others 1986; White and Reddy 1999) do not immediately change following the addition of PO_4 to oligotrophic soils.

Many studies have used the depth profile of radioisotopes to estimate the rates of P (Table 4) and peat accumulation. Mean estimates of P accumulation using ^{137}Cs or ^{210}Pb dating are greater in enriched areas with *Typha* (0.60 $g\ m^{-2}\ y^{-1}$) or mixed *Typha* and *Cladium* (0.38 $g\ m^{-2}\ y^{-1}$) than in unenriched areas with *Cladium* (0.09 $g\ m^{-2}\ y^{-1}$)

Table 4. Annual Soil P-Loading (g m^{-2} y^{-1}) Data for the Everglades

Typha		*Typha/Cladium*		*Cladium*	
Load	**Location**	**Load**	**Location**	**Load**	**Location**
0.39–0.47[24]	WCA-2A	0.25–0.35[9]	WCA-2A	0.01–0.02[24]	WCA-1
0.46[6]	WCA-2A	0.28–0.63[7]	WCA-2A	0.02–0.21[7]	WCA-2A
0.54–1.14[9]	WCA-2A			0.03[22]	WCA-2A
0.56–0.78[7]	WCA-2A			0.03–0.09[24]	ENP-SRS
				0.06[6]	WCA-2A
				0.06–0.07[24]	WCA-3A
				0.07–0.14[24]	WCA-2A
				0.08–0.23[6]	WCA-3A
				0.11–0.25[9]	WCA-2A
				0.14[6]	WCA-2B

Data are listed with corresponding location and macrophyte habitat.
References, indicated by superscripts, are listed in the Appendix.

(ANOVA: $n = 16$, $P<0.001$, multiple $R^2 = 0.84$) (Table 2). Soils in unenriched areas of the Everglades have lower P accumulation rates, but greater N accumulation rates, than other unenriched freshwater wetlands in the United States (Craft and Richardson 1998). Similar to rates of P accumulation, areas receiving nutrient-enriched water have higher organic soil accretion rates than oligotrophic areas. Organic soil accretion is highest near inflows and lowest near the center of WCA-2A, ranging from 1.13 to 0.27 cm y^{-1} (Reddy and others 1993). At similar locations in WCA-2A, Craft and Richardson (1993a) reported organic soil accretion ranging from 0.40 to 0.16 cm y^{-1} using ^{137}Cs activity and 0.66–0.03 cm y^{-1} with ^{210}Pb activity (Craft and Richardson 1993b). At enriched sites, organic soil accretion rates were substantially higher after the increase in P loading around 1960 than they were before this period (Craft and Richardson 1998). Organic soil accretion in unenriched areas ranges from 0.068 cm y^{-1} in the interior of WCA-2A (Scinto 1997) to 0.11–0.21 cm y^{-1} across the Everglades (Craft and Richardson 1998).

However, soil is one of the last ecosystem components to show changes after P enrichment begins, or the most difficult component to detect changes due to its high variability. No accumulation of P in soil was observed in the first 4 months after the initiation of P-loading mesocosm experiments in WCA-2A (McCormick and Scinto 1999). After 2 years of adding P to WCA-2B, Craft and others (1995) found statistically significant increased TP concentrations in the surface soils of *Cladium* (approximately 700 vs 1100 $\mu g\ g^{-1}$) and slough communities (approximately 350 vs 700 $\mu g\ g^{-1}$) only in the treatments with the highest dosing concentrations of P (4.8 vs 1.2 or 0.6 g m^{-2} y^{-1}); no differences were found in the mixed *Typha/Cladium* community. Following the eventual response of soil P concentration to enrichment (Table 2), the ability of the ecosystem to store P in the soil decreases with increased P loading. Craft and Richardson (1993a) calculated that the efficiency of P removal is lower at enriched sites (87% removal) than at unenriched areas (100% removal) of WCA-2A. Craft and Richardson (1993b) also estimated a 74% efficiency of P removal in the enriched areas of WCA-2A. This divergence between the reported rates of P removal from the same enriched areas of WCA-2A is due to the use of different P-accumulation and P-loading rates in the two Craft and Richardson (1993a, b) calculations.

Despite variation in published values, these estimates of P-removal efficiency suggest that in areas receiving water enriched in P, a front of P-enriched soils will move downstream as the ability of the ecosystem to accumulate P becomes saturated. This hypothesis is supported by studies that have found that soil P-adsorption rates decrease with high P concentrations in Everglades soil (Richardson and Vaithiyanathan 1995; Amador and others 1992). In contrast, soil total nitrogen (TN) concentrations do not vary along the same nutrient-enrichment gradients (Koch and Reddy 1992; Newman and others 1997; Craft and Richardson 1998; Vaithiyanathan and Richardson 1999), although enriched (*Typha*) areas have higher soil NH_4 concentrations (Koch and Reddy 1992; Newman and others 1997; Vaithiyanathan and Richardson 1997).

