I. Title: Marsh vegetation patterns and soil phosphorus gradients in the Everglades ecosystem

II. Names of Authors: Robert F. Doren, Thomas V. Armentano, Louis D. Whiteaker, and Ronald D. Jones

III. Postal Addresses: Robert F. Doren

Thomas V. Armentano

Louis D. Whiteaker

South Florida Natural Resource Center

40001 SR 9336

Homestead, Florida, 33034 USA

Ronald D. Jones

Florida International University

Southeast Environmental Research Program

University Park Campus

Miami, Florida 33199 USA.

IV. Telephone and fax number of corresponding author:

Robert F. Doren

Telephone: 305-242-7800

Fax: 305-242-7836

Email: Bob_Doren@NPS.GOV

V. Present Addresses of Author(s):

Louis D. Whiteaker

Bureau of Land Management

2795 Anderson Avenue

Bldg 25

Klamath Falls, Oregon 97603 USA

VI. Correspondence Address for Proofs:

Robert F. Doren, Acting Director

South Florida Natural Resource Center

Everglades National Park

40001 State Road 9336

Homestead, Florida 33034-6733 USA

Abstract

In order to test the hypothesis that phosphorous enrichment is modifiying Everglades marsh community composition, we sampled vegetation and soil phosphorus concentrations along four transects in separate areas representative of varying environmental conditions within the Everglades region. Every 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. Species frequency, and soil phosphorus data were collected.

We compared soil phosphorus levels and determined correlations for between-species occurrences and between-species frequencies and phosphorus concentrations with distance from nutrient source (water flow structure). We compared within-transect effects and between-transect effects from north to south across the Everglades region.

In all cases phosphorus levels and presence of Typha domingensis showed a negative relationship to distance from flow structure, while 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.

Key Words: Everglades, Macrophytes, Community Composition, Phosphorus, Eutrophication, Freshwater marsh

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 three to twelve months per year (Fig. 1) (Kushlan, 1990; Fennema et al., 1994). The original Everglades exceeded 10,000 km^2 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 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 to 5.0 μgL^{-1} as soluble reactive phosphorus (Boyd and Hess, 1970; Koch and Reddy, 1992) or lower and less than 100.0 μgL^{-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_2 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 leves, 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 (Gunderson, 1994; Kushlan, 1990; Wood and Tanner, 1990). Recently however, Typha spp. has been 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 althougth the presence of Thypha pollen suggensts 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 levels 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. Based on observation and prelimnary data we developed an a priori hypothesis that phosphorous enrichment is a major factor explaining the observed increase in Typha in the northern Everglades. The present work was conducted to provide information essential for testing the hypothesis - quantitative relationships between soil phosphorous levels and marsh species distribution in a range of sites varying in exposure to nutrient-enriched waters. 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 enrichments.

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 50cm 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 et al. (1948), and Gleason and Stone (1994).

2. Methods

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 approximately 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 approximately 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 approximately 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. Transects lengths were chosen in each area to ensure that each transect originated at flow structures or major canals directing 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/absence data were collected rather than cover estimates, since fire reduced cover in some areas of the transects and not others, but had not eliminated exisiting species (Streng, et al. 1995). 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 meter line parallel to each transect. A 1 m^2 frame divided into four 0.25 m^2 sample quadrants was placed at 3 locations along one side and 2 locations along the other side of the 10 meter 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^2 in area were sampled at each nutrient sampling point, exceeding the 2.5 m^2 area suggested by Porter (1967) as adequate for sampling prairies in southern Florida.

Cladium and wet prairie communities were sampled seperately 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. Histograms were produced using SPC Harvard Graphics ver. 2.3. 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.

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 to 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 (as described above), 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 (6 cores per station). Cores were transported to the laboratory and the top 10 cm screened for roots and large debris. Individual samples were then mixed until homogenous and placed in 125 ml cups and dried at 70˚C for 48 hours. Then the entire sample was ground to a fine powder in a Wiley Mill and stored in desiccating cabinet. After collecting samples using the PVC coring devices, samples from all transects were collected by hand from each community type at the same locations (4 composite samples each station). The TP content of soil samples did not differ significantly between collection techniques, therefore, only samples collected by hand were used for the remainder of the

sampling events. All data presented here were obtained from samples collected by hand. Soil TP was measured using the ashing/acid hydrolysis method described by Solorzano and Sharp (1980). The resulting soluble reactive PO_4 (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 µg of P per gram of dry weight soil. 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_2PO_4 were run with each batch of soil samples. In all cases comparison with NBS standards were within the precision of the NBS certificate. Values for each sample represent the mean for each sampling location.

