

# Decadal Change in Vegetation and Soil Phosphorus Pattern across the Everglades Landscape

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## ABSTRACT

Wetlands respond to nutrient enrichment with characteristic increases in soil nutrients and shifts in plant community composition. These responses to eutrophication tend to be more rapid and longer lasting in oligotrophic systems. In this study, we documented changes associated with water quality from 1989 to 1999 in oligotrophic Everglades wetlands. We accomplished this by resampling soils and macrophytes along four transects in 1999 that were originally sampled in 1989. In addition to documenting soil phosphorus (P) levels and decadal changes in plant species composition at the same sites, we report macrophyte tissue nutrient and biomass data from 1999 for future temporal comparisons. Water quality improved throughout much of the Everglades in the 1990s. In spite of this improvement, though, we found that water quality impacts worsened during this time in areas of the northern Everglades (western Loxahatchee National Wildlife Refuge [NWR] and Water Conservation Area [WCA] 2A). Zones of high soil P (exceeding 700 mg P kg<sup>-1</sup> dry wt. soil) increased to more than 1 km from the western margin canal into the Loxahatchee NWR and more than 4 km from northern boundary canal into WCA-2A. This doubling of the high soil P zones since 1989 was paralleled with an expansion of cattail (*Typha* spp.)-dominated marsh in both regions. Macrophyte species richness declined in both areas from 1989 to 1999 (27% in the Loxahatchee NWR and 33% in WCA-2A). In contrast, areas well south of the Everglades Agricultural Area, including WCA-3A and Everglades National Park (ENP), did not decline during this time. We found no significant decadal change in plant community patterns from 1989 and 1999 along transects in southern WCA-3A or Shark River Slough (ENP). Our 1999 sampling also included a new transect in Taylor Slough (ENP), which will allow change analysis here in the future. Regular sampling of these transects, to verify decadal-scale environmental impacts or improvements, will continue to be an important tool for long-term management and restoration of the Everglades.

WETLANDS RESPOND to nutrient enrichment of associated waters in a typical fashion: Usually, some shift in plant community composition occurs after nutrient levels in the soils increase, followed by changes in both aquatic and wetland-dependent animal communities (Mitsch and Gosselink, 2000). In oligotrophic wetlands, such as peatlands and ombrotrophic bogs, these responses to eutrophication may be more rapid, more dramatic, and longer lasting. The Florida Everglades is a peat-based subtropical wetland system that is characteristically oligotrophic (Davis and Ogden, 1994; Noe et al., 2001) and phosphorus limited (Koch and Reddy, 1992; Amador and Jones, 1993; McCormick et al., 1996). Everglades water column total P concentrations are typ-

ically <0.3  $\mu\text{M}$  (10  $\mu\text{g L}^{-1}$ ) and soluble reactive phosphorus (SRP) concentrations are often below detection limits (<5 nM; Walker, 1999). Since the 1970s, water flowing into Everglades wetlands has been considerably enriched in nutrients and other contaminants (Walker, 1991). In northern Everglades regions near agricultural activities, total P concentrations have often exceeded 3  $\mu\text{M}$  (100  $\mu\text{g L}^{-1}$ ; McCormick et al., 1996; Noe et al., 2001). In the 1990s, some progress was made in reducing phosphorus (P) loading to Everglades wetlands, particularly at water inflow points in more southern regions of the system (Walker, 1999).

Hydrologic modifications during the last 100 yr (including construction of more than 2500 km of canals and levees and hundreds of water control structures) have played an important role in the eutrophication of the Everglades (Light and Dineen, 1994; Sklar et al., 2001). These hydrologic modifications have had two important effects. First, the canal-levee network has segmented the remaining Everglades wetlands into several large impoundments, known as Water Conservation Areas (WCAs; Fig. 1A). The WCAs were designed to store water, discouraging the natural tendency of water to flow south (downstream) through the Everglades landscape to the Gulf of Mexico. Everglades National Park (ENP), which is downstream end of the WCA network, is the only region of the remaining Everglades in which some natural flow regime exists. Second, hydrologic compartmentalization of the Everglades has caused the remaining wetlands to receive surface water mainly as point-source inputs at canal structures. The result is focal points in the landscape for water inputs, whereas pre-drainage water movement was diffuse and distributed across the landscape (Sklar et al., 2001). Increased nutrient concentrations coupled with these point-source inputs has led to the formation of defined enrichment gradients (Koch and Reddy, 1992; Urban et al., 1993; Qualls and Richardson, 1995; Doren et al., 1997).

Quantifying the impacts and long-term implications of phosphorus-enriched water inputs to Everglades wetlands has been the focus of a great deal of research for nearly 20 years. The major issue associated with water quality impacts on Everglades wetland plant communities is cattail (*Typha domingensis* Pers.) dominance and expansion at the expense of sawgrass (*Cladium jamaicense* Crantz) marsh or slough communities. In some areas of the northern Everglades (e.g., WCA-2A; Fig. 1A), cattail expansion has occurred at rates as high as 4% per year, such that by 1991 one-third of WCA-2A was

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**Abbreviations:** EAA, Everglades Agricultural Area; ENP, Everglades National Park; NWR, National Wildlife Refuge; WCA, Water Conservation Area.

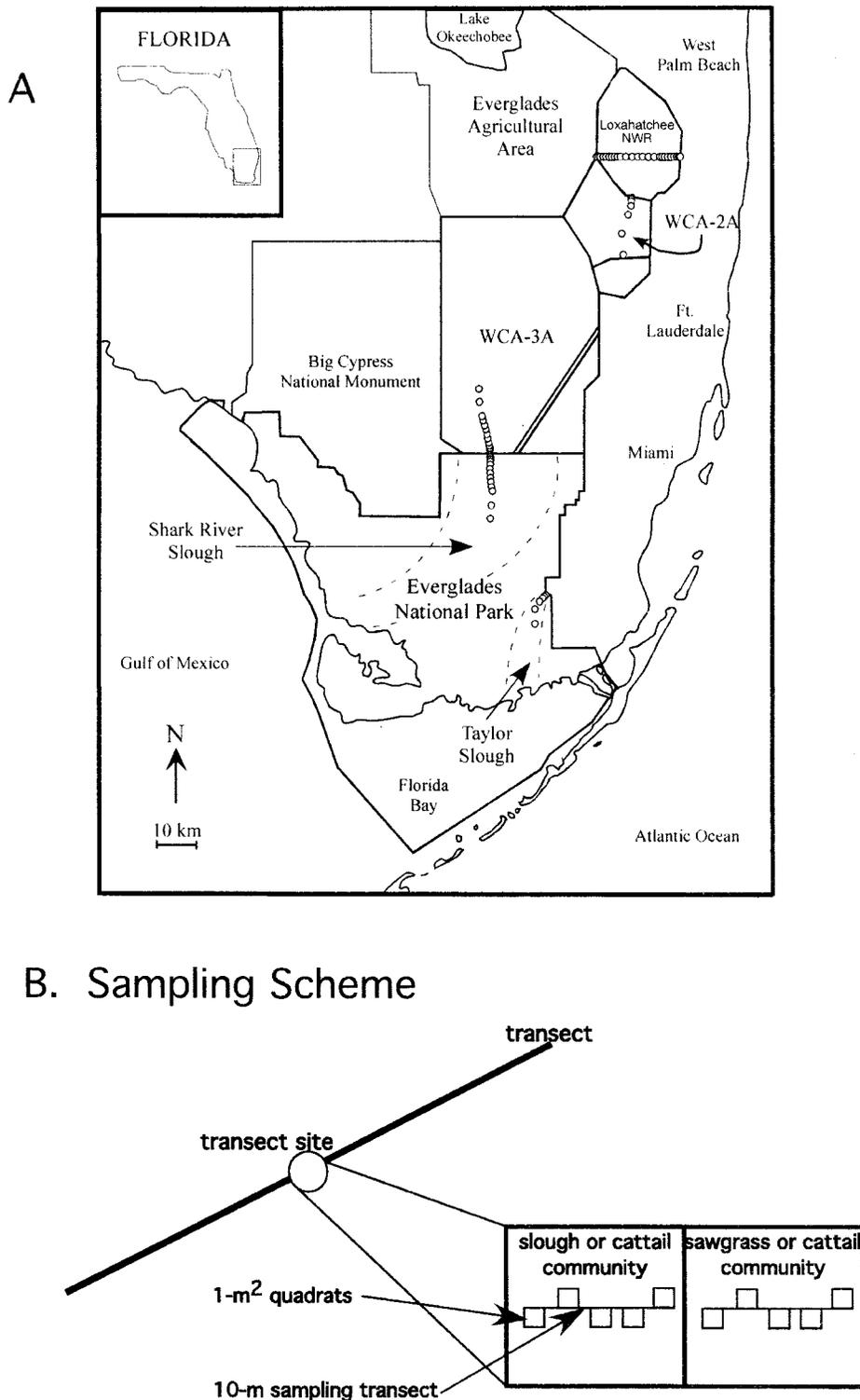


Fig. 1. (A) Map of southern Florida and the Everglades showing the location of the transects. (B) schematic of the sampling scheme used for macrophyte and soil sampling in 1989 (see Doren et al., 1997) and 1999.

dominated by cattail (Wu et al., 1997). Cattail is native to the Everglades, but it is adapted to soils higher in P than are typically found in unimpacted wetlands (Gunderson, 1994; Lorenzen et al., 2001); thus, large, expansive stands of cattail are relatively rare in unimpacted systems. Miao et al. (2000) found a strong positive rela-

tionship between soil P and both cattail seed germination and seedling success, suggesting that cattail establishment is limited to areas with relatively high soil P content ( $>700 \text{ mg P kg}^{-1} \text{ dry wt.}$ ). Both sawgrass and spikerush (*Eleocharis* spp.) are adapted to low soil P environments (Steward and Ornes, 1975, 1983; Newman

et al., 1996; Daoust and Childers, 1999; Lorenzen et al., 2001). Both appear to be easily out-competed by cattail when soil P levels increase (Newman et al., 1996; Miao and DeBusk, 1999). Lorenzen et al. (2001) substantiated this conclusion with hydroponic rhizotron experiments. Furthermore, it is becoming increasingly clear that hydroperiod changes alone cannot explain the expansion of cattail in impacted Everglades marshes (David, 1996; Newman et al., 1996; Richardson et al., 1999). Hydroperiod and soil P levels, as they are related to nutrient loading, are linked, but the P content of the soil appears to be the dominant controller of shifts in plant community structure in Everglades wetlands.

Soil nutrient levels are closely related to plant community composition in the oligotrophic Everglades, as in all wetlands (Mitsch and Gosselink, 2000). It seems intuitive that nutrients from enriched water inputs must first become part of the soil nutrient pool before they can affect plant productivity, competitive interactions, and ultimately community composition, though some wetland plants are able to use adventitious roots to take up nutrients directly from the water column (Howard-Williams, 1985; Noe et al., unpublished data, 2002). Unimpacted Everglades peat soils (with bulk densities < 0.15 g cm<sup>-3</sup>) typically have soil P concentrations of 200 to 400 mg P kg<sup>-1</sup> dry wt. soil (McCormick et al., 2001). At concentrations above about 600 to 700 mg P kg<sup>-1</sup> dry wt. soil, cattail begins to dominate the plant community (Noe et al., 2001). It seems clear that improvements in the quality of water flowing into Everglades wetlands may be reflected in reduced *expansion* of impacted, cattail-dominated areas. However, reductions in the overall *extent* of these areas will necessitate P reduction in soils, and thus will require a considerable length of time.

Our objective was to resample a series of wetland transects, representing a range of Everglades wetland environments, that were originally sampled in 1989 by Doren et al. (1997). Our goal was to determine the impacts of waterborne nutrient inputs to these wetlands during the intervening decade. In this paper, we present plant biomass, community composition, and soil P data from our 1999–2000 sampling and compare our results with those of Doren et al. (1997). We analyzed our plant community data with statistical techniques that were comparable with those of Doren et al. (1997). By comparing our species-specific information with similar data from WCA-2A (Vaithyanathan and Richardson, 1999) and Shark River Slough, ENP (Busch et al., 1998), we were able to address long-term changes in plant community composition across the greater Everglades landscape. Our analysis also included decadal comparisons of native and exotic plant species. In addition, we quantified plant aboveground biomass by species, plant tissue nutrient content, soil bulk density, and soil organic content. We present these additional data to establish an expanded baseline dataset for future decadal monitoring of these transects. We hypothesized that we would find relatively minor spatial changes along these transects since they were last sampled, given that the quality of water entering most of these Everglades marshes has improved during the intervening decade. Specifically,

we expected to see these spatial changes as the expansion of elevated soil P and cattail-dominated marsh. As a corollary to this hypothesis, we also did not expect to detect any reductions in soil P or improvements in plant community composition (e.g., a return to sawgrass or slough marsh species composition and relative abundance) in the impacted portions of these transects.

## MATERIALS AND METHODS

### Study Area

The Everglades landscape is part of a greater watershed that includes more than 28 000 km<sup>2</sup> of central and southern Florida, from near Orlando to Florida Bay. The expansive freshwater marshes, known popularly as the “river of grass,” dominate the southern portion of this landscape (Fig. 1A). Before drainage and canalization, water moved through the Everglades as a slow but pervasive surface flow from Lake Okeechobee through a mosaic of sawgrass marshes, wet sloughs, and forested islands along a topographic gradient of about 1 m per 56 km (Light and Dineen, 1994). Water flow was seasonal, driven by wet season precipitation (May through November) and overflow from the lake. In a typical dry season, many of the marshes along the slightly higher fringes were not inundated.

Hydrologic modifications have dissected the region into numerous subbasins. The 3059-km<sup>2</sup> Everglades Agricultural Area (EAA) has been completely drained. To the south, Everglades National Park (ENP) includes more than 4300 km<sup>2</sup> of the watershed; surface water flow in the park is regulated primarily by four water control structures along its northern border (known as S-12A–D). In between are five large Water Conservation Areas (WCA) that impound more than 3500 km<sup>2</sup> of Everglades marsh (Light and Dineen, 1994; Fig. 1A). Water management has increased the frequency and intensity of disturbance events, such as floods, droughts, and fire (DeAngelis and White, 1994; Gunderson, 1994). Canals, levees, and unnaturally deep water have greatly reduced wetland connectivity in the WCAs. This highly modified hydrologic regime has also altered patterns of flow, inundation, and P delivery in Everglades marshes. The EAA is a major source of P to the oligotrophic marshes, often by point-source canal inputs (Coale et al., 1994; Davis, 1994; Doren et al., 1997).