Based on an analysis of North American constructed wetlands, Richardson and others (1997) proposed the "1-gram rule"—that phosphorus loading into freshwater wetlands in excess of 1 g m^{-2} y^{-1} results in significant increases in outflow TP concentrations above baseline outputs (>40 μg L^{-1}). Near large inputs of P into WCA-2A, the threshold TP-loading rate at which water TP concentrations exceed 50 μg L^{-1} has been reported to be 0.6 g m^{-2} y^{-1} (Richardson and others 1997). It should be noted that water TP concentrations in oligotrophic areas of the Everglades are close to 10 μg L^{-1} (Table 2). Therefore, the loading rate that saturates the ecosystem's capacity to accumulate P and results in increases in outflowing water TP concentrations above background is much lower than 0.6 g m^{-2} y^{-1}. By comparison, net atmospheric P loading to the oligotrophic Everglades, and hence the bulk of total loading, is around 0.03 g m^{-2} y^{-1} and soil accumulation averages 0.09 g m^{-2} y^{-1}. Finally, such modeling of loading rates and outflowing concentrations does not consider the impact of increased P loading on the structure and function of the wetland.

The Macrophyte Component

The expansion of *Typha* has been correlated with the enrichment of soil P concentrations in WCA-2A (Urban and others 1993; Jensen and others 1995; Wu and others 1997), WCA-3B (David 1996), and throughout the entire Everglades system (Doren and others 1997). The soil TP level at which *Typha* invasion occurs varies from 650 μg g^{-1} (Wu and others 1997) to 1200 μg g^{-1} (data in Doren and others 1997). Vaithiyanathan and Richardson (1999) reported that *Typha domingensis* became common at 700–900 μg TP g^{-1} and that significant decreases in the frequency of oligotrophic species occurred at soil TP concentrations above 700 μg g^{-1}. However, shifts in plant communities may begin following small increases in P levels but then become more evident as P levels increase. *Typha domingensis* is also found in soils enriched with P compared to *Cladium* and *Eleocharis cellulosa* along a nutrient-enrichment gradient in tropical freshwater wetlands in Belize and Mexico (Rejmánkova and others 1996). Among unenriched wetlands in Belize, Rejmánkova and others (1995) measured average soil TP concentrations of about 70 μg g^{-1} in *Eleocharis cellulosa*, 140 μg g^{-1} in *Cladium*, and 180 μg g^{-1} in *Typha domingensis* marshes. Although increased soil P could cause *Typha* expansion, a shift to *Typha* from oligotrophic plant species can also increase soil P.

The spatial extent of *Typha* domination in the Everglades has increased in the recent past. Using satellite imagery of WCA-2A from 1973 to 1991, Jensen and others (1995) estimated that the total area of habitats with *Typha* increased from 2054 to 26,010 ha, whereas *Cladium* (including periphyton, open water, and slough) decreased from 41,047 to 26,504 ha. Subsequently, Rutchey and Vilchek (1999) concluded that the use of satellite imagery by Jensen and others (1995) overestimated the area occupied by *Typha* in WCA-2A but that trends in habitat shifts from 1973 to 1991 were valid. Rutchey and Vilchek (1999) concluded from analyses of aerial photographs that the total area occupied by *Typha* in WCA-2A increased from 5470 ha in 1991 to 9312 ha in 1995. In 1997, Wu and others utilized aerial imagery to estimate that *Typha* will be dominant in 50% of WCA-2A by 2003–10 if the driving forces of invasion remain unchanged. Other evidence for vegetation change in WCA-2A includes the distribution of recently (within 6–25 years) deposited macrophyte pollen in relation to soil P concentrations (Jensen and others 1999) and changes in seed banks in areas dominated by *Typha* (van der Valk and Rosburg 1997).

