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# Marsh vegetation patterns and soil phosphorus gradients in the Everglades ecosystem

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### Abstract

In order to test the hypothesis that phosphorous enrichment is modifying Everglades marsh community composition, we sampled vegetation and soil phosphorus concentrations along four transects in areas representative of varying environmental conditions within the Everglades region. Each transect originated at or near a canal flow control structure and extended towards the center of the marsh because the canal flow structures were seen as potential nutrient input sources from 'upstream' agricultural areas. Cladium jamaicense, wet prairie communities and Typha spp. dominated sites were sampled along each transect. Correlations for between-species occurrences and between-species frequencies and phosphorus concentrations with distance from nutrient source were determined. Within-transect effects and between-transect effects from north to south across the Everglades region were compared. In all cases phosphorus concentrations and presence of Typha domingensis showed a negative relationship to distance from nutrient source, while the presence of *Cladium* and other natural communities showed a positive one. The pattern in marsh community composition and soil phosphorus content seen in the four marsh transects indicates that a strong relationship exists between Typha expansion, decline of Cladium marsh and wet prairie communities and rising phosphorus concentrations, and that these trends are correlated with nutrient input sources associated with agricultural runoff.

Keywords: Macrophytes; Community composition; Eutrophication; Freshwater marsh

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## 1. Introduction

Much of the interior of southern peninsular Florida extending southward from Lake Okeechobee consists of freshwater marshes characterized by peat or marl soils and herbaceous vegetation inundated continuously for periods ranging from 3 to 12 months per year (Fig. 1) (Kushlan, 1990; Fennema et al., 1994). The original Everglades exceeded 10 000 km<sup>2</sup> in area and the predominant vegetation cover consisted of freshwater marshes dominated by *Cladium jamaicense* Crantz (sawgrass) and a host of associated species (Kushlan, 1990). Historically, rainfall and subsequent floodwaters, much of it originating as overflow from Lake Okeechobee and augmented by rainfall throughout the Kissimmee and Everglades basins, passed through a continuous expanse



Fig. 1. Map of southern Florida with general outline of the Everglades Agricultural Areas, the Conservation Areas, Everglades National Park and the Central and Southern Florida Water Management System. Map also shows locations of transects and sampling distances in kilometers, WCA11 (0-9km and 26-30km); WCA2A (0-8km); WCA3A (0-5km); ENP (0-6km).

of freshwater wetlands extending to the tidal estuaries of Florida Bay. Flowing over a shallow limestone plateau formed under marine conditions, the waters are low in plant nutrients (particularly phosphorus), giving rise to a distinct assemblage of paludal plant communities adapted to these oligotrophic conditions (Kushlan, 1990; Davis, 1991; and Gunderson, 1994).

Phosphorus concentrations in Everglades waters believed to be free of pollution average  $3.0-5.0 \,\mu g \, l^{-1}$  or lower as soluble reactive phosphorus (Boyd and Hess, 1970; Koch and Reddy, 1992) and less than  $100.0 \,\mu g l^{-1}$  nitrate-nitrogen, levels far lower than eutrophic marsh waters (Boyd and Hess, 1970; Walker, 1991). High N/P ratios, probably a result of microbial N<sub>2</sub> fixation, indicate that phosphorus may be limiting to plant growth in the Everglades region (Koch and Reddy, 1992). Since the 1920s, however, in order to encourage agricultural and urban development and limit flooding, an extensive system of canals, pumping stations and levees has been constructed to impound water within areas of sawgrass marsh now managed as water conservation areas (Fig. 1). The water management system, incorporating about 2400 km of canals and levees, has profoundly altered the natural water balance of the region. In addition, extensive development of agricultural land between Lake Okeechobee and undrained marshes to the south and east has enriched drainage waters with nutrients and other contaminants that enter the marshes. The effects of the increased nutrients on the structure and function of the Everglades marshes have been a major question under investigation over the past decade.