In this study, we revisited the four marsh transects sampled by Doren et al. (1997) in 1988–1989 to quantify how vegetation patterns had changed in the intervening 10 to 12 yr. We also sampled soils along the transects to investigate relationships between soil P and vegetation patterns. In addition to returning to their WCA-1 (Arthur R. Marshall Loxahatchee National Wildlife Refuge), WCA-2A, WCA-3A, and Shark River Slough (Everglades National Park) transects, we established and sampled a transect in Taylor Slough, the other major marsh watershed in ENP (Fig. 1A). As with Doren et al. (1997), our transects were anchored on major canals at sources of water input. In some cases, our transects extended further from the canal input point than did those of Doren et al. (1997): 16 km compared with 6 km in Shark River Slough, 16 km compared with 5 km in WCA-3A, and 16 km compared with 8 km in WCA-2A (Fig. 1A). As with Doren et al. (1997), we sampled approximately every kilometer along these transects during the 1999–2000 wet season (Table 1).

### Vegetation Sampling

We quantified macrophyte species frequency and stem density at each transect site (Fig. 1A, Table 1) with the sampling

protocol of Doren et al. (1997). This involved establishing a 10-m line transect in sawgrass, slough, or cattail communities at each site, whenever these community types were present (Fig. 1B). When both community types were not represented, it was nearly always because the site fell in a cattail stand. Thus, sites were designated as either sawgrass marsh (C), spikerush slough (S), or cattail marsh (T). Along these 10-m lines, we randomly located five 1-m<sup>2</sup> quadrats, with two quadrats on one side of the line and three on the other (Fig. 1B). Each 1-m<sup>2</sup> quadrat was divided into four 0.25-m<sup>2</sup> subquadrats. We counted the total number of stems or culms of each emergent plant species present (we did not sample submerged aquatic plants). Species frequencies (0–1.0) were calculated as the number of 0.25-m<sup>2</sup> subquadrats in which a plant species occurred divided by the total number of quadrats (20 per community type at each site). We quantified the aboveground biomass of each quadrat by clipping, drying, and weighing all plant material. Thus, we generated occurrence frequencies and stem densities for each plant species represented in a quadrat as well as total live and dead biomass for a 0.25-m<sup>2</sup> subsection of each quadrat, and scaled these data to grams dry weight per square meter.

To estimate total P pools in plant tissues, we analyzed samples for tissue nutrient content. During the 1999–2000 wet season sampling, triplicate individuals of the dominant species (sawgrass in C quadrats, spikerush species in S quadrats, and cattail in T quadrats) were subsampled for live aboveground tissue. These tissue samples were analyzed for P content in the SERC Analytical Lab at Florida International University as per Daoust and Childers (1999). We report these P data in g P kg<sup>-1</sup> dry weight. In a separate analysis and manuscript, we combined these values with species-specific dry weight biomass data to budget P into various ecosystem components at each transect location (Noe et al., unpublished data, 2002).

### Soil Sampling

We quantified soil nutrient and physical parameters at each transect site shown in Table 1 by collecting a soil core adjacent to each macrophyte quadrat. These cores were collected by inserting a 2.36-cm-i.d. cellulose–acetate–butyrate (CAB) plastic tube with a cutting edge (to reduce compaction) to 10 cm below the soil surface. Intact cores contained the water column and the flocculent detrital layer (floc) as well as the 10-cm soil core, which were decanted off after inserting a plug to the soil surface. The soil core was extruded into a sampling container.

Soil samples from the five quadrats at a given site were combined to result in one composite sample for each community type (C, S, or T) at each sampling site. Upon return to the laboratory, soil samples were homogenized and large anomalous material (white roots, snail shells, etc.) was removed. The homogenized soil samples integrated the upper 10 cm of the soil profile in all of our samples. We determined field bulk density (Mg m<sup>-3</sup>) from sample dry weight and core volume. Otherwise, our sample analysis followed Doren et al. (1997). Samples were dried at 80°C until constant weight (48–72 h), ground to a fine powder with a Wiley mill, and stored until analyzed for total P. Total P was measured with the ashing–acid hydrolysis method of Solorzano and Sharp (1980). The resulting soluble reactive phosphorus (SRP) was measured colorimetrically with an autoanalyzer. Values are expressed as mg P kg<sup>-1</sup> dry weight of material (hereafter mg P kg<sup>-1</sup>).

### Statistical Analyses

We used dendrogram analysis to identify significant plant species assemblages from species frequencies (PC Ord; McCune

**Table 1.** Details of all transect sites sampled in the 1999 wet season sampling, including site name, distance and direction of each site from the canal, and site coordinates.

Site†	Distance from canal	Direction from canal	Latitude	Longitude
	km			
WCA3A-0	0	NA‡	25°45.740'	80°43.786'
WCA3A-0.5	0.5	north	25°46.000'	80°43.929'
WCA3A-1	1	north	25°46.260'	80°44.043'
WCA3A-2	2	north	25°46.780'	80°44.400'
WCA3A-3	3	north	25°47.300'	80°44.593'
WCA3A-4	4	north	25°47.820'	80°44.786'
WCA3A-5	5	north	25°48.340'	80°44.529'
WCA3A-6	6	north	25°48.860'	80°42.629'
WCA3A-7	7	north	25°49.380'	80°42.314'
WCA3A-8	8	north	25°49.900'	80°42.815'
WCA3A-12	12	north	25°51.980'	80°42.900'
WCA3A-16	16	north	25°54.060'	80°43.005'
LOX-0	0	NA	26°28.227'	80°26.652'
LOX-0.5	0.5	east	26°28.227'	80°26.348'
LOX-1	1	east	26°28.227'	80°26.043'
LOX-2	2	east	26°28.227'	80°25.435'
LOX-3	3	east	26°28.227'	80°24.827'
LOX-4	4	east	26°28.227'	80°24.218'
LOX-5	5	east	26°28.227'	80°23.610'
LOX-6	6	east	26°28.227'	80°23.000'
LOX-7	7	east	26°28.227'	80°22.392'
LOX-8	8	east	26°28.227'	80°21.783'
LOX-10	10	east	26°28.227'	80°21.071'
LOX-12.5	12.5	east	26°28.227'	80°20.358'
LOX-15	15	center	26°28.227'	80°19.645'
LOX-17	13	center	26°28.227'	80°19.644'
LOX-19	11	center	26°28.227'	80°18.968'
LOX-21	9	center	26°28.227'	80°18.292'
LOX-23	7	west	26°28.227'	80°17.616'
LOX-24	6	west	26°28.227'	80°17.008'
LOX-25	5	west	26°28.227'	80°16.399'
LOX-26	4	west	26°28.227'	80°15.790'
LOX-27	3	west	26°28.227'	80°15.181'
LOX-28	2	west	26°28.227'	80°14.573'
LOX-29	1	west	26°28.227'	80°13.964'
LOX-29.5	0.5	west	26°28.227'	80°13.659'
LOX-30	0	NA	26°28.227'	80°13.355'
WCA2A-0	0	NA	26°22.171'	80°21.188'
WCA2A-0.5	0.5	south	26°21.895'	80°21.188'
WCA2A-1	1	south	26°21.618'	80°21.188'
WCA2A-2	2	south	26°21.092'	80°21.188'
WCA2A-3	3	south	26°20.474'	80°21.043'
WCA2A-4	4	south	26°20.000'	80°21.572'
WCA2A-5	5	south	26°19.645'	80°21.993'
WCA2A-6	6	south	26°19.145'	80°22.282'
WCA2A-7	7	south	26°18.746'	80°22.550'
WCA2A-8	8	south	26°16.855'	80°22.761'
WCA2A-12	12	south	26°16.197'	80°23.714'
WCA2A-15	14	south	near canal	near canal
TS-S332	0	NA	25°25.400'	80°35.400'
TS-S332D	0	NA	25°26.850'	80°35.400'
TS-0.5	0.5	south-southwest	25°25.143'	80°35.557'
TS-1	1	south-southwest	25°24.935'	80°35.729'
TS-2	2	south-southwest	25°24.494'	80°36.029'
TS-4	4	south-southwest	25°23.545'	80°36.471'
TS-8	8	south-southwest	25°21.377'	80°36.300'
SRS-0	0	NA	25°45.610'	80°43.629'
SRS-0.5	0.5	south	25°45.340'	80°43.629'
SRS-1	1	south	25°45.070'	80°43.629'
SRS-2	2	south	25°44.530'	80°43.629'
SRS-3	3	south	25°44.490'	80°43.629'
SRS-4	4	south	25°43.450'	80°43.629'
SRS-5	5	south	25°42.91'	80°43.629'
SRS-6	6	south	25°42.37'	80°43.629'
SRS-7	7	south	25°41.83'	80°43.629'
SRS-8	8	south	25°41.290'	80°43.629'
SRS-12	12	south	25°39.13'	80°43.629'
SRS-16	16	south	25°36.970'	80°43.629'

† LOX, Loxahatchee National Wildlife Refuge; WCA, Water Conservation Area; SRS, Shark River Slough; TS, Taylor Slough.  
‡ Not applicable.

and Mefford, 1999). We used Sorensen's distance measure with group average method to generate the similarity matrix for each dendrogram, and generated one dendrogram for each transect (total = 5). Dominant species were determined to be significant indicators with indicator species analysis methods of Dufrene and Legendre (1997). We used an additional ordi-

nation analysis (nonmetric multidimensional scaling; global NMS-PC Ord for Windows Version 4.14) to support the dendrogram results, but did not report these analyses for the sake of brevity. This support came from comparing groupings and identifying similarities (Clark, 1993). This particular method is well suited for data that are nonnormal or discontinuous as it tends to linearize environmental relationships. The dendrogram ordinations used Sorensen's distance measure, the variance-regression endpoint selection method, Euclidean axis projection geometry, and Euclidian residual distances. In these vegetation analyses, we assumed that locations with cattail communities were represented only by this community type while all other locations were assumed to have both sawgrass marsh and wet prairie slough communities, both of which we sampled. We described broad patterns of change in the frequency of dominant species along the transects without relying on inferential statistical tests of these changes because (i) stem densities were measured in 1999 but not in 1989 and (ii) tests of differences in species presence or absence among the five plots at each location had very low statistical power.

To determine if soil P varied among the plant community (dendrogram) groups, we used analysis of variance (ANOVA) to compare soil P among the plant species assemblages within transects. Tukey's Honestly Significant Difference post-hoc tests identified differences among plant assemblages when the ANOVA results were significant ( $p \leq 0.05$ ). In all cases, we log-transformed soil P data to achieve homoscedasticity and normality of the residuals.

We tested if soil P differed significantly between oligotrophic community types (C and S) along the transects with two-way ANOVA with community type and transect as main factors (Systat; SPSS, 1998). Upon finding no difference in the soil P between community types, and no community type X transect interaction, we opted to not distinguish soil P values between C and S community types within a given site in further analyses. Data were plotted as total P ( $\text{mg kg}^{-1}$ ) versus distance down-transect (km) and were fit to the equation:

$$C = C_0 e^{-kd} + b$$

where  $C$  was the soil P ( $\text{mg kg}^{-1}$ ) at a given location,  $C_0$  was an estimate of soil P at the transect anchor station or in proximity to the inflow canal (in most cases, these were the same);  $k$  was the slope of the exponential curve representing the rate of concentration change (decline) with distance ( $d$ , in km) from the transect anchor station, and  $b$  was a constant that predicted an asymptotic concentration that we considered to be representative of background or unimpacted conditions ( $\text{mg P kg}^{-1}$ ). Other equations could have been used to describe some of these data, occasionally providing a better fit. However, this equation allowed us to consistently compare soil P patterns among all transects, enhancing our ecological interpretation.

## RESULTS

### Loxahatchee National Wildlife Refuge (Water Conservation Area 1) Transect

Our Loxahatchee NWR transect ran west to east across the refuge from the S-6 pump structure to the L-40 boundary canal (Fig. 1A). In 1989, Doren et al. (1997) found cattail-dominated marsh extending to 0.5 km east from the S-6 pump structure, and at the 1-km site they found a mix of cattail- and sawgrass-dominated communities. A decade later, our data showed that cattail occurred in 100% of the quadrats at the 0-, 0.5-, and 1-km sites and had a 60% occurrence frequency 2

km from the western canal margin. At the 1-km site, the only plant species present was cattail, growing in a dense stand more than 3 m tall. Since 1989, sawgrass had been extirpated at all sites within 1 km of the canal (Fig. 2A). At the eastern end of this transect, though, we found no change since Doren et al. (1997): we found cattail marsh (100% cattail frequency) at only the site adjacent to the canal, while 0.5 km to the interior (west) the vegetation reflected an unimpacted marsh (Fig. 2A). Total aboveground live biomass during the 1999–2000 wet season was roughly equivalent at the cattail and sawgrass sites, while the spikerush slough sites had about an order of magnitude less biomass, both live (Fig. 2A) and dead (Fig. 2B). Spikerush and sawgrass plant tissues were consistently less than  $0.005 \text{ g P kg}^{-1}$  dry wt. whereas cattail plant tissues in the impacted marshes were two to four times higher than this (Fig. 2C).