Everglades vegetation has responded to experimental P enrichment. Craft and others (1995) found that aboveground tissue P concentrations and biomass of emergent vegetation increased only in response to the highest P-addition treatments (4.8 g m^{-2} y^{-1} compared to 0.6 or 1.2 g m^{-2} y^{-1}) in WCA-2B; *Cladium* root biomass increased in the medium P-addition treatment. Macrophyte biomass responses were observed only in the 2nd (final) year of fertilization, and species composition did not differ among nutrient-addition treatments (Craft and others 1995), suggesting that there is a lag between an increase in P and changes in vegetation. Newman and others (1996) found that the aboveground biomass of *Typha domingensis* increased in response to elevated water TP concentration (100 vs 50 μg L^{-1}) over 2 years in ex situ mesocosms. However, *Cladium* and *Eleocharis interstincta* did not respond to increased P concentrations (Newman and others 1996). No significant differences in aboveground biomass were detected among the three species at the lower nutrient level after 2 years (Newman and others 1996). Finally, Daoust (1998) added P to *Cladium* and wet prairie habitats in ENP. In this study, *Cladium* responded to P enrichment by increasing below ground biomass in the 1st year and adding aboveground biomass in the 2nd year (Daoust 1998). In contrast, *Eleocharis* sp. in the wet prairie did not respond until the 2nd year, when it increased stem turnover rates but did not change aboveground or belowground biomass (Daoust 1998).

Changes in P loading to the Everglades are concomitant with altered hydrology. Urban and others (1993) found that increased inundation was correlated with increases in *Typha* density through time in WCA-2A, although water depth is not related to distance along the WCA-2A transects (Urban and others 1993; McCormick and others 1996) and the spatial distribution of *Typha* was related to soil TP. In addition, Newman and others (1998) concluded that the proliferation of *Typha* in two small northern Everglades remnants with elevated soil nutrients was a result of flooding and fire. However, Wu and others (1997) found that *Typha* invasion rates in WCA-2A escalated with increases in water depth only where soil TP concentrations were low. The mesocosm experiment of Newman and others (1996) demonstrates that the aboveground biomass of *Typha domingensis*, and not *Cladium* or *Eleocharis*, increases in response to increased water depth, but only at lower nutrient levels. Finally, David (1996) used an analysis of vegetation change in WCA-3A to conclude that improved hydroperiod without water quality improvements may be inadequate for Everglades restoration because it will likely result in monotypic stands of *Typha domingensis*. Therefore, it is unlikely that *Typha* expansion would occur without P enrichment.

Macrophytes in oligotrophic Everglades marshes have very low tissue P concentrations (Table 1). Previous work has identified and reviewed the low nutrient concentrations in Everglades plants compared to other wetlands (Steward and Ornes 1975; Miao and DeBusk 1999). Total P concentrations in live aboveground macrophyte tissues increase in enriched habitats (ANOVA: $n = 16$, $P < 0.001$, multiple $R^2 = 0.94$). Mean TP concentration in *Cladium* vegetation is roughly 200 and 420 $\mu g\ g^{-1}$, respectively, in sloughs and wet prairies, whereas average *Typha* tissue concentrations are much higher, around 1500 $\mu g\ g^{-1}$ (Table 2). Bedford and others (1999) report an average live tissue TP concentration of 1400 $\mu g\ g^{-1}$ ($\pm$ 200 95% CI) for temperate North American wetland plant species; average TP concentrations in oligotrophic bogs (700 $\mu g\ g^{-1}$) and poor fens (600 $\mu g\ g^{-1}$) are also greater than in *Cladium* vegetation (Table 2). Plant tissue TP concentrations are also higher in temperate peatlands than in oligotrophic Everglades—roughly 750 $\mu g\ g^{-1}$ in bogs and 1100 $\mu g\ g^{-1}$ in fens (Aerts and others 1999). Mean tissue TP concentrations are lower in the oligotrophic Everglades than along a broad nutrient gradient in Central America, where *Cladium*, *Eleocharis cellulosa*, and *Typha domingensis* TP concentrations are 1170, 1210, and 1890 $\mu g\ g^{-1}$, respectively (Rejmánkova and others 1996). However, plant tissue TP concentrations in the oligotrophic marshes of Belize average 200 $\mu g\ g^{-1}$ in *Cladium*, 500 $\mu g\ g^{-1}$ in *Eleocharis cellulosa*, and 1400 $\mu g\ g^{-1}$ in *Typha domingensis* (Rejmánkova and others 1995).