3. Results

CA11 Transect

Three species assemblages along the transect are delineated by dendrogram (Fig. 3). The Group 1 assemblage, dominated by Typha, was found nearest the flow structures where soil phosphorus concentrations ranged from 1460 to 2380 $\mu g.g^{-1}$ (Fig. 3). 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 $\mu g.g^{-1}$ 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 of $\mu g.g^{-1}$. 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 $\mu g.g^{-1}$ 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 (Figs. 4 and 5). Total soil phosphorus declined by nearly six-fold within 4 km of the western flow structure and by more than half within 2 km of the eastern flow structure. Figure 4 and 5 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 to 1000 $\mu g.g^{-1}$ 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 spike rush distributions were positively correlated at statistically significant levels with each other and with distance from flow structures and negatively correlated with soil phosphorus levels and Typha presence (Table 1).

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-dominated "weedy" community (Fig. 6). A. australis and Rumex crispis were important secondary species found in the Thypha assemblages. Although some intermixture of Cladium and Typha communities occurred between 2 and 6 km from the transect origin at the canal (Fig. 7), the highest TP levels (2060 to 1790 $\mu g.g^{-1}$ of soil) were associated with Typha stands. The lowest TP (510 to 840 $\mu g.g^{-1}$) areas were occupied by Cladium and open marsh communities (Figs. 6 and 7). 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 6 km 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.

CA3A Transect

Like the previously discussed transects, vegetation patterns along transect CA3A differentiated into three associations: Cladium-dominated, Typha-dominated and open marsh communities dominated by Eleocharis spp., with Utricularia spp., Nymphaea odorata (Figs. 8, 9 and 10). 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. 9 and 10). 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 and periphyton occurred in every plot (Fig. 9 and 10).

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 ($r=-0.76$), 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 ($P<0.05$).

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. 11). 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 $\mu g.g^{-1}$ (Figs. 12 and 13). 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 distance and beyond (Fig. 13). 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 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 oppossed to a functional) relationship indicating that phosphorus enrichment caused the observed marsh compositional shifts. While we were not able to evaluate all the potential environemental 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, 1975b, 1983; Scheidt et al., 1989) and field analysis under ambient conditions (Davis, 1991, 1994; Richardson et al., 1990; Hayati and Proctor, 1990; Huenneke et al., 1990).

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 (Huenneke et al., 1990; Koide et al., 1988). 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, 1993; 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 conservation areas as our study 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 Amaranthus australis and Rumex 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 Phillipp, 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 (Uban et al. (in press).

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 (Hofstetter and Parsons, 1975; Werner, 1975; Herndon et al., 1991), particularly when fires kill sawgrass roots or is 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 (Herndon et al. 1991; Wade et al., 1980). Reestablishment of Cladium communities following damaging fire may take several years but does not involve Typha establishment (Herndon, et al. 1991; Wade et al., 1980). Typically, fires reduce above ground macrophyte biomass without eliminating them. Thus potentially confounding effects of fire on vegetation patterns in this study were reduced by relying on presence/absence data for analysing 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., 1994) 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 march 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 hae existed in the Everglades, ranging from deep-water sloughs flooded all year to marshes flooded vor only a month or two in most years. In non of these communities has Typha been more that 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 (1994). 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 to 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.

5. Acknowledgements

We thank Mark McMahon and Kathy Fanning for their expert assistance with field identifications. We thank Mark Maffei, Bob Payton, and Burkette Neely for their field and logistical support and we thank the Everglades National Park seasonal staff, especially K. O., who assisted with field data collection. We thank Barbara Bedford, Ron Raschke, George Dalrymple and Susan Bratton for their review of sampling techniques and analyses and we thank Paulette Johnson for her statistical review and assistance.