While we found a total of 30 plant species along the Loxahatchee NWR transect (Table 2), the species richness at a given site never exceeded  $8 \text{ m}^{-2}$ . Of these 30 species, only 11 were found in both 1989 and 1999 (Table 2). Four main species assemblages were delineated along this transect (Fig. 3A). Cattail dominated Group 1, which occurred at locations nearest the inflow canals where soil P concentrations were  $>450 \text{ mg kg}^{-1}$  and were significantly greater than the other groups (Fig. 2D). The sample sites that represent Group 1 had only four species present. Sawgrass dominated Groups 2 and 3 with a mixed presence of other native species (including some cattail at the 2-km location; Fig. 2). Group 3 (the slough sites) had higher species richness than Group 2, had more frequent presence of long hydroperiod species, and had lower soil P than the sawgrass-dominated Group 2. These species differences explained why Groups 2 and 3 showed a separation at about the 40% level (60% dissimilarity; Fig. 3A). Group 4 was dominated by waterlily (*Nymphaea odorata* Ait.) and Gulf Coast spikerush (*Eleocharis cellulosa* Torr.). These two species are characteristic of the longest hydroperiods, suggesting that these slough sites typically had deeper water and longer periods of inundation. Group 4 sites also had (marginally) significantly lower soil P than Group 2 sites ( $P = 0.065$ ), but were similar to soil P levels at Group 3 sites.

Soil P concentration at the 0- and 1-km sites was approximately  $900 \text{ mg kg}^{-1}$ , roughly three times higher than soil P at the 2- to 29-km sites (approximately  $300 \text{ mg kg}^{-1}$ ; Fig. 2D). Curve fitting showed an exponential decrease in soil P with distance ( $k = -0.52 \text{ mg kg}^{-1} \text{ km}^{-1}$ ,  $r^2 = 0.79$ ,  $p < 0.001$ ), excluding data from the 29.5- and 30-km sites (Fig. 2D). Background P levels were predicted to be  $288 \text{ mg kg}^{-1}$ . This value was similar to mean soil P from our 2- to 29-km sites and to a mean value of  $368 \text{ mg kg}^{-1}$  reported by Newman et al. (1997) for unimpacted, interior Loxahatchee NWR sites sampled in 1991.

### Water Conservation Area 2A Transect

Water Conservation Area 2A is most proximal to the EAA, and as a result virtually all of the nonatmospheric

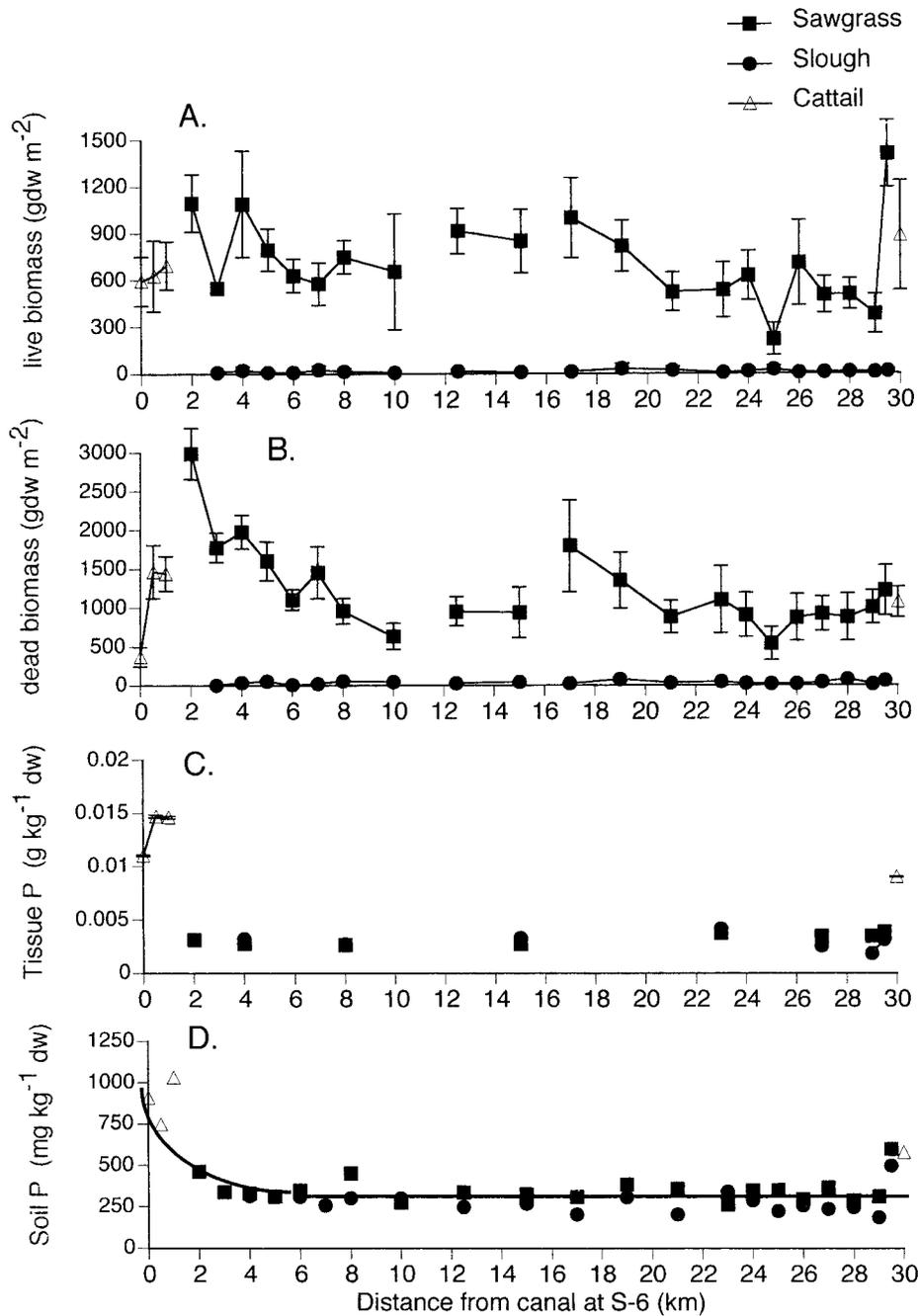


Fig. 2. Macrophyte and soils data from the Loxahatchee National Wildlife Refuge transect. (A) Total aboveground standing live biomass; (B) total aboveground standing dead biomass; (C) tissue phosphorus content of the dominant species (sawgrass, spikerush, or cattail); (D) soil phosphorus (curve fit for the 0- to 29-km sites:  $C = 288 + 695e^{(-0.52d)}$ ,  $r^2 = 0.79$ ,  $p < 0.001$ ).

inputs of water to this area have elevated nutrient concentrations. In 1989, Doren et al. (1997) found cattail in 100% of their sampling quadrats up to 2 km from the canal, and cattail occurred at sites as far away as 6 km. Sawgrass occurred in 10% of their sampled quadrats at the 2-km site, and was found in 100% of their quadrats at sites 3 to 6 km from the canal. In 1989, sawgrass marsh dominated at the 7- and 8-km sites. A decade later, our wet season data showed that the impacted cattail marsh (100% cattail occurrence) extended to the 4-km site. Sawgrass was no longer found within 2 km of the canal, and occurred at low densities and frequency (60%) at the 4-km site (Fig. 4). Sawgrass

marsh or spikerush slough was only found at the 8- and 15-km sites (Fig. 4A). Total aboveground live biomass was roughly equivalent at the cattail and sawgrass sites, while the spikerush slough sites had roughly an order of magnitude less biomass. The two spikerush sites had virtually no standing dead plant material during the wet season while dead biomass at the two sawgrass marsh sites was more than double the live biomass (Fig. 4B). Spikerush and sawgrass plant tissues were consistently less than  $0.005 \text{ g P kg}^{-1}$  dry wt. whereas cattail plant tissues at the impacted sites were two to four times higher than this (Fig. 4C).

We found a total of 16 plant species at our WCA-2A

**Table 2. Complete species list for all plants identified in either 1989 (Doren et al., 1997) or 1999. An "X" indicates that a given plant species was identified in any plot at any site on a given transect. The last of these categories includes species found along the Taylor Slough transect in 1999 only.**

Species		Site†								
Scientific name	Common name	LOX, 1989	LOX, 1999	WCA2A, 1989	WCA2A, 1999	WCA3A, 1989	WCA3A, 1999	SRS, 1989	SRS, 1999	TS, 1999
<i>Aeschynomene americana</i> L.	shyleaf					X		X	X	
<i>Amaranthus australis</i> (Gray) Sauer	southern amaranth	X		X		X				
<i>Andropogon</i> spp.	broomsedge	X								
<i>Annona glabra</i> L.	pond apple		X					X	X	
<i>Baccharis halimifolia</i> L.	groundsel tree			X						
<i>Bacopa caroliniana</i> (Walt.) B.L. Robins.	blue waterhyssop, lemon bacopa	X				X		X		
<i>Blechnum serrulatum</i> L.C. Rich	toothed midorus fern, swamp fern		X							
<i>Boehmeria cylindrica</i> (L.) Sw.	false nettle	X						X		
<i>Cephalanthus occidentalis</i> L.	common buttonbush		X	X	X	X	X			
<i>Chrysobalanus icaco</i> L.	coco plum		X							
<i>Cladium jamaicense</i> Crantz	sawgrass	X	X	X	X	X	X	X	X	X
<i>Conoclinium coelestinum</i> (L.) DC	blue mistflower	X					X			X
<i>Crinum americanum</i> L.	seven sisters, string-lily					X				
<i>Cynanchum</i> spp.	swallowwort				X		X		X	
<i>Cyperus haspan</i> L.	haspan flatsedge	X		X				X		
<i>Cyperus odoratus</i> L.	fragrant flatsedge							X		
<i>Diodia virginiana</i> L.	Virginia buttonweed	X						X		
<i>Echinochloa crusgalli</i> (L.) Beauv.‡	barnyardgrass	X		X				X	X	
<i>Eichhornia crassipes</i> (Mart.) Solms‡	common water hyacinth		X							
<i>Eleocharis cellulosa</i> Torr.	Gulf Coast spikerush	X	X	X	X	X	X	X	X	X
<i>Eleocharis elongata</i> Chapman	slim spikerush		X	X		X	X			
<i>Eleocharis interstincta</i> (Vahl) Roemer & J.A. Schultes	knotted spikerush								X	
<i>Eragrostis elliottii</i> S. Watson	Elliott's lovegrass									X
<i>Erechtites hieracifolius</i> (L.) Raf. ex DC.	burnweed	X								
<i>Eriocaulon</i> spp.	hatpins, pipeworts	X	X							
<i>Eupatorium capillifolium</i> (Lam.) Small ex Porter & Britton	dogfennel	X								
<i>Eupatorium mikanioides</i> Chapman	semaphore thoroughwort									X
<i>Fuirena scirpoidea</i> Michx.	southern umbrella-sedge		X						X	
<i>Gnaphalium obtusifolium</i> (L.) Hilliard & Burt ssp. <i>obtusifolium</i>	rabbit-tobacco	X								
<i>Hydrocotyle</i> spp.	water pennywort	X			X					
<i>Hymenocallis</i> spp.	spider-lily						X		X	X
<i>Ipomoea sagittata</i> Poir.	saltmarsh morning-glory			X					X	
<i>Justicia ovata</i> (Walter) Lindau	looseflower water-willow				X		X	X	X	X
<i>Kosteletzkya virginica</i> (L.) C. Presl ex A. Gray	Virginia saltmarsh mallow	X						X		
<i>Lachnanthes caroliniana</i> (Lam.) Dandy	Carolina redroot	X								
<i>Leersia hexandra</i> Sw.	southern cutgrass		X				X		X	X
<i>Lemna obscura</i> (Austin) Daubs	little duckweed			X						
<i>Ludwigia octovalvis</i> (Jacq.) Raven	Mexican primrose-willow	X				X				
<i>Ludwigia peruviana</i> (L.) Hara‡	Peruvian primrose-willow	X			X		X			
<i>Ludwigia repens</i> J.R. Forst.	creeping primrose-willow	X						X		
<i>Ludwigia</i> spp.	primrose-willow		X							
<i>Lygodium microphyllum</i> (Cav.) R. Br.‡	small-leaf climbing fern		X							
<i>Melothria pendula</i> L.	creeping cucumber			X						
<i>Mikania scandens</i> (L.) Willd.	climbing hempvine	X		X	X			X	X	X
<i>Murdannia nudiflora</i> (L.) Brenan‡	nakedstem dewflower				X					
<i>Myrica cerifera</i> (L.) Small	wax myrtle	X	X							
<i>Najas</i> spp.	waternymph			X		X				
<i>Nymphaea odorata</i> Ait.	American white waterlily		X	X	X	X	X		X	
<i>Nymphoides aquatica</i> (J.F. Gmel.) Kuntze	big floatingheart		X				X			X
<i>Osmunda cinnamomea</i> L.	cinnamon fern		X							
<i>Osmunda regalis</i> L.	royal fern		X							
<i>Oxypolis filiformis</i> (Walt.) Britt.	water cowbane									X
<i>Panicum dichotomum</i> (L.) Gould var. <i>dichotomum</i>	cypress panicgrass	X								
<i>Panicum hemitomon</i> J.A. Schultes	maidencane	X	X	X		X	X	X	X	X
<i>Panicum rigidulum</i> Bosc ex Nees	redtop panicgrass									X
<i>Panicum tenerum</i> Bey. ex Trin.	bluejoint panicgrass									X
<i>Paspalidium geminatum</i> (Forsk.) Stapf	Egyptian paspalidium	X	X			X	X		X	X
<i>Peltandra virginica</i> (L.) Schott	green arrow arum		X				X	X	X	
<i>Pennisetum purpureum</i> Schumach.‡	napierrgrass	X								
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	common reed	X								

Continued on next page.

Table 2. Continued.