The N:P ratio is useful for evaluating nutrient economy in plant communities (Koerselman and Meuleman 1996). Koerselman and Meuleman (1996) suggested that N-limitation occurs at molar N:P ratios below 31:1, whereas plant communities are limited by P at N:P ratios above 35:1. The N:P ratio in live aboveground tissues decreases in response to enrichment (ANOVA: $n = 17$, $P < 0.001$, multiple $R^2 = 0.81$). *Cladium* in the oligotrophic Everglades has very high molar N:P ratios, ranging from 46:1 to 139:1 (Table 3) and averaging 77:1 in the literature (Table 2), suggesting extreme P limitation. *Cladium* N:P ratios in the Everglades are much greater than vegetation N:P values in peat-based temperate wetland ecosystems (Table 2) (Bedford and others 1999). The N:P ratio of aboveground and belowground *Typha* tissues increases from an enriched (average for all tissue = 15:1) to an unenriched site (average for all tissue = 33:1) along a eutrophication gradient in WCA-2A (Koch and Reddy 1992). In addition, the average N:P ratio of all *Cladium* tissues increases from 20:1 to 139:1 along the same gradient (Koch and Reddy 1992). Miao and Sklar (1998) found similar trends in *Typha* and *Cladium* N:P ratios. *Typha* may be N-limited in enriched areas, as suggested by the literature's average N:P ratio of 17:1 (Table 2). In contrast, *Cladium* N:P ratios (average = 77:1) (Table 2) are much higher than the P-limitation threshold suggested by Koerselman and Meuleman (1996), and *Cladium* shoot and root growth are responsive to the addition of P but not N (Steward and Ornes 1983). However, observations of N:P ratios of multiple species in an oligotrophic area of ENP suggest that not all species are necessarily P-limited (Daoust and Childers 1999). This assertion relies on the generality of the community-level N:P threshold for P limitation for individual species in communities, which has not been confirmed (Koerselman and Meuleman 1996). To summarize, Everglades macrophytes are in general highly limited by P in oligotrophic areas but may become N-limited in areas enriched with P. The degree of P limitation of macrophyte growth in the oligotrophic Everglades appears to be greater than in other wetland ecosystems.

The low P concentrations in the live tissue of vegetation in the oligotrophic Everglades and efficient resorption of P from senescing leaves (Richardson and others 1999) result in low P concentrations in macrophyte detritus (Davis 1991). TP concentrations in the standing dead leaves of *Cladium* are less than 100 μg g^{-1} in interior, less-enriched areas of WCA-2A (DeBusk and Reddy 1998; Qualls and Richardson 2000). The nutrient content of detritus is an important determinant of decomposition rates (Webster and Benfield 1986; Enriquez and others 1993), and the litter of Everglades macrophytes has low decomposition (Amador and Jones 1993) and P-mineralization rates (Amador and Jones 1995). Low decomposition rates in long-hydroperiod areas of the Everglades are evidenced by a thick peat layer. In the Everglades, *Cladium* has decreased P nutrient use efficiency at high soil P (Richardson and others 1999). In addition, *Typha* has higher P in aboveground (Miao and Sklar 1998) and all tissues (Koch and Reddy 1992). *Typha* in highly enriched areas (DeBusk and Reddy 1998), as well as in oligotrophic areas (Qualls and Richardson 2000), also has higher TP concentrations in standing dead leaves than *Cladium* in oligotrophic areas of the Everglades, indicating that *Typha* is less proficient at P resorption (*Sensu* Killingbeck 1996) than *Cladium*. The increase in tissue nutrient levels and a shift to species with higher tissue nutrient concentrations in response to P enrichment in the Everglades results in altered rates of detrital decomposition (Davis 1991; DeBusk and Reddy 1998; Qualls and Richardson 2000). Thus, P enrichment may initiate a positive feedback cycle following the conversion of vegetation to *Typha*.

Dead macrophyte tissue is an important sink for P in the Everglades. At intermediate to highly enriched water-column P concentrations, P is immobilized in macrophyte detritus and P content increases during decomposition, whereas the P content of detritus does not change at low water-column P concentrations (Davis 1991; Qualls and Richardson 2000). The P immobilization rate for macrophyte detritus (0.07 g m^{-2} y^{-1}) (Davis 1991) is similar to estimates of total soil P load in unenriched areas (Table 2). However, the detritus immobilization rate of P in enriched areas (1.42 g m^{-2} y^{-1}) (Davis 1991) is greater than total soil loading estimates (Table 2). This difference in macrophyte detrital immobilization rates compared to total soil loading rates in enriched areas (Table 4) suggests that some detrital P is eventually exported downstream to less impacted marshes instead of accreted to soil following P enrichment.

The Consumer Component

Due in part to the oligotrophy of the ecosystem, the oligotrophic Everglades has very low fish and aquatic invertebrate biomass relative to other freshwater wetlands (Turner and others 1999). The Everglades faunal community is very responsive to P enrichment, suggesting food web limitations by P. Rader and Richardson (1992, 1994) observed an increase in the number of species, including species not found in oligotrophic marshes, and an increase in the density of most invertebrate and small fish species in sweep nets and soil cores from nutrient-enriched sloughs of WCA-2A. However, they (1994) found that the density of the freshwater shrimp (*Palaemonetes paludosus*) decreased drastically in P-enriched sloughs, from 54.5 to 1.2 m^{-3}.