References

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

Belanger, T.V., Scheidt, D.J., and Platko II, J.R., 1989. Effects of Nutrient Enrichment on the Florida Everglades. Lake and Reservoir Management (5)1: 101-111.

Boyd, D.E. and Hess, L.W., 1970. Factors in influencing shoot production and mineral nutrient levels in Typha latifolia. Ecology 51: 276-300.

Covin, J.D. and Zedler, J.B., 1988. Nitrogen effects on Spartina foliosa and Salicornia virginica in the salt marsh at Tijuana Estuary, California.

Craighead, F.C., 1971. The Trees of South Florida. University of Miami Press, Coral Gables, Florida. 212 pp.

Day, R.T., Keddy, P.A., McNeill, J, and Carleton, T.J., 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. Ecology 69(4): 1044-1054.

Davis, J. H. 1946. The peat deposits of Florida. Florida Geological Survey Bulletin. No. 30.

Davis, S.M., 1991. Growth, decomposition and nutrient retention of Cladium jamaicense Crantz and Typha domingensis Pers. in the Everglades. Florida Aquatic Botany 40: 203-224.

Davis, S.M., 1994. Phosphorous inputs and vegetation sensitivity in the Everglades. In: S.M. Davis and J.C. Ogden (Editors), Everglades the Ecosystem and Its Restoration, St. Lucie Press, Delray Beach, Fl. pp. 357-378.

Doren, R.F., Platt, W.J. and Whiteaker, L.D., 1992. Density and size structure of slash pine stands in the Everglades region of south Florida. Forest Ecology and Management 59:295-311.

Ehrenfeld, J.G., 1983. The effects of changes in land-use on swamps of the New Jersey pine barrens. Biological Conservation 25: 353-375.

Fennema, R.J., Neidrauer, C.J., Johnson, R.A., MacVicar, T.K. and Perkins, W.A., 1994. In: S.M. Davis and J.C. Ogden (Editors), Everglades the Ecosystem and Its Restoration, St. Lucie Press, Delray Beach, Fl. pp. 249-289.

Gleason, P.J. and Stone, P., 1994. Age, Origin and Landscape Evolution of the Everglades Peatland. In: S.M. Davis and J.C. Ogden (Editors), Everglades the Ecosystem and Its Restoration, St. Lucie Press, Delray Beach, Fl. pp. 149-197.

Gorham, E., 1956. The ionic composition of some bog and fen waters in the English Lake District. Journal of Ecology 44: 142-152.

Gosselink, J.G. and Turner, R.E., 1978. The role of hydrology in freshwater wetland ecosystems. In: R.E. Good (Editor), Freshwater Wetlands. Academic Press, New York, N.Y. pp. 63-78.

Green, R.H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York. 257pp.

Grimshaw, H.J., Rosen, M., Swift, D.R., Rodberg, K. and Noel, J.M, 1993. Marsh phosphorus concentrations, phosphorus content and species compositions of Everglades periphyton communities. Archiv. Hydrobiologie 128(3): 257-276.

Gunderson, L.H., 1989. Historical Hydropatterns in Wetland Communities of Everglades National Park. Freshwater Wetlands and Wildlife, Conf-8603101, DOE Symposium Series No. 61, R.R. Sharitz and J.W. Gibbons (Eds.), USDOE Office of Scientific and Technical Information, Oak Ridge, Tennessee.

Gunderson, L.H., 1994. Vegetation of the Everglades: determinants of community composition. In: S.M. Davis and J.C. Ogden (Editors), Everglades the Ecosystem and Its Restoration, St. Lucie Press, Delray Beach, Fl. pp. 323-340.

Guntenspergen, G.R. and Stearns, F., 1981. Ecological limitations on wetland use for waste-water treatment. Proc. Midwest Conf. on Wetland Values and Management. Minnesota Water Planning Board, Minneapolis. p. 273-284.

Hayati, A.A. and Proctor, M.C.F., 1990. Plant distribution in relation to mineral nutrient availability and uptake on a wet-heath site in south-west England. Journal of Ecology 78: 134-151.