Species		Site†								
Scientific name	Common name	LOX, 1989	LOX, 1999	WCA2A, 1989	WCA2A, 1999	WCA3A, 1989	WCA3A, 1999	SRS, 1989	SRS, 1999	TS, 1999
<i>Phyla nodiflora</i> (L.) Greene	turkey tangle fogfruit									X
<i>Pluchea rosea</i> Godfrey	rosy camphorweed	X		X				X		X
<i>Polygonum densiflorum</i> Meisn.	denseflower knotweed		X						X	
<i>Polygonum hirsutum</i> Walt.	hairy smartweed				X		X			
<i>Polygonum hydropiperoides</i> Michx.	swamp smartweed	X		X		X		X		X
<i>Polygonum setaceum</i> Baldw.	bog smartweed	X		X				X		X
<i>Pontederia cordata</i> L.	pickerelweed	X	X		X	X	X	X	X	X
<i>Proserpinaca palustris</i> L.	marsh mermaidweed	X								
<i>Rhynchospora inundata</i> (Oakes) Fern.	narrowfruit horned beaksedge		X			X	X		X	X
<i>Rhynchospora microcarpa</i> Baldw. ex Gray	southern beaksedge	X	X				X		X	X
<i>Rhynchospora</i> spp.	beaksedge		X				X			
<i>Rhynchospora tracyi</i> Britt.	Tracy's beaksedge	X	X			X		X	X	X
<i>Rumex crispus</i> L.‡	curly dock			X	X		X			
<i>Sabatia grandiflora</i> (Gray) Small	largeflower rose gentian					X				
<i>Saccharum giganteum</i> (Walt.) Pers.	sugarcane plumegrass									X
<i>Sagittaria lancifolia</i> L.	bulltongue arrowhead	X		X	X	X	X	X	X	X
<i>Salix caroliniana</i> Michx.	coastal plain willow		X	X				X		
<i>Sarcostemma clausum</i> (Jacq.) Schult.	white twinevine	X		X						
<i>Scirpus tabernaemontani</i> (K.C. Gmel.) Palla	softstem bulrush				X		X	X	X	
<i>Scleria triglomerata</i> Michx.	whip nutrush	X								
<i>Solidago leavenworthii</i> Torr. & Gray	Leavenworth's goldenrod	X								
<i>Stillingia</i> spp.	queen's delight									X
<i>Typha domingensis</i> Pers.	cattail	X	X	X	X	X	X	X	X	
<i>Utricularia</i> spp.	bladderwort			X		X		X		
<i>Woodwardia virginica</i> (L.) Sm.	Virginia chainfern	X								
<i>Xyris</i> spp.	yellow-eyed grass	X	X			X				
<i>Zizaniopsis miliacea</i> (Michx.) Doell & Aschers.	giant cutgrass								X	

† LOX, Loxahatchee National Wildlife Refuge; WCA, Water Conservation Area; SRS, Shark River Slough; TS, Taylor Slough.

‡ Exotic.

sites (Table 2), but no more than five species at any given site. Of the 16 total species found in 1999, only eight also occurred along this transect in 1989 (Table 2). Three primary species assemblages were delineated along our WCA-2A transect (Fig. 3B). Group 1 (all sites 0–4 km from the canal) was dominated by cattail, but also had a high abundance of swallowwort (*Cynanchum* spp.), a plant that is not typical of these areas and is often considered a weed, as well as a number of woody species. Notably, swallowwort was not present in 1989 (Table 2). The sawgrass sites at 8 and 15 km (Group 2) had a relatively high presence of cattail, and thus were more than 60% dissimilar from the slough sites at the same locations (Group 3; Fig. 3B). Group 3 was dominated by waterlily, with a high presence of Gulf Coast spikerush, both typical of longer hydroperiod sloughs.

Our soil P data showed high concentrations (1200–1600 mg kg<sup>-1</sup>) at the 0- to 4-km sites (vegetation Group 1), with the exception of the 0.5-km site, which had uncharacteristically marly soils (Fig. 4D). Marl soils have higher bulk density and lower organic matter content than peat soils, and thus generally have lower P content, when reported on a per-weight basis (Harris and Hurt, 1999). This pattern suggested that the soil P retention capacity was saturated within 4 km of the canal, with an exponential reduction to less impacted soils. From the 4-km site, we found a dramatic logarithmic decline in soil P toward the interior of WCA-2A (Fig. 4D). The exponential curve fit to data from these sites was marginally significant ( $p < 0.10$ ,  $r^2 = 0.89$ ), probably because our WCA-2A

transect had only three sites between 4 and 14 km. Phosphorus concentrations at the 8- and 14-km sites (vegetation Groups 2 and 3) ranged from 283 to 609 mg kg<sup>-1</sup> and averaged 418 mg kg<sup>-1</sup>. Group 3 slough sites had lower soil P than the Group 1 cattail sites, but there were no significant differences in soil P between Groups 1 and 2 or Groups 2 and 3.

### Water Conservation Area 3A Transect

Water Conservation Area 3A is managed as one of the wettest regions of the Everglades, particularly at the southern margin where our transect was located (Fig. 1A). Water tends to impound at this southern margin, and rarely flows north from Tamiami Canal (Light and Dineen, 1994; Fig. 1A). Thus, this transect is different from the other four we report here in that the transect is not oriented along a gradient of canal influence. We found cattail only adjacent to the canal (0 km, 40% frequency), the same pattern reported by Doren et al. (1997) for their 1989 sampling. We found a total of 24 plant species along our WCA-3A transect in 1999, only 11 of which were also present in 1989 (roughly 46% temporal coherence). Although total plant species richness was 24 species in 1999, we never found more than five species per square meter at a given site. Total above-ground live biomass was about fivefold greater at the sawgrass sites compared with the spikerush sites, and neither showed any clear patterns with distance (Fig. 5A). The spikerush sites had virtually no standing dead plant

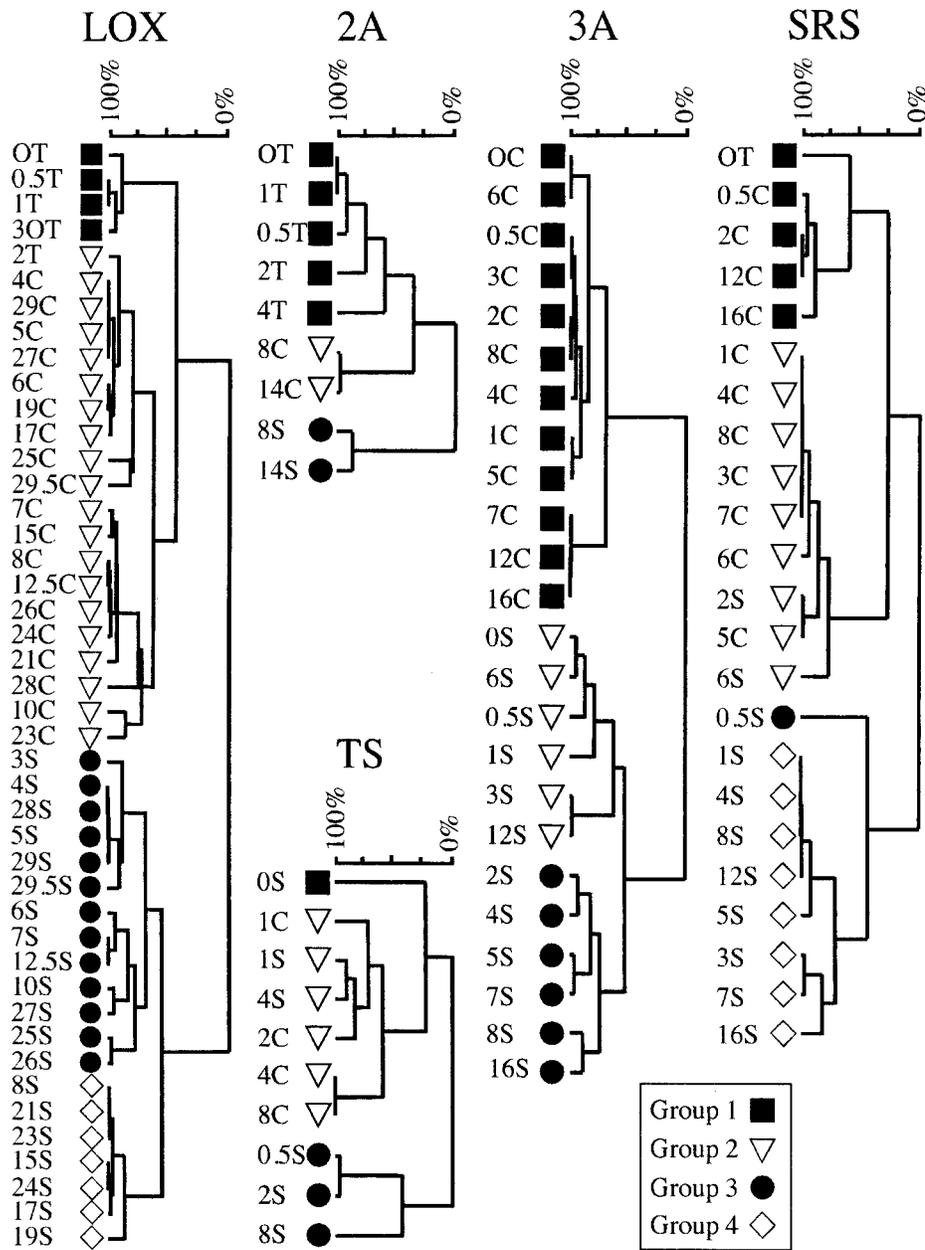


Fig. 3. Dendrogram of plant community groupings for all transects based on Sorensen's distance similarity with analysis of variance (ANOVA) post-hoc test results for soil P similarity shown in parentheses (same letters indicate no significant difference in soil P). (A) Loxahatchee National Wildlife Refuge (soil P results: Group 1 A, Group 2 B, Group 3 C, Group 4 BC); (B) Water Conservation Area (WCA) 2A (soil P results: Group 1 A, Group 2 AC, Group 3 BC); (C) WCA-3A (soil P results: Group 1 A, Group 2 B, Group 4 B, none for Group 3); (D) Shark River Slough, Everglades National Park (soil P results: Group 2 A, Group 3 A, none for Group 1); (E) Taylor Slough, Everglades National Park.

material, while dead biomass at the sawgrass sites was often five times live biomass (Fig. 5B). Spikerush and sawgrass plant tissues were consistently about 0.005 g P kg<sup>-1</sup> dry wt. Notably, this WCA-3A transect was the only one in which we found no elevated plant tissue P values (Fig. 5C).

Three primary species assemblages were delineated from our WCA-3A transect macrophyte data (Fig. 3C). Group 1 was made up of only sawgrass sites, and included all of the sawgrass marsh sites. Groups 2 and 3 were both spikerush slough groupings, and the differen-

tiation between these groups was less clear (with <50% dissimilarity between them; Fig. 3C). There was a tendency for Group 2 sites to have higher stem counts of Egyptian paspalidium [*Paspalidium geminatum* (Forsk.) Stapf] and waterlily, perhaps suggesting that these slough sites were deeper water environments. However, given that virtually the entire length of the transect was represented by the slough sites in both of these groups, this community distinction may primarily be showing small-scale heterogeneity in slough habitats.

Because Tamiami canal water does not regularly flow

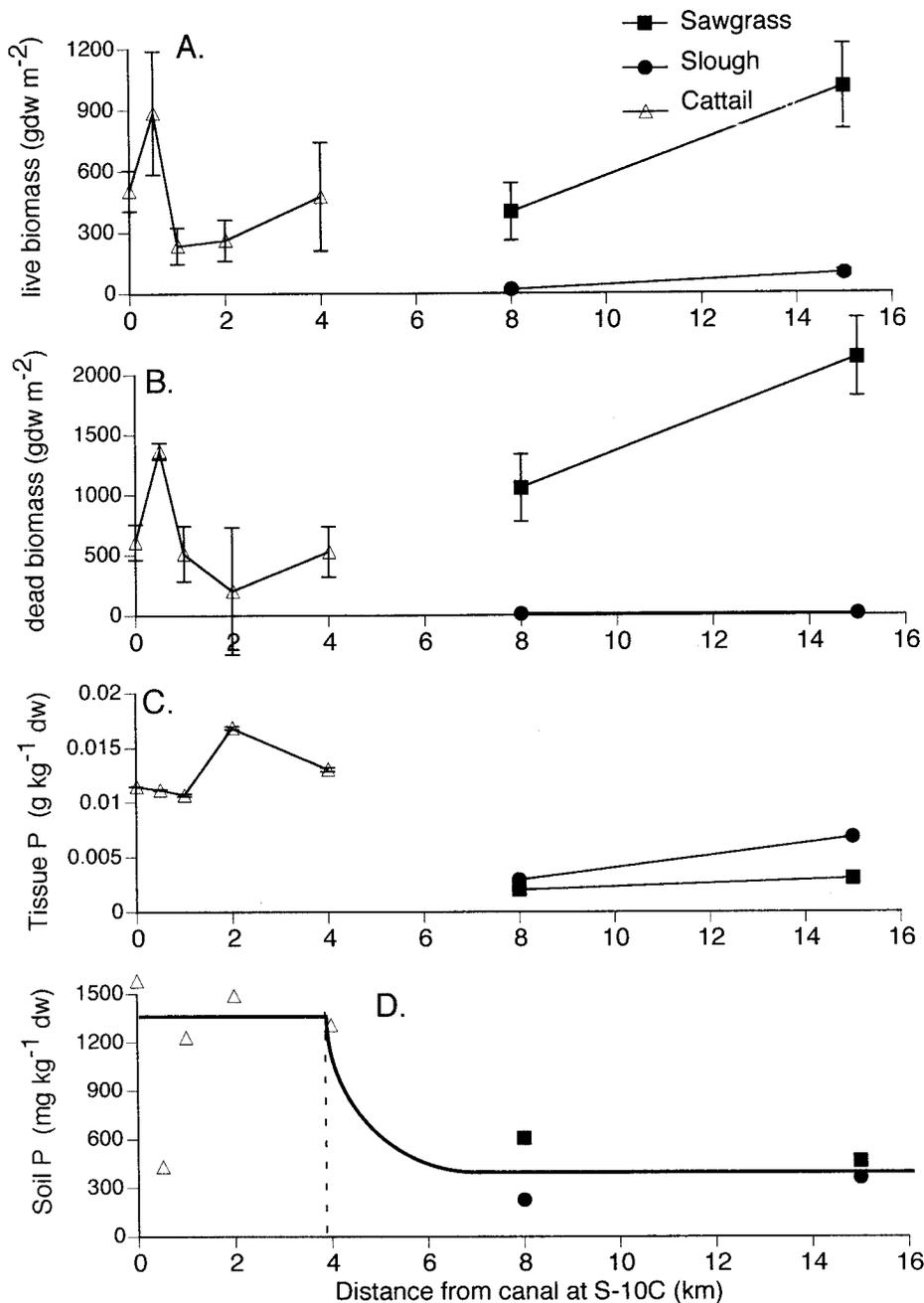


Fig. 4. Macrophyte and soils data from the Water Conservation Area (WCA) 2A transect. (A) Total aboveground standing live biomass; (B) total aboveground standing dead biomass; (C) tissue phosphorus content of the dominant species (sawgrass, spikerush, or cattail); (D) soil phosphorus (curve fit for the 4- to 14-km sites:  $C = 417 + 889e^{(-1.74d)}$ ,  $r^2 = 0.89$ ,  $p < 0.10$ ).

north into WCA-3A, we did not see the same exponential decline in soil P with distance from the canal that characterized the WCA-2A and even the Loxahatchee National Wildlife Refuge transects (Fig. 5D). We found divergent soil P values at the 0-km sites ( $C = 799$  and  $S = 413$  mg kg<sup>-1</sup>, respectively). With the exception of the high P concentration at this 0-km sawgrass site, soil P concentrations in WCA-3A averaged 362 mg kg<sup>-1</sup> and ranged between 260 and 479 mg kg<sup>-1</sup>. In addition, soil P was not significantly different among the three plant assemblages (Fig. 3C).