Experimental studies in C. jamaicense Crantz (sawgrass) marshes, have shown, as in many wetlands, that the addition of nutrients, particularly phosphorus, to marsh waters, shifts plant community composition favoring species such as Typha latifolia L. and, Typha domingensis Pers., which are relatively unimportant in native environments (Kushlan, 1990; Wood and Tanner, 1990; Gunderson, 1994). Recently however, Typha spp. (cattail) has spread into and replaced Cladium and spikerush-wet prairie marsh in the northern Everglades (Craighead, 1971), particularly near canals and water control structures, where phosphorus concentrations in soil and water have increased (Kushlan, 1990; Davis, 1991). There appears to be no historical precedent for the presence of Typha in high densities over areas of thousands of hectares (Wood and Tanner, 1990) as now occurs in the northern Everglades. Thus analysis of Everglades peat deposits reveals no evidence of Typha peat although the presence of Typha pollen suggests its role as a colonizing species in certain areas (Gleason and Stone, 1994). In contrast Cladium and white water lily (Nymphea odorata) peats have been a major freshwater component of Everglades histosols for approximately 4000 years (McDowell et al., 1969). Contrasting with Typha, Cladium growth is not stimulated by additions of ortho-phosphate at concentrations greater than twice natural background levels and has a far more limited capacity to retain nitrogen and phosphorus (Steward and Ornes, 1975a, 1983; Davis, 1991, 1994). These results suggest that *Cladium* is neither adapted to higher concentrations of phosphorus nor able to compete with nutrient-responsive species in the presence of phosphorus enrichment. In contrast, the increased importance of Typha in the phosphorus-enriched areas is consistent with its apparent ability to grow in the presence of higher phosphorus concentrations. Based on observation and preliminary data we developed a hypothesis that phosphorous enrichment is a major factor in the increase of *Typha* in the northern Everglades. The present work was conducted to provide information essential for testing the hypothesis—marsh species distributions and composition are directly related to increases in soil phosphorus concentrations due to nutrient source runoff. Consequently, the purpose of this study was to quantitatively describe compositional change in Everglades marsh communities and relate the change to soil phosphorus concentrations found over areas varying in nutrient enrichment.

# 2. Methods

#### 2.1. Study area

The study area is located within the greater Shark River Slough basin, the major drainage-way within the Everglades region south of Lake Okeechobee (Fig. 1). The slough can be described as a broad, shallow river approximately 200 km long and 40–60 km wide that conveys water from wetlands north of Everglades National Park, through the Park, to the adjacent Gulf of Mexico. Water depths within the slough vary seasonally and annually depending on rainfall and on water delivery schedules determined by the South Florida Water Management District. Where depths exceed 50 cm and inundation period exceeds 6–10 months, *Cladium* is partially or totally replaced by wet prairie marsh (Craighead, 1971; Kushlan, 1990; Gunderson, 1994) dominated by *Eleocharis* spp. (spikerush), *Rhynchospora* spp. (beakrush), with increasing importance of *Sagittaria* spp., *Utricularia* spp., *Nymphaea odorata* Ait., and *Panicum hemitomon* Schultes, as hydroperiod lengthens (Craighead, 1971; Gunderson, 1994). In most sites the two principal community types are clearly distinguishable by visual inspection. Everglades soil types and their associations are well described by Davis (1946), Jones (1948), and Gleason and Stone (1994).

# 2.2. Transect sampling

Vegetation and soil phosphorus concentrations were sampled along four transects varying from 6 to 26 km in length and established in separate fresh-water marsh areas representative of varying environmental conditions within the region. All transects originated at a canal or flow structure and extended away from the flow structures, towards the center of the marsh areas (Fig. 2). Transect CA11 within Loxahatchee National Wildlife Refuge (Water Conservation Area 1), a tract of 56 203 ha, consisted of two segments, one extending 4 km westward from structure S-6 and the second 9 km eastward of the most western extension of this transect at the L-40 canal. Transect CA2A, within Water Conservation Area 2A, an area of 41 895 ha, extended approximately 8 km southwesterly of the S-10C structure, while Transect CA3A, within Water Conservation Area 3A, which extends over 199 440 ha, extended due north of the S-12C structure and was 5 km long. Transect ENP located within Everglades National Park, an area covering 609 688 ha, extended 6 km due south from the S12C gate structure on the C-4 canal into the marshes of Shark River Slough. Transect lengths were chosen in each area to ensure that each transect originated at flow structures or major canals directing



Fig. 2. Dendrogram of Transect CA11 delineating among- and within-group species similarity along the transect with distance from the 0.0 km point and total soil P ( $\mu$ gg<sup>-1</sup>) at each sampling location. Sites S1 through S19 were sampled along the 9 km transect segment and S20 through S27 along the 4 km transect segment.