Herndon, A., Gunderson, L., and Stenberg, J., 1991. Sawgrass (Cladium jamaicense) survival in a regime of fire and flooding. Wetlands 11(1): 17-27.

Hofstetter, R.H., 1973. Appendix K. Part 1. Effects of fire in the ecosystem: an ecological study of the effects of fire on the wet prairie, sawgrass glades, and pineland communities of south Florida. Final Report (EVER-N-48. USDI National Park Service, NTIS No. PB 231940. 156 p.

Hofstetter, R.H. and Parsons, F., 1975. Effects of fire in the ecosystem: an ecological study of the effects of fire on the wet prairie, sawgrass glades and pineland communities of south Florida. Final Rep. part 2. USDI National Park Service. EVER-N-48 NTIS No. BP 264463.

Hough, R.A., Fornwall, M.D., Negele, B.J., Thompson, R.L. and Putt. D.A.., 1989. Plant community dynamics in a chain of lakes; principal factors in the decline of rooted macrophytes with eutrophication. Hydrobiologia 173(3): 199-218.

Huenneke. L.F., Hamburg, S.P., Koide, R., Mooney, H.A., and Vitousek, P.M., 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grasslands. Ecology 71(2): 478-491.

Jones, L.A., 1948. Soils, geology, and water control in the Everglades region. University of Florida Agricultural Experiment Station Bulletin, No. 442.

Kadlec, R.H. and Bevis, F.B., 1990. Wetlands and waste-water. Kinross, Michigan. Wetlands 10: 77-95.

Klukas, R.W., 1973. Control burn activities in Everglades National Park. Proc. Tall Timbers Fire Ecol. Conf. Lubbock, TX., June 1972. 12:397-425.

Koch, M.S. and Reddy, K.R., 1992. Distribution of soil and plant nutrients along a trophic gradient in the Florida Everglades. Soil Sciences Society Am. Journal 56: 1492-1499.

Koide, R.T., Huenneke, L.F., Hamburg, S.P. and Mooney, H.A., 1988. Effects of applications of fungicide, phosphorus and nitrogen on the structure and productivity of an annual serpentine plant community. Functional Ecology 2(3): 335-344.

Kushlan, J.A., 1990. Freshwater marshes. In: R.L. Myers and J.J. Ewel (Editors), Ecosystems of Florida, University of Central Florida Press, Orlando, FL. pp. 324-364.

Moore, D.R.J., Keddy, P.A., Gaudet, C.L. and Wisheu, I.C., 1989. Conservation of wetlands: Do infertile wetlands deserve a higher priority? Biological Conservation 47: 203-217.

Morgan, M.D. and Philipp, K.R., 1986. The effect of agricultural and residential development on aquatic macrophytes in the New Jersey pine barrens. Biological Conservation 35: 143-158.

Mueller-Dombois, D., and Ellenberg, H., 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York. 547 pp.

Odum, H. T.,Ewel, K.C., Mitsch, W.J. and Ordway, J.W., 1975. Recycling treated sewage through cypress wetlands in Florida. In: F.M. D'itri (Editor), Waste-water Renovation and Reuse. Marce Dekker, New York. pp. 35-67.

Streng, D.R., Glitzenstein, J.S., and Platt, W.J., 1993. Evaluating season of burn in longleaf pine forests: a critical literature review and some results from an ongoing long-term study. Proceedings Tall Timers Fire Ecology Conference, No. 18, The longleaf Pine Ecosystem: ecology, restoration and management, Sharon M. Hermann (Ed.), Tall Timbers Research Station, Tallahassee, Florida.

Porter, C.L., 1967. Composition and productivity of a subtropical prairie. Ecology 48(6): 937-942.

Raschke, R.L., 1992. Diatom (Bacillariophyta) community response to phosphorus in the Everglades National Park, USA. Phycologia 32(1): 48-58.

Richardson, J.R., Bryant, W.L., Kitchens, W.M., Mattson, J.E. and Pope, K.R., 1990. An evaluation of refuge habitats and relationship to water quality, quantity and hydroperiod. A Synthesis Report to Arthur R. Marshall Loxahatchee National Wildlife Refuge, Boynton Beach, Florida. Florida Cooperative Fish and Wildlife Research Unit, Univ. of Florida, Gainesville.