### Shark River Slough Transect

The Shark River Slough transect in Everglades National Park was located immediately across the Tamiami Canal from the WCA-3A transect. In 1989, Doren et al. (1997) found cattail in 90% of their sampling quadrats at the 0-km site, adjacent to the Tamiami canal, but they did not find it at any other site. Sawgrass was found in 100% of their quadrats at sites 0.5 to 5 km from the canal. A decade later, we found that cattail was still present at the 0-km site nearest the canal (at 100% frequency). We located and sampled both sawgrass or spikerush

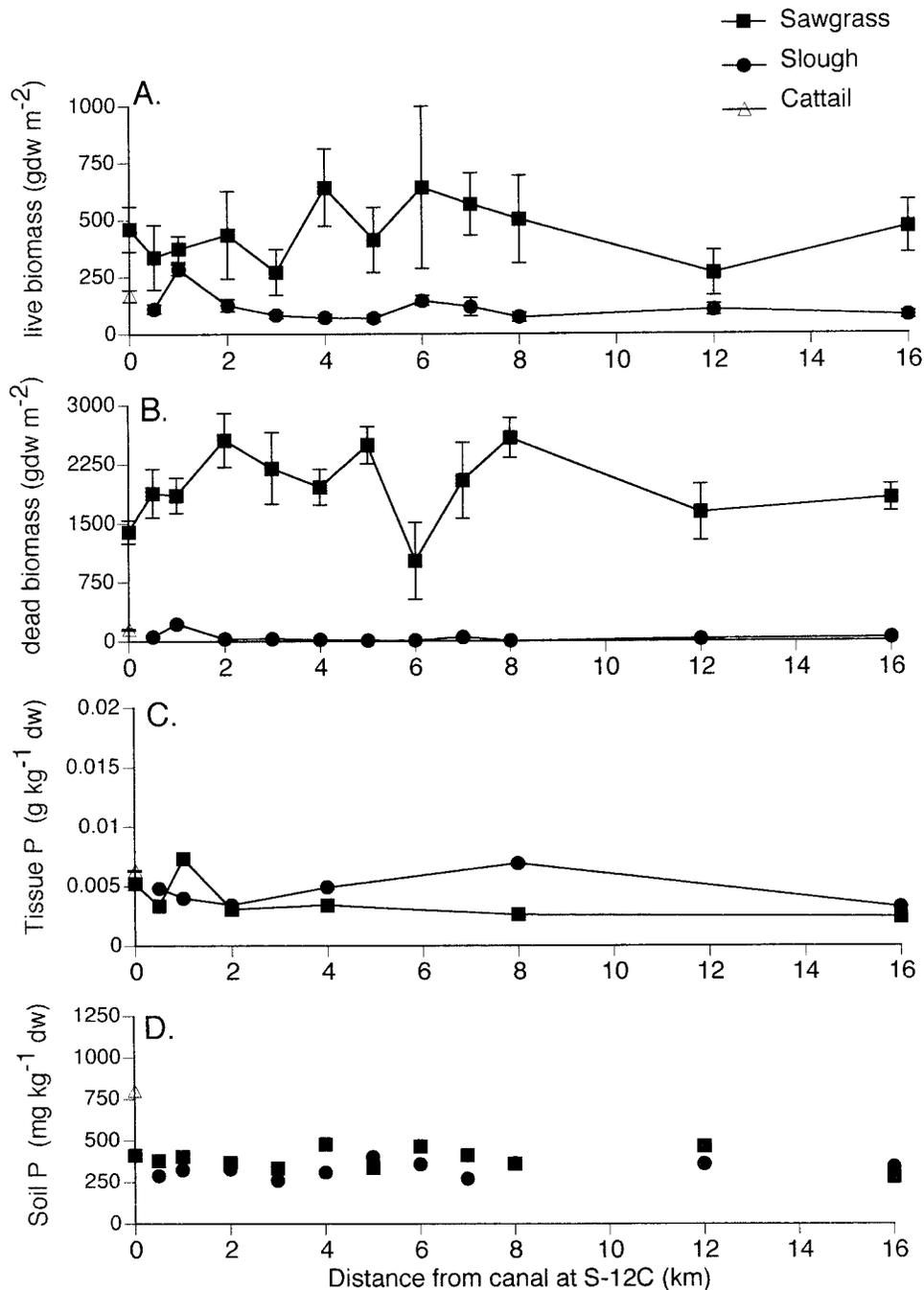


Fig. 5. Macrophyte and soils data from the Water Conservation Area (WCA) 3A transect. (A) Total aboveground standing live biomass; (B) total aboveground standing dead biomass; (C) tissue phosphorus content of the dominant species (sawgrass, spikerush, or cattail); (D) soil phosphorus (transect mean = 361 ± 61 mg kg<sup>-1</sup>, range = 260–479 mg kg<sup>-1</sup> excluding the 0-km cattail site).

marsh plots at all other sites along our 16-km transect (Fig. 6). A total of 27 plant species were found along the Shark River Slough transect, compared with 26 species in 1989 and 14 species present both times (Table 2). However, species richness at a given site never exceeded five species per square meter. Total aboveground live biomass ranged from 400 to 800 g dry wt. m<sup>-2</sup> in the sawgrass plots compared with less than 200 g dry wt. m<sup>-2</sup> in the spikerush plots, and neither showed any clear patterns with distance (Fig. 6A). Notably, live biomass at the 0-km cattail site was less than at the 0.5 slough site, because this particular slough habitat was dominated by

dense maidencane (*Panicum hemitomom* J.A. Schultes) (Fig. 6A). The rest of the slough sites had virtually no standing dead plant material, while dead biomass at the sawgrass sites was roughly equal to live biomass (Fig. 6B). Spikerush and sawgrass plant tissues were consistently less than 0.005 g P kg<sup>-1</sup> dry wt. (Fig. 6C), with the exception of sawgrass 0.5 km from the canal, where tissue P content was 0.013 g P kg<sup>-1</sup> dry wt., or nearly as high as the P content of the cattail at the 0-km site (Fig. 6C).

Four primary species assemblages were delineated from the Shark River Slough transect (Fig. 3D). Group 1

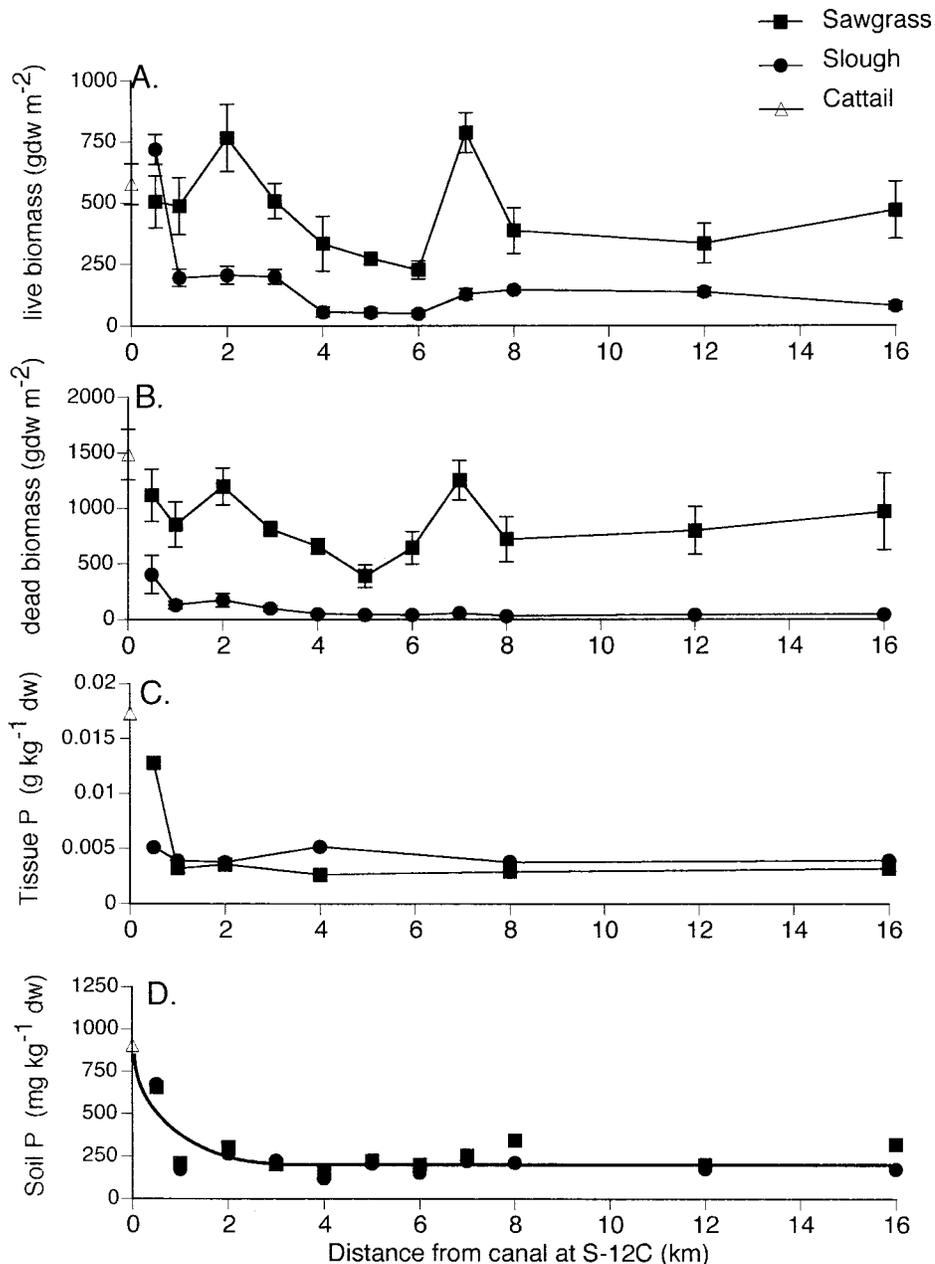


Fig. 6. Macrophyte and soils data from the Shark River Slough (Everglades National Park) transect. (A) Total aboveground standing live biomass; (B) total aboveground standing dead biomass; (C) tissue phosphorus content of the dominant species (sawgrass, spikerush, or cattail); (D) soil phosphorus (curve fit:  $C = 210 + 746e^{-1.65d}$ ,  $r^2 = 0.82$ ,  $p < 0.001$ ).

included the 0-km cattail site, but also included sawgrass sites from the entire 16-km length of this transect. Sawgrass sites also dominated Group 2, although the 2- and 6-km slough sites were also included in this group. The remainder of the slough sites were clearly distinguished in Groups 3 and 4 (Fig. 3D). The 0.5-km slough site formed its own group (Group 3) because it contained a greater mix of longer hydroperiod species than Group 2 and was dominated by *Panicum* spp.

The plant assemblages segregated based on soil P. Group 1, which included a cattail site and an enriched sawgrass site, had significantly higher soil P compared with Groups 2 and 4 (Fig. 3D). The slough (Group 4) and sawgrass assemblages (Group 2) had similar and lower soil P. The single site in Group 3, a *Panicum* spp.–

dominated slough, had moderately enriched soil. We found elevated P in soils only at sites less than 1 km from the canal (Fig. 6D). At sites 1 km from the canal inflow and further, soil P concentrations were relatively constant, averaging 218 mg kg<sup>-1</sup> and ranging between 120 and 346 mg kg<sup>-1</sup>. Our exponential model of soil P concentrations with distance was highly significant ( $r^2 = 0.82$ ,  $p < 0.001$ ) and predicted a baseline, unimpacted soil total P concentration of 210 mg kg<sup>-1</sup> (Fig. 6D).

### Taylor Slough Transect

The Taylor Slough transect was established in this study. While we were not able to make comparisons with 1989 transect data, we felt these data should be pre-

sented here to facilitate future transect comparisons. Taylor Slough is hydrologically separate from the Central Everglades drainage, which includes our other transects (Fig. 1A). It is part of a much smaller and more localized watershed, and the freshwater marshes here have shorter hydroperiods and marly soils. Both of these features complicate comparisons with our other 1999 transect data. However, the Taylor Slough transect is anchored at the main canal water input point. Notably, until late 1999, water entered Taylor Slough through the S-332 pump structure (Light and Dineen, 1994). Since then, water has been introduced to Taylor Slough via overbank flooding from the L-31W (from which the S-332 once pumped water) that is driven by the new

S-332D pump structure located upstream from the S-332 (Sklar et al., 2001).

Some cattail occurs in the deep-water pool immediately downstream of the S-332 pump structure, but because we sampled only marsh sites of typical water depth, we did not find cattail at any of our Taylor Slough transect sites. Overall, we found 25 plant species in Taylor Slough, and up to eight species per square meter at a given site. This was the highest species richness per square meter of the five transects. High diversity is typical of shorter hydroperiod Everglades wetlands, most of which are now found only in Everglades National Park (Gunderson, 1994; Busch et al., 1998). Total aboveground live biomass was less than 600 g dw m<sup>-2</sup>.