Furthermore, in a comparison of litterbag colonization in eutrophic (*Typha*) and nonimpacted areas (*Cladium*) of WCA-2A, Urban (unpublished in Davis 1994) found a near absence of snails, an absence of isopods, a doubling of annelids, and in general fewer taxa in eutrophic sites. There is no difference in total macroinvertebrate standing crop between *Typha* communities and *Cladium* or wet prairie (nonenriched) communities in WCA-2A and ENP, although the total fish biomass is greater in enriched areas (Turner and others 1999). Turner and others (1999) hypothesized that a trophic cascade was operating and that the fish (primarily carnivorous) were reducing the invertebrate biomass in the nutrient-enriched areas. Finally, Richardson and others (1999) documented increased herbivory of *Cladium* leaves in P-enriched areas compared to less enriched areas of WCA-2A. This increase in herbivory occurs in conjunction with a decrease in herbivore-deterring phenolic secondary compounds and an increase in TP concentration in *Cladium* leaves (Richardson and others 1999).

There are no published data on P concentrations in Everglades consumers. A preliminary estimate of average TP concentrations is 38,500 μg g^{-1} (dry mass) in three dominant fish species of the Everglades (C. Stevenson unpublished). In contrast, mean TP concentrations in fish from Laurentian oligotrophic lakes is 14,900 μg g^{-1} (Sterner and George 2000). A review of whole-fish P concentrations by Sterner and George (2000) indicated that typical TP concentrations in fish range from roughly 20,000 to 40,000 μg g^{-1}. These preliminary data suggest that fish in the Everglades may have high TP concentrations relative to those in other ecosystems. The fact that fish in extremely P-limited Everglades marshes may potentially be sequestering, or bioaccumulating, more P than fish in other ecosystems is particularly intriguing and warrants further investigation.

Palaemonetes paludosus is a dominant invertebrate (61% of total invertebrate biomass) (Turner and others 1999) and an important part of the Everglades food web (Kushlan and Kushlan 1980); fish consume large numbers of them (Hunt 1952). The diet of *P. paludosus* comes primarily from periphyton mats (Hunt 1952) and from a periphyton/macrophyte detritus mix (Browder and others 1994). Therefore, the loss of the calcareous periphyton–*Utricularia* assemblage and the concurrent decrease in *P. paludosus* density in nutrient-enriched areas should also affect higher trophic levels. An interpretation of data presented in Rader and Richardson (1994), and similar to the trophic evaluation of Rader (1994), indicates that the proportion of individuals that were detritivorous increased from about 33% in unenriched areas to 42% in enriched areas, whereas the proportion that was herbivorous decreased from about 44% to 25% with nutrient enrichment. Therefore, a shift from a grazer-based to a detritivore-based consumer community has occurred in enriched areas of WCA-2A. Finally, the shift in periphyton composition toward less palatable species and an alteration in the structure of the periphyton mat may both decrease the food value of periphyton and the habitat value of the mat, resulting in changes to primary and secondary productivity in the Everglades (Browder and others 1994). These cascading effects of periphyton loss on ecosystem dynamics need further study.

The number of nesting wading birds in the southern and central Everglades is thought to have declined 90% from the period of early drainage (around the 1930s) to the 1980s in response to altered hydrology (Ogden 1994). Historically, P deposition by wading birds was locally important at colonial nesting sites on tree islands. This relocation and concentration of P has become less important as the number of wading birds nesting in the Everglades has declined; P deposition by wading birds at nesting sites may have been as high as 331 g m^{-2} y^{-1} in 1934, but it was only 0.90 g m^{-2} y^{-1} in 1987 (Frederick and Powell 1994). This historic estimate of P deposition by wading birds is four orders of magnitude greater than atmospheric deposition rates (approximately 0.03 g m^{-2} y^{-1}), whereas the recent loading rate is only 30 times greater than atmospheric sources of P. However, avian P deposition has been very localized because of the patchy distribution of colonial nesting sites in the landscape. In addition to declines in the magnitude of deposition, the spatial location of most P deposition by wading birds has shifted from the mangrove zone at the estuarine fringe of Florida Bay to the water conservation areas, especially WCA-3, due to the shift in nesting sites (Frederick and Powell 1994). The large decline in the rate of P deposition and the different locations of these birds has undoubtedly affected the cycling of P at both the landscape and the local scales.