runoff from 'upstream' agricultural areas where suspected nutrient-induced vegetation changes were obvious and extended well into natural communities without apparent nutrient-induced changes. Transects CA11 and ENP crossed areas that burned in 1989, while transects CA2A and CA3A had not burned for many years. Both cover and density of vegetation were differentially affected by fire. Therefore species presence data were collected rather than cover estimates, since fire reduced cover in some areas of the transects and not others, but had not eliminated existing species (Streng et al., 1993). Species frequency has proved a reliable surrogate for species abundance in species-poor areas, such as aquatic and marsh plant communities (Mueller-Dombois and Ellenberg, 1974) and is especially valuable in delineating species–environment relationships (Green, 1979).

Sample sites were accessed primarily by helicopter. Aircraft speed, held constant after departing from the 0.0 km point, was used to sight landmark features corresponding with the predetermined distances between sampling points along the transect(s). At each sampling point, the two principal vegetation communities (*Cladium* and wet prairie) nearest the identified landmark were sampled. Sampling intervals and locations were chosen independent of overall community locations or patterns in order to provide unbiased sample locations. Vegetation was sampled at approximately 0.5 km or 1 km intervals along the transects, along a 10 m line parallel to each transect. A 1 m<sup>2</sup> frame divided into four 0.25 m<sup>2</sup> sample quadrants was placed at three locations along one side and two locations along the other side of the 10 m line, so frame locations on opposite sides of the line were not adjacent to one another. Presence or absence of each species was recorded within each quadrant. Thus, a total of 20 sample quadrants totalling 5 m<sup>2</sup>

in area were sampled at each nutrient sampling point, exceeding the  $2.5 \text{ m}^2$  area suggested by Porter (1967) as adequate for sampling prairies in southern Florida.

*Cladium* and wet prairie communities were sampled separately wherever present at a 10 m transect site. But where these two community types could not be distinguished, either because only one 'type' was present, or they were already altered by *Typha* invasion, the prevalent vegetation type at the sampling station was sampled and the data for the two samples were combined and considered as one sample for that particular location. These were called combined-sites. For all plots, frequencies were calculated as the number of plots in which the species occurred divided by the total number of sample plots times 100.

Spearman Rank correlation between species frequencies, and soil phosphorus concentrations, and between species frequencies and distance to nearest water flow structure were determined using STSC Statgraphics ver. 5.0. Spearman Rank correlation was used to generate the matrices. Species lists also were created from each transect. Frequency data for each transect were analyzed using the dendrogram cluster analyses program, MVSP ver. 1.3 (Multivariate Statistical Package). Pearson product moment correlation, using the average linkage cluster–unweighted pair group method, was used to generate the similarity matrix for input into the cluster program.

## 2.3. Soil total phosphorus sampling

Nutrient sampling locations coincided with the vegetation sample locations along each transect and within each vegetation community type. Soil samples for total phosphorus content (TP) were collected along all transects within 1-2 weeks of vegetation sampling. Sample locations were identical to those described above. Cladium and wet prairie communities were sampled separately when present. In areas where combined community samples were made, twice the number of samples was collected. Samples were collected using a polyvinylchloride (PVC) tube 5 cm in internal diameter by 80 cm long with one end sharpened. Soil cores were obtained by manually forcing the tubes into the soil to a depth of 25 cm. Triplicate cores were taken at each location (six cores per station), and the top 10 cm screened for roots and large debris. Individual samples were then mixed until homogenous, dried at 70°C for 48 h, ground to a fine powder in a Wiley Mill and stored in a desiccating cabinet. Samples from all transects were also collected by hand from each location (four composite samples each station). The TP content did not differ significantly between collection techniques, therefore, only samples collected by hand were used. Soil TP was measured using the ashing/acid hydrolysis method described by Solorzano and Sharp (1980). The resulting soluble reactive PO4 (SRP) was measured as phosphoantimonylamolybdenum complex within an absorbance maximum at 880 nm using an RFA-300 rapid flow analyzer (Alpkem Corp.). All samples were ashed, hydrolyzed in duplicate and analyzed for SRP in triplicate. Values were expressed as  $\mu g P g^{-1}$  soil dry weight. Analytical precision was better than 2% and the detection limit was  $< 10 \,\mu g \, g^{-1}$  soil. Standards of NBS orchard leaves and analytical standards of KH<sub>2</sub>PO<sub>4</sub> were run with each batch of soil samples. Values for each sample represent the mean for each sampling location.