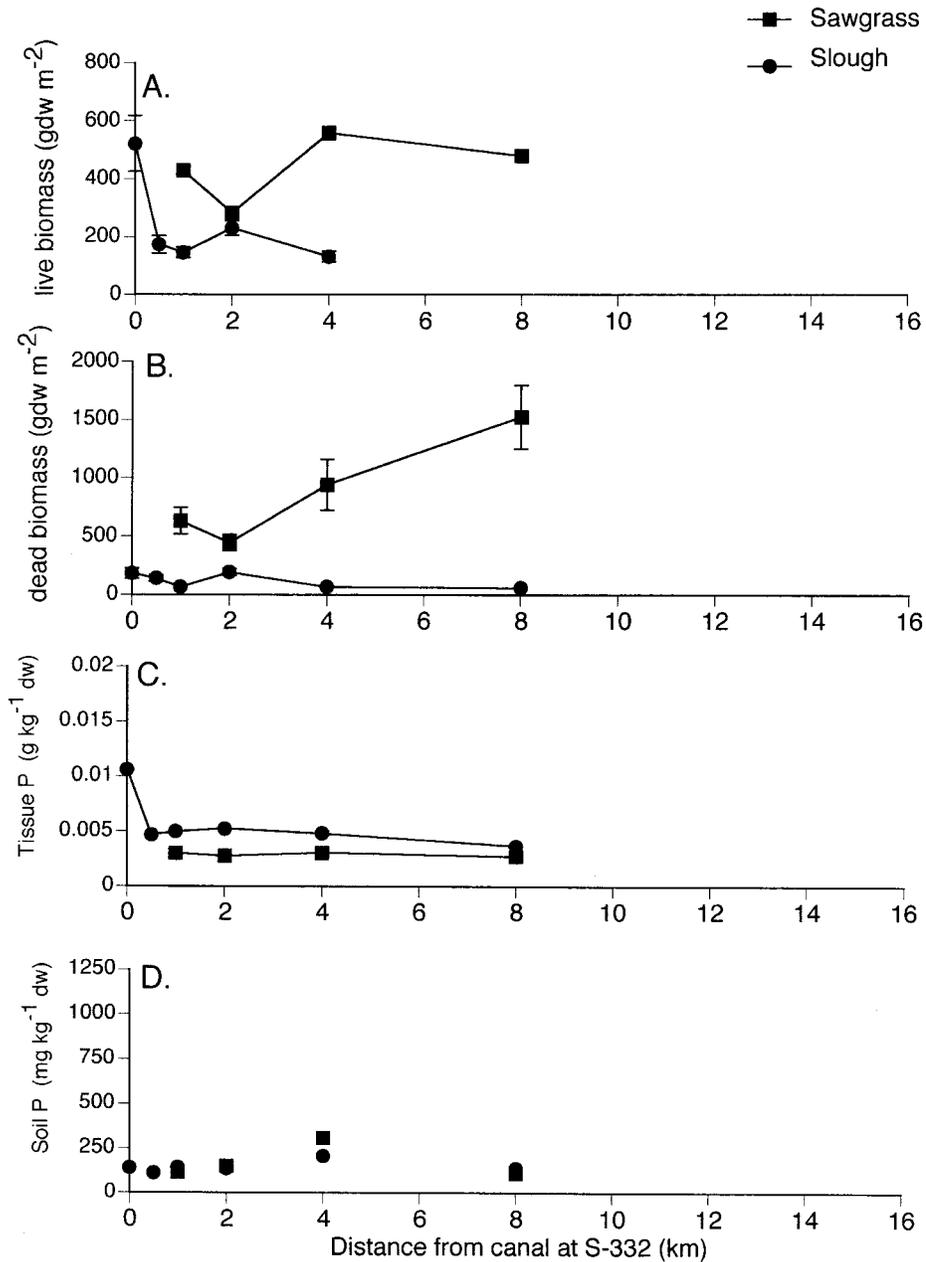


Fig. 7. Macrophyte and soils data from the Taylor Slough (Everglades National Park) transect. (A) Total aboveground standing live biomass; (B) total aboveground standing dead biomass; (C) tissue phosphorus content of the dominant species (sawgrass, spikerush, or cattail); (D) soil phosphorus (transect mean = 131 ± 16 mg kg<sup>-1</sup>, range = 109–151 mg kg<sup>-1</sup> excluding both 4-km marl soil sites).

$m^{-2}$  in the sawgrass plots and 200 g dry wt.  $m^{-2}$  in the slough plots, although the spikerush site adjacent to the canal had considerably higher biomass (Fig. 7A). As with most of our slough sites, we found virtually no standing dead plant material in Taylor Slough sites, but dead biomass at the sawgrass sites was approximately double the live biomass (Fig. 7B). Phosphorus in spikerush and sawgrass plant tissue was less than  $0.005 \text{ g P kg}^{-1}$  dry wt. except in spikerush immediately adjacent to the canal, where tissue P content was  $0.011 \text{ g P kg}^{-1}$  dry wt. (Fig. 7C). Because tissue P content in spikerush is highly sensitive to P enrichment (Daoust and Childers, 1999), this may be an early indication of P impacts associated with L-31W canal water inputs. Our soil P data at this 0-km site do not support this, however (see Fig. 7D).

The Taylor Slough plant community sampled along our 1999 transect separated into three primary species assemblages (Fig. 3E). Group 1 contained only the 0-km slough site, and differentiated from the other groups (by nearly 80% dissimilarity) because sawgrass was not present here, as it was in most slough and all sawgrass sites. Group 3 included the three slough sites with the highest species diversity per square meter, and Group 2 was made up of all remaining sawgrass and slough sites (Fig. 3E).

Soil P did not vary among the plant assemblages (Fig. 3E). We found soil P levels in Taylor Slough to be among the lowest measured for all transects (Fig. 7D). These soils were predominantly marl, while the other four transects were dominated by peat soils. The mean ash content of these soils exceeded 66%, compared with generally  $<20\%$  for most of the other soils studied. The P content of soils along this transect were generally between 110 and  $150 \text{ mg kg}^{-1}$  and averaged  $131 \text{ mg kg}^{-1}$ , with the exception of the 4-km site (Fig. 7D). At this site, soils were an organically enriched marl with an ash content of 49% by weight, making this particular site more analogous to the peat soils of our other transects than to the marl soils typical of Taylor Slough. There was no canal effect, so this transect did not conform to the exponential model.

## DISCUSSION

The Loxahatchee National Wildlife Refuge (also known as WCA-1) is the northernmost wetland region in the remaining Everglades (Fig. 1A). This 57 234-ha area is surrounded by a canal system but is not isolated by levees (Light and Dineen, 1994). Some of the deepest peat soils in the Everglades are found in WCA-1, and minor topographic variation in the depth of this peat results in a gradient of increasing water depth and hydroperiod from north to south (Jordan et al., 1997). The hydrologic regime is closely regulated by water level management (hence water table management) in the peripheral canals. This management intensifies the natural hydrologic gradient of dry conditions in the northern areas of WCA-1 and the ponding of water in the southern areas (Light and Dineen, 1994; Jordan et al., 1997). The water budget of WCA-1 is based largely on rainfall inputs, making it the most ombrotrophic system in the remaining Everglades (Loveless, 1959; Gunderson, 1994).

Although the peripheral canals do not represent large point sources of water to the Loxahatchee NWR, water quality impacts have been noted in wetlands near these canals (Doren et al., 1997). These effects are more pronounced in western Loxahatchee, along the L-7 and L-39 canals, which are closest to enriched agricultural water from the EAA (Fig. 1A). Between 1960 and 1987, the area of WCA-1 impacted by cattail-dominated marsh increased from 1 to 4%, and this western area accounted for much of this change (Richardson et al., 1990; Newman et al., 1997). A spatially intensive sampling of soil P levels throughout the Loxahatchee NWR showed the same pattern (Newman et al., 1997). Our macrophyte data showed that, in the past decade, these impacts have continued to worsen along the southwestern fringes (Fig. 2). Doren et al. (1997) found a total of 41 macrophyte species along their 1989 Loxahatchee transect. By 1999, species richness had dropped to 30 (a 27% decline), of which only 11 were found in both 1989 and 1999 (Table 2). This decadal decrease in species richness and shift in species composition was even more dramatic for native plant species (Fig. 8). Some of these changes

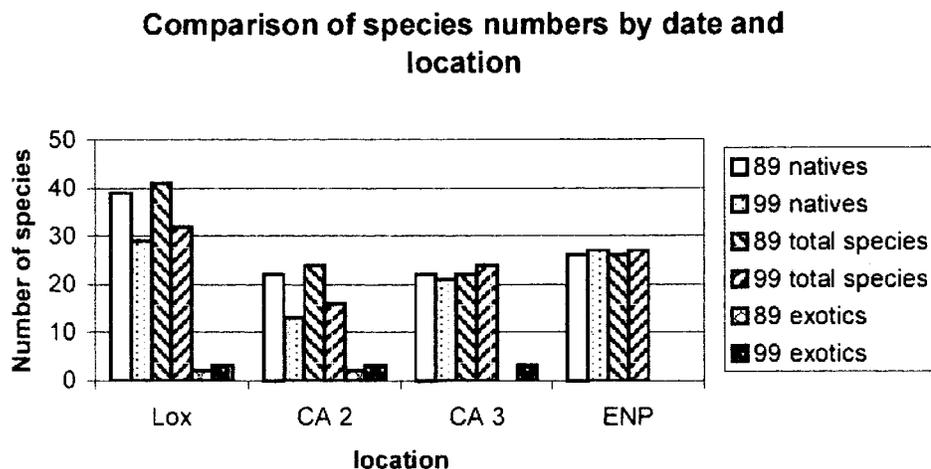


Fig. 8. Comparison of plant biodiversity from 1989 to 1999 by transect for the Loxahatchee, Water Conservation Area (WCA) 2A, WCA-3A, and Shark River Slough transects, including total numbers of native species versus exotic species from both samplings.

may be associated with floristic variability in plant presence depending on the time of year samples were collected, or with the microscale heterogeneity that typifies Everglades marsh plant community composition. However, we feel that these large-scale changes in community richness were real because we sampled a large number of vegetation quadrats along each transect, then pooled species presence data by transect. Few other Everglades studies have shown such marked changes in wetland plant community structure during only a 10-yr period of time (Davis and Ogden, 1994).

Stober et al. (2001) reported a decline in soil P concentrations from 1995 to 1999 in the Loxahatchee NWR, WCA-3A, and Shark River Slough, and they attributed this to some degree to the implementation of best management practices in the EAA. A comparison of our transect soil P data with those reported in Doren et al. (1997) also showed a systematic decline in soil P across the Everglades landscape from 1989 to 1999. However, we attribute this apparent system-wide change in soil P content to differences in sampling methods and analytical techniques, and temporal variability. Doren et al. (1997) collected soils as grab samples, which probably represented variable depths of the soil horizon, whereas we consistently sampled and homogenized the top 10 cm of soil. Furthermore, in 1989, some sites in the Loxahatchee NWR and Shark River Slough were sampled shortly after marsh fires, and ash probably enhanced surficial soil P levels reported for these sites by Doren et al. (1997; Faulkner and De La Cruz, 1982). Another source of consistent temporal variability between 1989 and 1999 is the fact that all 1989 samples were collected during a period of extended drought in south Florida, which may have generated anomalously high soil P concentrations related to the oxidation of surficial detritus and soil. In spite of these complications, patterns of soil P reported by Doren et al. (1997) can be compared with our data without direct comparisons of absolute P values. Both studies found elevated soil P concentrations across the western 2 km and the eastern 0.5- to 1-km fringes of the Loxahatchee NWR. This similarity of pattern suggests that dramatic changes have not occurred in soil total P in the intervening 10 years.

Virtually all of the nonatmospheric inputs of water to WCA-2A have elevated nutrient concentrations because of its proximity to the EAA. This 43 281-ha conservation area was first impounded with both canals and levees in the early 1950s (Light and Dineen, 1994). In the 1970s, it was decided that excess water in the EAA would be pumped south, into these canals, rather than north, into Lake Okeechobee (Sklar et al., 2001). At this point, P loading to WCA-2A increased dramatically (Walker, 1991). In the years immediately following this change in water management, the rate of change of sawgrass marsh or spikerush slough to impacted cattail marsh increased from 1% per year in 1973 to 4% in 1987, and the total area of impacted cattail marsh increased from 2054 ha (5% of total area) in 1973 to 16 017 ha (>33% of total area) in 1987 (Wu et al., 1997). This impacted area has continued to expand, and water qual-

ity is largely acknowledged to now be the primary control on vegetation change in WCA-2A (Urban et al., 1993; Rutchey and Vilchek, 1999; Wu et al., 1997). Soil P concentrations range from 400 to as high as 1650 mg kg<sup>-1</sup> dry wt. (Koch and Reddy, 1992; Debusk et al., 1994). Although some interior areas of WCA-2A are often called unimpacted, it is widely recognized the interior of WCA-2A may no longer be considered oligotrophic (Davis, 1994; Wu et al., 1997).

While WCA-2A is the most impacted region of the remaining Everglades, it is also the best studied. It is not possible in this venue to review all of the research conducted in WCA-2A. Numerous investigators have quantified soil P content with spatially articulate sampling regimes (Koch and Reddy, 1992; Craft and Richardson, 1993; and Debusk et al., 1994, among others). Vegetation change has been well documented, and the interacting effects of eutrophication, hydroperiod, and fire have been investigated here (e.g., Urban et al., 1993; Newman et al., 1996; Wu et al., 1997). Our focus was on revisiting a single transect oriented along the topographic flow trajectory from a key canal input (Fig. 1A). Most canal water enters WCA-2A along the northeast margin, through the S-10 spillway structures. The topographic gradient of nearly 1.5 m runs north-south, although some water does enter the system at the western and southern margins. Our transect macrophyte data showed that the impacted cattail zone had roughly doubled its width, from 2 km in 1989 to 4 km in 1999 (Fig. 4). Even more striking, within 4 km of the canal, where cattail dominated, we found that sawgrass had been completely extirpated from the community.