Research Gaps

Our review of the literature, in the context of other freshwater wetland ecosystems, revealed several significant gaps in our understanding of P biogeochemistry and the effects of P enrichment on the Everglades and other oligotrophic ecosystems. First, most research on P in the Everglades has focused on WCA-2A (Table 1), the most enriched hydrologic unit of the Everglades. Thus, there is a dearth of data on P in the other WCAs and ENP. Furthermore, the way in which periphyton facilitates the removal of P by adsorption to $CaCO_3$ or precipitation with Ca has not been adequately quantified. Although gradients in soil TP concentrations along nutrient and macrophyte habitat gradients are well documented, the order in which ecosystem components respond to and are changed by P additions is not clear. Nor have consumer trophic dynamics and P relations been adequately studied. In addition, the role of the flocculent detrital layer in P biogeochemistry needs further evaluation. P cycling in different ecosystem components needs further study. Finally, more controlled experimental additions of P should be done to separate the effects of concurrent N and P additions (such as discharge from EAA) from P fertilization alone, so that we can assess the effects of low levels of P enrichment and document the events that occur when an Everglades marsh is first exposed to P additions. This research will help to alleviate controversy by identifying TP concentrations in water entering the Everglades that can "prevent an imbalance in the natural populations of aquatic flora or fauna" (Everglades Forever Act). Filling in these gaps in our understanding of P will improve efforts to manage and restore the Everglades.

Ecosystem Functional Analogies

There are several similarities between the Everglades and other P-limited wetland ecosystems, including their hydrogeomorphology, the microbial dominance of P cycling, and their soils. For example, the wetlands of the Yucatan Peninsula in Belize and Mexico have a flat limestone bedrock and a climate similar to the Everglades (Rejmánkova and others 1995) and an analogous ecosystem structure and function. Freshwater wetlands with a plant community structure similar to the Everglades also occur on the Zapata Peninsula of Cuba, an area with similar hydrology and flat karstic limestone bedrock (Borhidi and others 1983). Phosphorus is also very limiting in spring-fed calcareous wetlands in England (Boyer and Wheeler 1989). Wetlands receiving water from a carbonate-dominated landscape are likely to be P-limited due to the biologically mediated or abiotic removal of P by precipitation with Ca or adsorption to $CaCO_3$ (see, for example, Boyer and Wheeler 1989).

Hydrology may also influence P limitation in wetlands. The large flat bedrock of the Everglades results in a hydrology that is primarily driven by precipitation; similarly, ombrotrophic temperate bogs have lower leaf P concentrations than temperate fens in which the hydrology is controlled by precipitation, surface water, and groundwater (Aerts and others 1999). In contrast, leaf N concentrations do not differ among fens and bogs (Aerts and others 1999). In other words, the conservative nature of P cycling necessitates the presence of an external supply of P. A low level of allochthonous P inputs to ecosystems will likely result in P limitation.

Another characteristic that the Everglades shares with other P-limited wetlands is the microbial control of P uptake and cycling. In a Michigan fen, Richardson and Marshall (1986) demonstrated that microbes control initial P uptake and cycling in surface waters. In addition, microbial processes strongly influence the supply of available P in P-limited pocosin wetlands in North Carolina (Walbridge 1991). As in the Everglades, periphyton mats are also abundant in the P-limited freshwater wetlands of the Yucatan Peninsula (Rejmánkova and other 1995). Periphyton has also been shown to dominate P uptake and cycling in the oligotrophic littoral zone of a coastal lake (Howard-Williams and Allanson 1981). In arctic wetlands, soil microbes immobilize P after fertilization and control the availability of P to plants (Jonasson and others 1996). When microbial populations crash in the winter, P is released in arctic wetlands (Chapin and others 1978). In the subtropical Everglades, there are no prolonged freezes to lyse microbial cells; therefore, microbes are likely to be strong competitors for P throughout the year.

However, it should be noted that the microbial control of P cycling in the Everglades and other P-limited wetlands could be a response to ecosystem P limitation rather than the cause of P limitation. Microbes may dominate nutrient cycling in oligotrophic wetlands because their high surface area–to-volume ratio makes them more competitive assimilators of available P. The importance of periphyton to the primary production and P cycling of many areas of the Everglades may be due to its competitive uptake of P and a position in the water column that allows it to capture scarce P inputs.