# 3. Results

## 3.1. CAll transect

Three species assemblages along the transect are delineated by dendrogram (Fig. 2). The Group 1 assemblage, dominated by *Typha*, was found nearest the flow structures where soil phosphorus concentrations ranged from 1460 to 2380  $\mu$ g g<sup>-1</sup> (Fig. 2). Exotic weedy species, such as pigweed (*Amaranthus australis* (Gray) Sauer), also were established near flow structures. The Group 2 assemblage consisted mainly of *Cladium* marsh with the occasional presence of other native species. Total phosphorus concentrations ranged from 480 to 1180  $\mu$ g g<sup>-1</sup> of soil throughout the *Cladium*-dominated marshes. Group 2 can be subdivided at approximately the 40% within-group similarity into a *Cladium* assemblage with an important spikerush component. Where spikerush was more important TP fell within 480 to 630  $\mu$ g g<sup>-1</sup>. Group 3, a spikerush–wet prairie assemblage, was generally dominated either by beakrush, spikerush or white water lily. This assemblage, typically found in somewhat deeper waters than *Cladium* marsh, also was associated with lower phosphorus levels, in this case between 440 and 640  $\mu$ g g<sup>-1</sup> of soil.

Analysis of TP across the entire 30 km length of the CA11 transect reveals a strong association of P levels and proximity to water management structures (Fig. 3). Total soil phosphorus declined nearly six-fold within 4 km of the western flow structure and by



CA11 TP/CATTAIL/SAWGRASS/RHYNC

Fig. 3. Histogram comparing presence of *Typha*, *Cladium* and *Rhyncospora* with distance and total P concentrations along Transect CA11.

Table 1

Correlation matrix comparing sawgrass marsh/combined sites, and spikerush marsh and combined sites along Transect CA11

a. Sawgrass marsh and combined sites

	Sawgrass	Total P	Cattail	· · · · · · · · ·
Total P	- 0.79			
	(14)			
	0.004			
Cattail	- 1.0	0.79		
	(14)	(14)		
	0.0	0.004		
Distance	0.73	- 0.87	- 0.73	
	(14)	(14)	(14)	
	0.009	0.002	0.009	

b. Spikerush marsh and combined sites

	Total P	Cattail	Spikerush	Eleocharis	
Cattail	0.74				
	(17)				
	0.003				
Rush	-0.57	- 0.65			
	(17)	(17)			
	0.02	0.01			
Eleocharis	-0.61	- 0.86	0.53		
	(17)	(17)	(17)		
	0.01	0.0006	0.03		
Distance	- 0.65	- 0.69	0.73	0.51	
	(17)	(17)	(17)	(17)	
	0.01	0.005	0.003	0.04	

Figures given are: Coefficient; sample size (given in paretheses); significance level.

more than half within 2 km of the eastern flow structure. Fig. 3 represents both combined-sites and *Cladium* marsh sample sites. The high frequency of *Cladium* and spikerush where total soil phosphorus concentration falls below approximately 500–1000  $\mu$ gg<sup>-1</sup> and their replacement by *Typha* at higher phosphorus concentrations is apparent on both sides of the Conservation Area. *Typha* frequency was negatively correlated (P < 0.05) with frequency of the major indigenous marsh species and with distance from flow structure and positively correlated with soil phosphorus levels (Table 1). In contrast, *Cladium*, beakrush and spikerush distributions were positively correlated at statistically significant levels with each other and with distance from flow structures, and negatively correlated with soil phosphorus levels (Table 1).