A more detailed look at the macrophyte community in WCA-2A showed a 33% decline in species richness from 1989 to 1999 (from 24 to 16 species; Table 2). Of the 24 plant species found by Doren et al. (1997), we found only eight in 1999, suggesting an even more dramatic elimination of 66% of plant species and an even more dramatic decline in native species (Fig. 8). Vaithyanathan and Richardson (1999) found a total of 39 macrophyte species at the 51 sites in WCA-2A that they spot-sampled in 1994. Of these, only 20 species also occurred on our WCA-2A transects, in either 1989 or 1999. They identified 6 of these 39 plant species as being indicative of unimpacted marshes, and 6 as being indicative of impacted marshes, and our comparison of these 12 species with Table 2 showed good coherence, with only two impacted species [inland leatherfern (*Acrostichum danaeifolium* Langsd. & Fisch.) and denseflower knotweed (*Polygonum densiflorum* Meisn.)] not found in our WCA-2A transects in either 1989 or 1999. Interestingly, 11 of the 39 species reported by Vaithyanathan and Richardson (1999) for WCA-2A in 1994 did not occur in any quadrat at any of our sites anywhere in the Everglades, in 1989 or 1999.

Soil P concentrations in WCA-2A showed an exponential decrease with distance beginning 4 km from the canal (Fig. 4D), while in 1989 this decline began 3 km from the canal (Doren et al., 1997). In both cases, soil P content was consistently high at sites 3 to 4 km from

the canal, suggesting that (i) the soil had reached P saturation within this zone in 1989 and (ii) this region of saturation had expanded 1 km further by 1999 (Fig. 4D). Similarly, Reddy et al. (1998) found that this impacted area of WCA-2A had increased in extent between 1990 and 1997.

Water Conservation Area 3A is the largest of these impounded and managed regions. It is in the heart of the "ridge and slough" portion of the Everglades landscape, where sawgrass ridge strands and tree islands alternate with deeper sloughs in an orientation parallel to the direction of historical water flow (Davis, 1943; Loveless, 1959). Water Conservation Area 3A is hydrologically divided into northern and southern regions by "Alligator Alley" (Interstate Highway 75; Fig. 1A). The northern area of WCA-3A has inundation frequencies ranging from 32 to 61% of the year and mean water depths ranging from 10 to 18 cm (1972–1984 data; David, 1996). In contrast, southern WCA-3A is managed as one of the wettest regions of the Everglades, with the marsh inundated more than 96% of the time to mean depths of more than 60 cm (1972–1984; David, 1996) near where our transect was located (Fig. 1A). Water no longer flows from north to south through the WCA-3A region. Water tends to impound at the southern margin, and there is essentially never flow from Tamiami Canal north into WCA-3A (Light and Dineen, 1994; Fig. 1A). Thus, this transect was different in that it was not oriented along a gradient of canal influence. Our soil P data reflect this lack of canal nutrient loading (Fig. 5D). One site in direct proximity to the canal had elevated soil P compared with the remaining sites. This was probably a canal effect on canal bank soils that did not extend into the marsh.

The macrophyte data also suggested an abatement of nutrient loading impacts to southern WCA-3A. In 1989, Doren et al. (1997) found cattail in 100% of their sampling quadrats at the site adjacent to the Tamiami canal. A decade later, we still found cattail at the slough site nearest the canal (0 km), but it did not occur at any other site (Fig. 5). Plant community composition changes from 1989–1999 were very different in WCA-3A compared with WCA-2A or Loxahatchee NWR. Doren et al. (1997) found a total of 21 plant species in southern WCA-3A in 1989, and by 1999 this had increased to 22 species (Fig. 8). It is difficult to conclude a trend of increasing biodiversity in the WCA-3A plant community from these data, but it is clear that the 28 and 33% decline in species richness seen in the Loxahatchee NWR and WCA-2A, respectively, did not happen here. Interestingly, this slight increase in species richness was a result of 13 new species in 1999 while 11 of the 1989 plants were not found a decade later (Table 2).

The Shark River Slough transect (ENP) was located across the Tamiami Canal from the WCA-3A sampling, in both the Doren et al. (1997) study and our work. Between 1989 and 1999, water levels and water flow into Shark River Slough were controlled mainly by four large gated structures along this canal: the S-12 structures (Light and Dineen, 1994; the 1989 and 1999 tran-

sects were anchored at the S-12C structure). Management of the S-12 structures has decreased water levels, hydroperiods, and flow velocities in Shark River Slough compared with pre-drainage estimates (Light and Dineen, 1994). Although such hydrologic changes are expected to influence all biotic components of the Everglades ecosystem, this influence may be manifest in complex ways (Gunderson, 1994). For example, Busch et al. (1998) were unable to find a clear relationship between overall marsh macrophyte cover and water depth at three Shark River Slough sites, and they attributed this to complexities associated with hydrologic history, fire frequency, and nutrient effects. This transect study was designed to address changes in the latter between 1989 and 1999.

In 1999, cattail was still present at the 0-km site nearest the canal, but this community had not expanded to the 0.5-km site (Fig. 6). Shark River Slough was not characterized by the same aggressive advancement of cattail that we documented in WCA-2A and along the western margin of the Loxahatchee NWR. Of the 27 plant species found along the Shark River Slough transect, 14 were also found in 1989, when Doren et al. (1997) found a total of 26 plant species (Table 2). Thus, neither Shark River Slough nor WCA-3A showed the large decline in plant species richness, from 1989–1999, that we observed in WCA-2A and the Loxahatchee NWR. Notably, none of the 13 plant species found in 1999 but not in 1989 were newly invaded exotics (Table 2, Fig. 8). Busch et al. (1998) conducted tri-annual plant surveys of selected sites in Shark River Slough from 1985–1995. Of the 30 species identified in their surveys, 20 occurred in the species list of either this study, the 1989 study, or both. The remaining 10 species tended to either be submerged aquatic plants (e.g., *Chara* spp., *Valisneria* spp., and *Potamogeton* spp.), which we did not sample, or had only one occurrence in the Busch et al. (1998) dataset (e.g., *Phyla* spp., *Thalia* spp., and *Muhlenbergia* spp.).

Phosphorus in plant tissues was elevated at only the 0-km cattail site (0.017 g kg<sup>-1</sup> dry wt.) and the 0.5-km sawgrass marsh site in Shark River Slough (0.013 g kg<sup>-1</sup> dry wt.). Background (unimpacted) tissues from both spikerush and sawgrass were less than 0.005 g P kg<sup>-1</sup> dry wt. (Fig. 6C). We found similar and consistent tissue P values at unimpacted sites of all four transects. Sawgrass is quite sensitive to increases in P availability, and its tissue P content increases rapidly with P enrichment (Steward and Ornes, 1983; Daoust and Childers, 1999; Lorenzen et al., 2001). It is thus possible that sawgrass tissue P content may be an early indicator of enrichment conditions that will (eventually) lead to cattail invasion. The elevated tissue P in sawgrass at our 0.5-km site corresponded with soil P concentrations of approximately 660 mg kg<sup>-1</sup> at this site (Fig. 6C,D), suggesting canal impacts, although cattail has not yet advanced this far into the marsh. In 1999, we found elevated P soils only at sites less than 1 km from the canal. These values contrast with the 1989 pattern that showed soil P above background levels (about 300 mg kg<sup>-1</sup>) at sites up to 4 km from the Tamiami Canal (Doren et al., 1997). This

area of Shark River Slough, like many portions of the southern Everglades, contains a mosaic pattern of peat soils mixing with marl soils, and marl soils tend to have lower P concentrations per unit dry weight. Data on the ash content of our 1999 Shark River Slough soils (not shown) suggested that several sites had soils with relatively high mineral matter. We do not know the number of 1989 samples that were peat versus marl soils. However, in such spatially heterogeneous conditions, even very small differences in sampling locations between 1989 and 1999 could account for substantial differences in soil P.

In 1999, we encountered most exotic plants near canals in areas with elevated soil P levels and cattail. However, small-leaf climbing fern [*Lygodium microphyllum* (Cav.) R. Br.] (an exotic viny fern) was found at several sawgrass sites in mid- to eastern portions of Loxahatchee NWR. Small-leaf climbing fern was first reported in 1989, and had spread to more than 12% (9175 ha) of Loxahatchee NWR by 1997 (Brandt and Black, 2001). Most exotics tended to occur in Loxahatchee NWR and WCA-2A, the northern WCA most proximal to the EAA. Five of the six exotic species found in either 1989 or 1999 occurred in WCA-1 or WCA-2A (Table 2). Among all four transects, we found a total of four exotic species in 1989 (barnyardgrass [*Echinochloa crusgalli* (L.) Beauv.], Peruvian primrose-willow [*Ludwigia peruviana* (L.) Hara], napiergrass [*Pennisetum purpureum* Schumach.], and curly dock [*Rumex crispus* L.]) and five in 1999 (barnyardgrass, common water hyacinth [*Eichhornia crassipes* (Mart.) Solms], small-leaf climbing fern, nakedstem dewflower [*Murdannia nudiflora* (L.) Brenan], and curly dock) (Table 2, Fig. 8). Water hyacinth, a floating aquatic plant that was only observed at the 0-km site at WCA-1 in 1999, may have been introduced into the cattail marsh from the adjacent canal. Overall, while the number of exotic species increased along most transects, this increase was not statistically significant and may not have been directly tied to nutrient additions. However, continued environmental alterations have clear implications for future increases in both the number and extent of exotic species invasions (Cuddigy and Stone, 1990; Cronk and Fuller, 1995).

## CONCLUSIONS

Our objective in this study was to resample a series of wetland transects, representing a range of Everglades wetland environments, that were originally sampled in 1989 (Doren et al., 1997). Our goal was to determine the extent to which the impacts of P inputs to these wetlands have changed in the intervening decade. We hypothesized that the expansion cattail-dominated marsh would be minor along these transects, given that the quality of water entering most of these Everglades marshes has improved during the intervening decade. At the same time, we did not expect to detect any reductions in soil P or return from cattail marsh to sawgrass or spikerush slough marsh in the impacted portions of these transects.

Our hypothesis tested true along both northern Everglades transects. The impacted cattail marsh along the southwest margin of the Loxahatchee NWR, adjacent to the S-6 pump structure, had expanded from 0.5 to 1 km into the marsh from 1989–1999. Sawgrass was extirpated within 1 km of the canal during this time, and at our 2-km site we found a cattail–sawgrass mixed community. In WCA-2A, the impacted cattail marsh expanded from 2 to 4 km from the canal during this decade, and sawgrass was no longer present within 4 km of the canal in 1999. This pattern did not follow in our more southern transects. Along both the WCA-3A and Shark River Slough transects, we found cattail only immediately adjacent to the canal (at the 0-km sites), and were able to sample both sawgrass and spikerush marsh plots at all sites along our 16-km transects. Doren et al. (1997) reported the same patterns, suggesting little change in plant community status in northern Everglades National Park during the 1990s.

Differences in sampling intensity (and thus sampling area) between the 1989 and 1999 surveys complicated interpretation of decadal changes in species richness in the northern Everglades. However, in our 1999 sampling we either sampled a greater area (e.g., Loxahatchee NWR: 27 sites in 1989 vs. 45 sites in 1999) or a nearly equivalent area (e.g., WCA-2A: 13 sites in 1989 vs. 9 sites in 1999), and still found that plant species richness declined significantly ( $p < 0.001$ ) in both areas during this time. A reduction of species richness due to nutrient enrichment of wetlands, particularly oligotrophic wetlands such as the Everglades, has been widely reported (Odum et al., 1975; Whigham and Simpson, 1978; Guntenspergen and Stearns, 1981). We observed little change in species richness in the more southerly areas of the Everglades, although we sampled more sites in 1999 (e.g., WCA-3A: 13 sites in 1989 vs. 24 sites in 1999; Shark River Slough: 15 sites in 1989 vs. 23 sites in 1999). The decline in species richness in WCA-2A and Loxahatchee NWR from 1989 to 1999 did not appear to be an artifact of different sampling intensities.

We also saw dramatic changes in species composition along all four transects from 1989 to 1999. Only three species were present in all locations in all years: sawgrass, spikerush, and cattail. Such changes in plant community composition is also widely recognized as an effect of nutrient additions in wetlands (Gorham, 1956; Gosselink and Turner, 1978; Aerts and Berendse, 1988; Hayati and Proctor, 1990). While no trends or patterns to the vegetation shifts are yet discernable from our two samplings, these dramatic shifts in species composition have huge implications for southern Florida restoration efforts. The widespread conversion of slough communities to sawgrass marsh since the 1960s represents a similar shift in species composition within communities that has been attributed to alterations in hydroperiod and fire regimes (Davis et al., 1994) and to dramatic reductions in water flow (McVoy and Crisfield, 2001). These shifts seem to be tied to anthropogenic perturbations rather than environmental stochasticity. As such, the trajectories of these vegetative community changes are unpredictable and may lead to shifts in species domi-

nance that will dramatically alter the aspect and ecology of the Everglades.

Soil P patterns generally mirrored the vegetation patterns. We found elevated soil P values up to 1 km from the canal along our Loxahatchee transect, as did Doren et al. (1997). Cattail marsh had expanded to this distance by 1999, but the community at this site in 1989 was a cattail-sawgrass mix, suggesting that vegetation changes lagged soil P increases here. In WCA-2A, the saturated zone of high soil P had moved from 3 km in 1989 to more than 4 km in 1999, which was consistent with the expansion of cattail and extirpation of sawgrass during the same time period at these locations. We found no canal impacts on soil P patterns along the southern margin of WCA-3A. We found Shark River Slough soils to be impacted within 1 km from the canal and our Taylor Slough transect data suggested that variable organic matter content had a stronger influence on soil P than did canal impacts. Soil P patterns in WCA-2A were similar between 1989 and 1999, and the zone of P saturation increased. This suggested that, although water column total P concentrations decreased in the 1990s in the northern Everglades (e.g., WCA-2A, Loxahatchee NWR) as a result of higher rainfall, greater water depths, and agricultural best management practices (Walker, 1999; Smith and McCormick, 2001), there was no reduction in the spatial extent of soil P impacts. One recent report suggested a synoptic decrease in soil P levels throughout the Everglades landscape during the 1990s (Stober et al., 2001), but we were unable to substantiate this decrease with any other published studies. In fact, DeBusk et al. (2001) documented an increase in soil total P concentrations in the northern Everglades (WCA-2A) from 1990 to 1998, both in enriched cattail marsh and interior sawgrass marsh. Regular sampling of these transects in the future, and consistency in field and analytical techniques in these samplings, will continue to add data that are valuable for critical management decisions and the adaptive management of Everglades restoration efforts.