Finally, soils with a high organic content are also more likely to be limited by P. Peatlands, including bogs and fens, are often P-limited, but marshes with mineral-rich soils are generally N-limited (Bedford and others 1999). N:P ratios in soils and the live tissues of plants in temperate wetlands are, on average, significantly higher in peat than in mineral soils (Bedford and others 1999). This is probably due to the low mineral content of organic soils and the resulting lack of imported P from minerals. Soils low in P, as well as N, are also more likely to accumulate organic matter in the soil due to their low decomposition rates. In general, wetlands are more likely to be P-limited when inputs of P are restricted.

CONCLUSIONS

The oligotrophic Everglades is extremely P-limited due to a suite of factors. This sensitivity to P enrichment is ultimately due to the low-relief limestone bedrock and large spatial extent of the Everglades, as well as the conservative nature of P cycling. Other wetland ecosystems share some of the same causes of P limitation, but we found none that included all of these factors. Very little exogenous P is available to the Everglades from mineral rock weathering or allochthonous sediments, and water flow rates are low. Thus, the primary natural source of P to the oligotrophic Everglades is atmospheric deposition, which supplies low levels of P. In addition, high Ca concentrations and pH remove P from the water column by the precipitation of Ca-P minerals and the adsorption of PO_4 onto $CaCO_3$. As a consequence of the low supply and availability of P to the ecosystem, water-column TP concentrations in oligotrophic areas average about 10 $\mu g\ L^{-1}$. Periphyton is very abundant compared to other wetlands and rapidly removes available P from the water column, while *Cladium* is able to grow at low P levels. The biomass of fish and aquatic invertebrates is also smaller than in other wetlands. In addition, the soil profile is oxidized to slightly reduced, even in peat soils. Finally, the uniqueness of the Everglades is evident in the very low P concentrations in plants and very high N:P ratios in its soils and plants, as compared to other wetlands (see Table 2). Therefore, the P biogeochemistry of the Everglades is likely unique.

Phosphorus enrichment modifies the structure and function of the Everglades ecosystem. Increased P loading increases the concentration of P in most components (water, periphyton, soil, and macrophytes), alters biogeochemical processes, eliminates calcareous periphyton mats, deoxygenates soils, stimulates the invasion of *Typha*, and increases the abundance of fish. Some of these changes may be beneficial, such as the potential benefit to wading birds from increased fish abundance. However, at the same time, fish may be less available to wading birds in areas where the vegetation structure has been altered by thick stands of *Typha*. In general, P enrichment leads to a distinctly different ecosystem than the historic oligotrophic Everglades.

We sought to identify the causes and indications of P limitation in wetlands. The functional similarities between the Everglades and other P-limited wetlands include their hydrogeomorphology, the microbial dominance of P cycling, and their soils. Not surprisingly, wetlands in general tend to be limited by P when supply rates are low or removal rates are high. Two common causes of low P supply to wetlands are a hydrology that is predominantly controlled by precipitation and their location in a watershed with low content or availability of mineral-bound P in bedrock and soils. Finally, common mechanisms for P removal in wetlands include location in a calcareous landscape and microbial dominance of P cycling. In a limestone-dominated watershed, P availability can be limited by $CaCO_3$ adsorption or Ca-P precipitation. Microbes often dominate the cycling of P in P-limited wetland ecosystems; however, this may be a response to, rather than a cause of, limitation.

Our review of Everglades P cycling and our analysis of this system in the context of other nutrient-poor freshwater wetland ecosystems has led us to consider the relationship between oligotrophy and P limitation in a more general way. To that end, we hypothesize that most oligotrophic freshwater wetland ecosystems are P-limited. The biota of oligotrophic ecosystems can offset N limitation by the fixation of atmospheric N_2 (Redfield 1958; Schindler 1977; Howarth and others 1988; Short and others 1990; Vitousek and Howarth 1991; Levine and Schindler 1992), whereas P cycling is conservative. Similarly, oligotrophic freshwater lakes are predominantly limited by P (Downing and McCauley 1992) and there is a trend toward increasing N limitation with eutrophication (Smith 1998). Therefore, N-limited oligotrophic wetlands should be rare, and the status of nutrient limitation in wetlands is likely determined by P loading. We hope that these hypotheses on the general causes of P limitation within and among wetland ecosystems will stimulate more research and synthesis on the nature of P biogeochemistry.

ACKNOWLEDGMENTS

We thank Joy Zedler and the *Ecosystems* editors for inviting this review. Many colleagues from the South Florida Wetland Ecosystems Lab, Southeast Environmental Research Center (SERC), and Department of Biological Sciences at Florida International University provided valuable insights on phosphorus in the Everglades and made useful comments on the manuscript. This review was made possible through funding to the Southeast Environmental Research Center from the United States Department of the Interior, Everglades National Park, Arthur R. Marshall Loxahatchee National Wildlife Refuge, and the South Florida Water Management District. This is SERC publication series contribution no. 144.