# 3.2. CA2A transect

Three assemblages were delineated, a *Cladium*-dominated marsh, a spikerush/wet prairie marsh, typified by *Eleocharis* spp. and *Nymphaea odorata* and a *Typha*-



Fig. 4. Dendrogram of Transect CA2A delineating among- and within-group species similarity along the transect with distance from the 0.0km point and total soil P ( $\mu gg^{-1}$ ) at each sampling location.

dominated 'weedy' community (Fig. 4). A. australis and Rumex crispus were important secondary species found in the Typha assemblages. Although some intermixture of Cladium and Typha communities occurred between 2 and 6km from the transect origin at the canal (Fig. 5), the highest TP levels (2060–1790  $\mu$ g g<sup>-1</sup> of soil) were associated with Typha stands. The lowest TP (510–840  $\mu$ g g<sup>-1</sup>) areas were occupied by Cladium and open marsh communities (Fig. 5). The correlations between distance from canal structure and TP was highly negative (P < 0.01), as was the relationship between Cladium and TP (P < 0.05) (Table 2). Despite the intermixing of Typha and Cladium between 2 and 6km from the canal structures, the distribution of the two species were negatively correlated (r = -0.84; P < 0.05) over the whole extent of the transect.

## 3.3. CA3A transect

Like the previously discussed transects, vegetation patterns along transect CA3A differentiated into three associations: *Cladium*-dominated, *Typha*-dominated and open



CA2A **TOTAL P/CATTAIL/SAWGRASS** 

Fig. 5. Histogram comparing presence of Typha and Cladium with distance from nutrient source and total P concentrations along Transect CA2A.

marsh communities dominated by Eleocharis spp., with Utricularia spp., Nymphaea odorata (Fig. 6). Total soil phosphorus concentrations along CA3A were lower than along the transects in the other conservation areas, peaking at  $1210 \mu g g^{-1}$  adjacent to the canal (Figs. 6 and 7). Here Typha occurred in every plot whereas Cladium and periphyton were absent. At 0.5 km from the canal structure and beyond, soil TP declined to  $350-630 \mu g g^{-1}$ . No Typha occurred at any of the sites between 0.5 and 5.0 km distance but Cladium occurred in every plot (Fig. 7).

The smaller range in TP, and the intermixing of the Cladium and open marshes resulted in relatively low correlations between variables (Table 3). Cladium and Typha

Correlation matrix comparing sawgrass marsh/combined sites along Transect CA2A				
	Distance	Total P	Sawgrass	
Total P	- 0.97			
	(9)			
	0.006			
Sawgrass	0.84	- 0.84		
	(9)	(9)		
	0.02	0.02		
Cattail	- 0.84	0.79	-0.84	
	(9)	(9)	(9)	
	0.02	0.02	0.02	

Figures given are: Coefficient; sample size (given in parentheses); significance level.

Table 2



Fig. 6. Dendrogram of Transect CA3A delineating among- and within-group species similarity along the transect with distance from the 0.0km point and total soil P ( $\mu$ gg<sup>-1</sup>) at each sampling location.

(r = -0.76), Cladium and TP (r = -0.53) and Typha and TP (r = 0.61) trends for example, correlated as expected but the coefficients were not statistically significant (P > 0.05). Only the relationship between Cladium and distance (r = -0.80) was strong enough to reach significance (P < 0.05).

# 3.4. ENP transect

The vegetation pattern in the ENP transect resembled the pattern of the CA3A transect, with *Typha*, *Cladium* marsh and open marsh communities delineated by the cluster analysis (Fig. 8). Total soil phosphorus concentrations were lowest in this southernmost transect. Peak values were  $1420 \,\mu g \, g^{-1}$  in soil adjacent to the canal, with values from 0.5 to 6 km away ranging from 1040 down to  $320 \,\mu g \, g^{-1}$  (Fig. 9). As in CA3A, *Typha* was restricted to the proximity of the canal and was replaced by intermixed *Cladium* and open marsh with extensive periphyton development at 0.5 km



CA3A TOTAL P/CATTAIL/SAWGRASS

Fig. 7. Histogram comparing presence of *Typha* and *Cladium* with distance from nutrient source and total P concentrations along Transect CA3A.

## Table 3

 $Correlation\ matrix\ comparing\ sawgrass\ marsh/combined\ sites,\ and\ spikerush\ marsh\ and\ combined\ sites\ along\ Transect\ CA3A$ 

	Distance	Sawgrass	Cattail	
Sawgrass	0.80			
	(7)			
	0.049			
Cattail	-0.61	-0.76		
	(7)	(7)		
	0.13	0.06		
Total P	- 0.71	-0.53	0.61	
	(7)	(7)	(7)	
	0.08	0.19	0.13	
b. Spikerush marsh	and combined sites			
	Distance	Periphyton	Cattail	
Periphyton	0.79	· · · · · · · · · · · · · · · · · · ·		
	(7)			
	0.05			
Cattail	-0.61	-0.65		
	(7)	(7)		
	0.13	0.11		
Total P	-0.61	-0.63	0.61	
	(7)	(7)	(7)	
	0.14	0.12	0.13	

a. Sawgrass marsh and combined sites

Figures given are: Coefficient; sample size (given in parentheses); significance level.