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#### REFERENCES

Aerts, R., and F. Berendse. 1988. The effect of increased nutrient availability on vegetation dynamics in heathlands. *Vegetatio* 76: 63–69.

- Amador, J.A., and R.D. Jones. 1993. Nutrient limitations on microbial respiration in peat soils with different total phosphorus content. *Soil Biol. Biochem.* 25:793–801.
- Brandt, L.A., and D.W. Black. 2001. Impacts of the introduced fern, *Lygodium microphyllum*, on the native vegetation of tree islands in the Arthur R. Marshall Loxahatchee National Wildlife Refuge. *Fla. Sci.* 64:191–196.
- Busch, D.E., W.F. Loftus, and O.L. Bass, Jr. 1998. Long-term hydrologic effects on marsh plant community structure in the southern Everglades. *Wetlands* 18:230–241.
- Clark, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18:117–143.
- Coale, F.J., F.T. Izuno, and A.B. Bottcher. 1994. Phosphorus drainage water from sugarcane in the Everglades Agricultural Area as affected by drainage rate. *J. Environ. Qual.* 23:121–126.
- Craft, C.B., and C.J. Richardson. 1993. Peat accretion and phosphorus accumulation along a eutrophication gradient in the northern Everglades. *Biogeochemistry* 22:133–156.
- Cronk, W.C.B., and J.L. Fuller. 1995. Plant invaders: The threat to natural systems. Chapman & Hall, London.
- Cuddigy, L.W., and C.P. Stone. 1990. Alteration of native Hawaiian vegetation: Effects of humans, their activities and introductions. Univ. of Hawaii Press, Honolulu.
- Daoust, R.J., and D.L. Childers. 1999. Controls on emergent macrophyte composition, abundance, and productivity in freshwater Everglades wetland communities. *Wetlands* 19:262–275.
- David, P.G. 1996. Changes in plant communities relative to hydrologic conditions in the Florida Everglades. *Wetlands* 16:15–23.
- Davis, J.H. 1943. The nature features of southern Florida, especially the vegetation and the Everglades. *Florida Geol. Survey Bull.* 25.
- Davis, S.M. 1994. Phosphorus inputs and vegetation sensitivity in the Everglades. p. 357–378. *In* S.M. Davis and J.C. Ogden (ed.) *Everglades: The ecosystem and its restoration*. St. Lucie Press, Delray Beach, FL.
- Davis, S.M., L.H. Gunderson, W.A. Park, J.R. Richardson, and J.E. Mattson. 1994. Landscape dimension, composition, and function in a changing Everglades ecosystem. p. 419–444. *In* S.M. Davis and J.C. Ogden (ed.) *Everglades: The ecosystem and its restoration*. St. Lucie Press, Delray Beach, FL.
- Davis, S.M., and J.C. Ogden. 1994. *Everglades: The ecosystem and its restoration*. St. Lucie Press, Delray Beach, FL.
- DeAngelis, D., and R. White. 1994. Ecosystems as products of spatially and temporally varying driving forces, ecological processes, and landscapes: A theoretical perspective. p. 9–27. *In* S.M. Davis and J.C. Ogden (ed.) *Everglades: The ecosystem and its restoration*. St. Lucie Press, Delray Beach, FL.
- DeBusk, W.F., S. Newman, and K.R. Reddy. 2001. Spatio-temporal patterns of soil phosphorus enrichment in Everglades Water Conservation Area 2A. *J. Environ. Qual.* 30:1438–1446.
- DeBusk, W.F., K.R. Reddy, M.S. Koch, and Y. Wang. 1994. Spatial distributions of soil nutrients in a northern Everglades marsh: Water Conservation Area 2A. *Soil Sci. Soc. Am. J.* 58:543–552.
- Doren, R.F., T.V. Armentano, L.D. Whiteaker, and R.D. Jones. 1997. Marsh vegetation patterns and soil phosphorus gradients in the Everglades ecosystem. *Aquat. Bot.* 56:145–163.
- Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol. Monogr.* 67:345–366.
- Faulkner, S.P., and A.A. De La Cruz. 1982. Nutrient mobilization following winter fires in an irregularly flooded marsh. *J. Environ. Qual.* 11:129–133.
- Gorham, E. 1956. The ionic composition of some bog and fen water in the English Lake District. *J. Ecol.* 44:142–152.
- Gosselink, J.G., and R.E. Turner. 1978. The role of hydrology in freshwater wetland ecosystems. p. 63–78. *In* R.E. Good (ed.) *Freshwater wetlands*. Academic Press, New York.
- Gunderson, L.H. 1994. Vegetation of the Everglades: Determinants of community composition. p. 323–340. *In* S.M. Davis and J.C. Ogden (ed.) *Everglades: The ecosystem and its restoration*. St. Lucie Press, Delray Beach, FL.
- Guntenspergen, G.R., and F. Stearns. 1981. Ecological limitations on wetland use for waste-water treatment. p. 273–284. *In* Proc. Midwest Conf. on Wetland Values and Management. Minnesota Water Planning Board, Minneapolis.

- Harris, W., and W. Hurt. 1999. Introduction to soils of subtropical Florida. p. 143-170. *In* K.R. Reddy et al. (ed.) Phosphorus biogeochemistry in subtropical ecosystems. Lewis Publ., New York.
- Hayati, A.A., and M.C.F. Proctor. 1990. Plant distribution in relation to mineral nutrient availability and uptake on a wet-heath site in south-west England. *J. Ecol.* 78:134-151.
- Howard-Williams, C. 1985. Cycling and retention of nitrogen and phosphorus in wetlands: A theoretical and applied perspective. *Freshwater Biol.* 15:391-431.
- Jordan, F., H.L. Jelks, and W.M. Kitchens. 1997. Habitat structure and plant community composition in a northern Everglades wetland landscape. *Wetlands* 17:275-283.
- Koch, M.S., and K.R. Reddy. 1992. Distribution of soil and plant nutrients along a trophic gradient in the Florida Everglades. *Soil Sci. Soc. Am. J.* 56:1492-1499.
- Light, S.S., and J.W. Dineen. 1994. Water control in the Everglades: A historical perspective. p. 47-84. *In* S.M. Davis and J.C. Ogden (ed.) Everglades: The ecosystem and its restoration. St. Lucie Press, Delray Beach, FL.
- Lorenzen, B., H. Brix, I.A. Mendelsohn, K.L. McKee, and S.L. Miao. 2001. Growth, biomass, allocation and nutrient use efficiency in *Cladium jamaicense* and *Typha domingensis* as affected by phosphorus and oxygen availability. *Aquat. Bot.* 70:117-133.
- Loveless, C.M. 1959. A study of the vegetation in the Florida Everglades. *Ecology* 40:1-9.
- McCormick, P.V., S. Newman, S. Miao, D.E. Gawlik, D. Marley, K.R. Reddy, and T. Fontaine. 2001. Effects of anthropogenic phosphorus inputs on the Everglades. p. 83-126. *In* J.W. Porter and K.G. Porter (ed.) The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. CRC Press, Boca Raton, FL.
- McCormick, P.V., P.S. Rawlik, K. Lurding, E.P. Smith, and F.H. Sklar. 1996. Periphyton-water quality relationships along a nutrient gradient in the northern Florida Everglades. *J. North Am. Benthol. Soc.* 15:433-449.
- McCune, B., and M.J. Mefford. 1999. PC Ord: Multivariate analysis of ecological data. Version 4.14. MjM Software Design, Gleneden Beach, OR.
- McVoy, C., and E. Crisfield. 2001. The role of water and sediment in the ridge and slough landscape. South Florida Water Management Dist., West Palm Beach, FL.
- Miao, S., and W.F. DeBusk. 1999. Effects of phosphorus enrichment on structure and function of sawgrass and cattail communities in the Everglades. p. 275-299. *In* K.R. Reddy et al. (ed.) Phosphorus biogeochemistry in subtropical ecosystems. Lewis Publ., New York.
- Miao, S., S. Newman, and F.H. Sklar. 2000. Effects of habitat nutrients and seed sources on growth and expansion of *Typha domingensis*. *Aquat. Bot.* 68:297-311.
- Mitsch, W.J., and J.G. Gosselink. 2000. Wetlands. 3rd ed. John Wiley & Sons, New York.
- Newman, S., J.B. Grace, and J.W. Koebel. 1996. Effects of nutrients and hydroperiod on *Typha*, *Cladium*, and *Eleocharis*: Implications for Everglades restoration. *Ecol. Appl.* 6:774-783.
- Newman, S., K.R. Reddy, W.F. DeBusk, Y. Wang, G. Shih, and M.M. Fisher. 1997. Spatial distribution of soil nutrients in a northern Everglades marsh: Water Conservation Area 1. *Soil Sci. Soc. Am. J.* 61:1275-1283.
- Noe, G.B., D.L. Childers, and R.D. Jones. 2001. Phosphorus biogeochemistry and the impacts of phosphorus enrichment: Why is the Everglades so unique? *Ecosystems* 4:603-624.
- Odum, H.T., K.C. Ewel, W.J. Mitsch, and J.W. Ordway. 1975. Recycling treated sewage through cypress wetlands in Florida. p. 35-67. *In* F.M. D'itri (ed.) Waste-water renovation and reuse. Marce Kelder, New York.
- Qualls, R.G., and C.J. Richardson. 1995. Forms of soil phosphorus along a nutrient enrichment gradient in the northern Everglades. *Soil Sci.* 160:183-198.
- Reddy, K.R., Y. Wang, W.F. DeBusk, M.M. Fisher, and S. Newman. 1998. Forms of soil phosphorus in selected hydrologic units of the Florida Everglades. *Soil Sci. Soc. Am. J.* 62:1134-1147.
- Richardson, J.R., W.L. Bryant, W.M. Kitchens, J.E. Mattson, and K.R. Pope. 1990. An evaluation of refuge habitats and relationships to water quality, quantity, and hydroperiod. A synthesis report. ARM Loxahatchee NWR, Boynton Beach, FL.
- Richardson, C.J., G.M. Ferrel, and P. Vaithianathan. 1999. Nutrient effects on stand structure, resorption efficiency, and secondary compounds in Everglades sawgrass. *Ecology* 80:2182.
- Rutchev, K., and L. Vilchek. 1999. Air photointerpretation and satellite imagery analysis techniques for mapping cattail coverage in a northern Everglades impoundment. *Photogramm. Eng. Remote Sens.* 65:185-191.
- Sklar, F., C. McVoy, R. VanZee, D.E. Gawlik, K. Tarboton, D. Rudnick, S. Miao, and T. Armentano. 2001. Effects of altered hydrology on the ecology of the Everglades. p. 39-82. *In* J.W. Porter and K.G. Porter (ed.) The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. CRC Press, Boca Raton, FL.
- Smith, E.P., and P.V. McCormick. 2001. Long-term relationship between phosphorus inputs and wetland phosphorus concentrations in a northern Everglades marsh. *Environ. Monit. Assess.* 68:153-176.
- Solorzano, L., and J.H. Sharp. 1980. Determination of total dissolved P and particulate P in natural waters. *Limnol. Oceanogr.* 25:754-758.
- SPSS. 1998. Systat 8.0 for Windows. SPSS, Chicago, IL.
- Steward, K.K., and W.H. Ornes. 1975. The autecology of sawgrass in the Florida Everglades. *Ecology* 56:127-140.
- Steward, K.K., and W.H. Ornes. 1983. Mineral nutrition of sawgrass (*Cladium jamaicense* Crantz) in relation to nutrient supply. *Aquat. Bot.* 16:349-359.
- Stober, Q.J., K. Thornton, R. Jones, J. Richards, C. Ivey, R. Welch, M. Madden, J. Trexler, E. Gaiser, D. Sheidt, and S. Rathbun. 2001. South Florida ecosystem assessment: Phase I/II (summary)—Everglades stressor interactions: Hydropatterns, eutrophication, habitat alteration, and mercury contamination. 904-R-01-002. USEPA, Atlanta, GA.
- Urban, N.H., S.M. Davis, and N.G. Aumen. 1993. Fluctuations in sawgrass and cattail densities in Everglades Water Conservation Area 2A under varying nutrient, hydrologic, and fire regimes. *Aquat. Bot.* 46:202-223.
- Vaithianathan, P., and C.J. Richardson. 1999. Macrophyte species changes in the Everglades: Examination along a eutrophication gradient. *J. Environ. Qual.* 28:1347-1358.
- Walker, W.W. 1991. Water quality trends at inflows to Everglades National Park. *Water Resour. Bull.* 27:59-72.
- Walker, W.W. 1999. Long-term water quality trends in the Everglades. p. 447-466. *In* K.R. Reddy et al. (ed.) Phosphorus biogeochemistry in subtropical ecosystems. Lewis Publ., New York.
- Whigham, F.F., and R.L. Simpson. 1978. Nitrogen and phosphorus movement in a freshwater tidal wetland receiving sewage and effluent. p. 2189-2203. *In* Coastal Zone '78. Proc. Symp. Technical, Environmental, Socioeconomic and Regulatory Aspects of Coastal Zone Management. ACSE, San Francisco, CA.
- Wu, Y., F.H. Sklar, and K. Rutchev. 1997. Analysis and simulations of fragmentation patterns in the Everglades. *Ecol. Appl.* 7:268-276.