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Appendix. Survey of Literature Included in the Meta-analysis

No.	Study	Soil Depth	Date	Notes on Interpretation and Usage
1	Steward and Ornes 1975	NR	1971	
2	Davis 1991	n/a	1975–80	Only live aboveground tissues included. *Cladium* = lowest SRP, *Typha* = highest SRP.
3	Walker 1991	n/a	1977–89	Median concentration.
4	Koch and Reddy 1992	5 cm	1990	*Typha/Cladium* reported as range. Macrophyte data is an average of leaves and roots.
5	Amador and Jones 1993	10 cm	NR	*Typha* = "high." *Cladium* = "low and intermediate."
6	Craft and Richardson 1993a	1964 or 10 cm	1989	Soil sampled down to peak ^{137}Cs depth (accumulation since 1964), or if no accumulation, 10 cm.
7	Craft and Richardson 1993b	1964	1990	Soil sampled down to peak ^{137}Cs depth (1964). *Typha* = St. 1, *Typha/Cladium* = 2–3, *Cladium* = 4–6.
8	Grimshaw and others 1993	n/a	1978–79	*Typha* = B1–2, *Cladium* and slough/wet prairie = B5–10.
9	Reddy and others 1993	1964	1990	Soil TP load and N:P data sampled down to peak ^{137}Cs depth (1964).
10	Urban and others 1993	n/a	1986–91	All sites classified as *Typha/Cladium*.
11	Coale and others 1994	n/a	1988–90	Only data from typical (fast) drainage practice included.
12	DeBusk and others 1994	10 cm	1990	
13	Diaz and others 1994	n/a	NR	
14	Vymazal and others 1994	n/a	1990	Control plots only.
15	Craft and others 1995	30 cm	1990	Control plots only. Macrophyte aboveground biomass is an average weighted by species biomass. Slough macrophyte average includes *Utricularia* with associated periphyton. Soil depth = 15 cm in slough/wet prairie.
16	Vymazal and Richardson 1995	n/a	1991–92	Range is for detached and attached periphyton, through time.
17	McCormick and O'Dell 1996	n/a	1995	Water data presented in #20. E1, E2, F2 = *Typha*. E3, F3, E4, F4 = *Typha/Cladium*. Other sites = *Cladium* and slough/wet prairie.
18	McCormick and others 1996	n/a	1994–95	Site classification identical to #19.
19	Doren and others 1997	25 cm	NR	*Typha/Cladium* = both *Typha* and *Cladium* have more than 25% frequency.
20	Grimshaw and others 1997	n/a	1994–95	"Unenriched slough" in Table 1 described as slough and *Cladium* = slough/wet prairie.
21	Newman and others 1997	10 cm	1991	Interior plots = *Cladium* and slough/wet prairie
22	Scinto 1997	9 cm	1993–95	Soil TP averaged over surface 9 cm.
23	Vaithiyanathan and Richardson 1997	2.5 cm	1993–95	Sites less than 2 km downstream = *Typha*; sites between 2 and 6 km = *Typha/Cladium*; sites more than 6 km = *Cladium*.
24	Craft and Richardson 1998	n/a	NR	Accretion data includes both ^{137}Cs (1964) and ^{210}Pb estimates (1962).
25	Miao and Sklar 1998	NR	1994–95	*Typha/Cladium* reported as range. Macrophyte data are an average of leaf, root, shoot base, and rhizome, weighted by relative biomass.
26	Vaithiyanathan and Richardson 1998	5 cm	1993–96	Range in macrophyte concentration is the range of species means (*Nymphaea* = average of petiole and leaf).
27	Daoust and Childers 1999	n/a	1995–96	*Cladium* datum is an average of wet and dry seasons. Average was weighted by species-relative biomass.
28	Jensen and others 1999	5 cm	1996	*Typha/Cladium* = both species denser than "nearby" or "sparse."
29	Richardson and others 1999	n/a	1990–96	Only *Cladium* data published for *Typha/Cladium* habitat. Soil data already published, not included.
30	Rudnick and others 1999	n/a	1984–95	Flow-weighted average concentration.
31	Turner and others 1999	10 cm	1996	WCA-2A soils data not used, reported in #12.
32	Vaithiyanathan and Richardson 1999	5 cm	1993–95	*Typha* = P-enrichment category 4–5. *Typha/Cladium* = 1–3, *Cladium* and slough/wet prairie = 0.

NR, not reported; n/a, not applicable