Fig. 8. Dendrogram of Transect ENP delineating among- and within-group species similarity along the transect with distance from the 0.0 km point and total soil P ( $\mu g g^{-1}$ ) at each sampling location.





Fig. 9. Histogram comparing presence of *Typha* and *Cladium* with distance from nutrient source and total P concentrations along Transect ENP.

Table 4

Correlation matrix comparing sawgrass marsh/combined sites, and spikerush marsh and combined sites along Transect ENP

a. Sawgrass marsh and combined sites

	Total P	Cattail	Sawgrass	
Cattail	0.58			
	(8)			
	0.13			
Sawgrass	-0.58	- 1.0		
-	(8)	(8)		
	0.13	0.0		
Distance	- 0.95	-0.58	0.58	
	(8)	(8)	(8)	
	0.01	0.13	0.13	
b. Spikerush and co	mbined sites			
	Total P	Cattail	Periphyton	
Cattail	0.58			
	(8)			
	0.13			
Periphyton	-0.58	- 1.0		
	(8)	(8)		
	0.13	0.0		
Distance	-0.88	-0.58	0.58	
	(8)	(8)	(8)	
	0.02	0.13	0.13	

Figures given are: Coefficient; sample size (in parentheses); significance level.

distance and beyond (Fig. 9). The open marsh included *Eleocharis*, *Rhynchospora* spp. and *Utricularia* spp.

Total soil phosphorus declined significantly with distance (P < 0.05), while periphyton and *Typha* exhibited a negative relationship (P < 0.001) (Table 4). Other relationships were not statistically significant but were consistent with patterns noted along other transects (Table 4).

## 4. Discussion

The pattern in marsh community composition and soil phosphorus content seen in the four marsh transects indicates that a clear relationship exists between *Typha* expansion, decline of natural marsh communities and elevated phosphorus concentrations. The trends appear to be traceable to agricultural drainage waters conveyed to study sites by water management structures. These results show a clear statistical (as opposed to a functional) relationship indicating that phosphorus enrichment caused the observed marsh compositional shifts. While we were not able to evaluate all the potential environmental variables that might explain these relationships, our results conform with other lines of evidence for the Everglades, from both experimental treatments (Steward

and Ornes, 1975a,b, 1983; Scheidt et al., 1989) and field analysis under ambient conditions (Hayati and Proctor, 1990; Huenneke et al., 1990; Richardson et al., 1990; Davis, 1991Davis, 1994).

Change in vegetation composition is widely recognized as an effect of nutrient additions in a variety of wetland types (Gorham, 1956; Gosselink and Turner, 1978; Aerts and Berendse, 1988; Hayati and Proctor, 1990). For example, in cypress dome pools, Odum et al. (1975) reported that increased nitrogen and phosphorous cause floating hydrophytes of several species to replace *Utricularia* spp., and *Nymphaea odorata*, two taxa that declined in our study. Species replacement, among other changes, also occurs as a result of nutrient enrichment in freshwater tidal wetlands (Whigham and Simpson, 1978), estuarine wetlands (Covin and Zedler, 1988), temperate marshes (Guntenspergen and Stearns, 1981; Kadlec and Bevis, 1990), fens and bogs (Vermeer and Berendse, 1983; Hayati and Proctor, 1990), riverine wetlands (Day et al., 1988) and grasslands (Koide et al., 1988; Huenneke et al., 1990). Moreover the changes in periphyton cover observed (those results are not reported) during our study are consistent with the response of Everglades periphyton communities to experimental nutrient enrichment (Raschke, 1992; Grimshaw et al., 1993).

Thus, loss of periphyton is understandable as a consequence of water quality alterations, as demonstrated by Swift (1984) who found major changes in Everglades periphyton species composition and growth rates in the same areas as our study that were associated with differences in phosphorus concentration, pH and ion content of marsh waters. Similarly the restriction of non-indigenous 'weedy' marsh species such as *A. australis* and *R. crispus* L. to the vicinity of canals and sites of higher phosphorus concentrations suggests that water quality alterations are a factor in altering habitat suitability for native communities and species (Ehrenfeld, 1983; Morgan and Philipp, 1986; Hough et al., 1989).

Nutrient stock alone cannot explain the wetland species distributions in the Everglades. Nutrients, fire and hydroperiod are perhaps the key factors that interact to determine the spatial extent and frequency of wetland plants, including *Typha*, and its expansion and dominance in disturbed areas (Urban et al., 1993).

Both lack of fire (Wade et al., 1980) and intense dry season fires (Hofstetter, 1973; Hofstetter and Parsons, 1975) can change species composition in *Cladium* marshes (Werner, 1975; Hofstetter and Parsons, 1975; Herndon et al., 1991), particularly when fires kill sawgrass roots or are followed by a rapid rise in water level (Herndon et al., 1991). Such cases appear to be exceptional however, and result only temporarily in apparent elimination of *Cladium* (Wade et al., 1980; Herndon et al., 1991). Reestablishment of *Cladium* communities following damaging fire may take several years but does not involve *Typha* establishment (Wade et al., 1980; Herndon et al., 1991). Typically, fires reduce above ground macrophyte biomass without eliminating species. Thus potentially confounding effects of fire on vegetation patterns in this study were reduced by relying on presence/absence data for analyzing spatial patterns. Because fire continues to be a dominant long-term force in the Everglades (Craighead, 1971; Klukas, 1973; Wade et al., 1980; Doren et al., 1993) and *Typha* invasion is a recent phenomenon, fire probably is not a deciding factor in the invasion and replacement of *Cladium* and other marsh communities by *Typha*.

Hydrology undoubtedly is a factor in structuring Everglades wetland plant communities. Construction of canal systems in the Everglades resulted in disturbed substrate and altered water depths and flooding duration. These changes can be assumed to have influenced community composition to some extent. Because the conservation areas have been operated under regulation schedule for several decades, water levels have, at times, been deeper or shallower than would have occurred under natural conditions, depending on location and climate. In addition, regulatory schedules have been revised and even experimentally modified. Thus the marsh communities have been exposed, over several decades, to a widely fluctuating hydrologic regime that would be difficult to quantitatively relate to species composition, particularly without long-term data, as concluded by Wood and Tanner (1990). The lack of a predictable relationship between plant marsh community type and interannual water level records in ENP marshes near the study area as found by Gunderson (1989) provides further evidence of this difficulty. Over the same period, however, the communities have experienced a gradual trend of nutrient enrichment that relates quantitatively to community composition and co-occurrence of species dominants. Equally important, perhaps, is the recognition that a variety of wetland communities have existed in the Everglades, ranging from deep-water sloughs flooded all year to marshes flooded for only a month or two in most years. In none of these communities has Typha been more than a sporadic component and where it is found, the sites are generally nutrient-enhanced through animal activity. Furthermore, in one of the few attempts to disentangle the effects of hydrology and nutrients, Richardson et al. (1990) report that in the center of CA1 where flooding depths resemble areas near canals but nutrient levels are much lower, Typha is absent except for locally nutrient-enhanced sites while it dominates the canal-side marshes.

The tendency for soil phosphorus levels to decline with increasing distance from nutrient runoff sources across all four transect areas strongly suggests that gradual enrichment (eutrophication) is progressing into the Everglades marshes as reported by Belanger et al. (1989), Koch and Reddy (1992) and Walker (1991). Additionally, the decline in phosphorus levels from north to south across the four transect areas suggests that nutrient enrichment is progressing southward from the agricultural areas in the north. This trend is also supported by the pronounced decrease in overall spatial extent of *Typha*-dominated areas to relative to *Cladium*, spikerush and white water lily marsh dominance that is seen when moving from the northernmost study site, Conservation Area 1 to the southernmost study site, Everglades National Park, as noted by Moore et al. (1989), Belanger et al. (1989), Koch and Reddy (1992) and Davis (1994). Thus from the perspective of both within-transect patterns and between-transect patterns of soil TP content and plant species distributions there is a firm basis for serious concern for the long-term effects of added nutrients on the Everglades marsh ecosystem.

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