Scheidt, D.J., Flora, M.D. and Walker, D.R., 1989. Water quality management for Everglades National Park. In: D.W. Fisk (Editor), Proc. of the Symposium on Wetlands: Concerns and Successes. Tampa, Florida. Sponsored by The American Water Resources Association.

Steward, K.K. and Ornes, W.H., 1975a. The autecology of sawgrass in the Florida Everglades. Ecology 56: 162-171.

Steward, K.K. and Ornes, W.H., 1975b. Assessing a marsh environment for wastewater renovation. Jour. of Water Pollution Control Fed. 47:1880-1891.

Steward , K.K. and Ornes, W.H., 1983. Inorganic Nutrient Utilization by Aquatic Vegetation of the Florida Everglades. United States Department of Agriculture, Agricultural Research Service, Washington, D. C. Final Report. pp. 107.

Swift, D.R.,1984. Periphyton and water quality relationships in the Everglades Water Conservation Areas. pp. 97-117 In: P. J. Gleason (ed.) Environments of South Florida Present and Past II. Miami Geological Society. Coral Gables, Florida.

Urban, N.H., Davis, S.M. and Aumen, N.G., In press. Fluctuations in sawgrass and cattail densities in Everglades Water Conservations Area 2A under varying nutrient, hydrologic and fire regimes. Aquatic Botany.

Vermeer, J.G. and Berendse, F., 1983. The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. Vegetatio 53: 121-126.

Wade, D., Ewel, J. and Hofstetter, R., 1980. Fire in South Florida Ecosystems. U.S. Department of Agriculture Forest Service General Technical Report SE-17, 125 p. Southeast Forest Experiment Station, Asheville,

N.C.

Walker, W.W., 1991. Water Quality Trends at Inflows to Everglades National Park. Water Resources Bulletin 27(1): 59-72.

Werner, H.W., 1975. The effects of fire on sawgrass in Shark Slough. Mimeo. Rep. USDI National Park Service. Homestead, FL. 67 p.

Whigham, D.F. and Simpson, R.L., 1978. Nitrogen and phosphorus movement in a freshwater tidal wetland receiving sewage effluent. In: Coastal Zone '78. Proc. Symp. Technical, Environmental, Socioeconomic and Regulatory Aspects of Coastal Zone Management ACSE, San Francisco, CA. p. 2189-2203.

Wood, J.M. and Tanner, G.W., 1990. Graminoid Community Composition and Structure within four Everglades Management Areas. Wetlands 10(2):127-149.

Tables:

Table 1. Correlation Matrix comparing sawgrass marsh/combined sites, and spikerush-wet prairie/combined sites along Transect CA11.

Table 2. Correlation Matrix comparing sawgrass marsh/combined sites along Transect CA2A.

Table 3. Correlation Matrix comparing sawgrass marsh/combined sites, and spikerush-wet prairie/combined sites along Transect CA3A.

Table 4. Correlation Matrix comparing sawgrass marsh/combined sites, and spikerush-wet prairie/combined sites along Transect ENP.

Figure Captions:

Figure 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.

Figure 2. Map of Conservation Areas and Everglades National Park showing locations of sampling transects.

Figure 3. 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 in $\mu g.g^{-1}$ 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.

Figure 4. Histogram comparing presence of Typha and Rhyncospora with distance and Total P concentrations along Transect CA11.

Figure 5. Histogram comparing presence of Typha and Cladium with distance from nutrient source and Total P concentrations along Transect CA11.

Figure 6. Dendrogram of Transect CA2A delineating among and within group species similarity along the transect with distance from the 0.0 km point and Total Soil P in $\mu g.g^{-1}$ at each sampling location.

Figure 7. Histogram comparing presence of Typha and Cladium with distance from nutrient source and Total P concentrations along Transect CA2A.

Figure 8. Dendrogram of Transect CA3A delineating among and within group species similarity along the transect with distance from the 0.0 km point and Total Soil P in $\mu g.g^{-1}$ at each sampling location.

Figure 9. Histogram comparing presence of Typha and periphyton with distance from nutrient source and Total P concentrations along Transect CA3A.

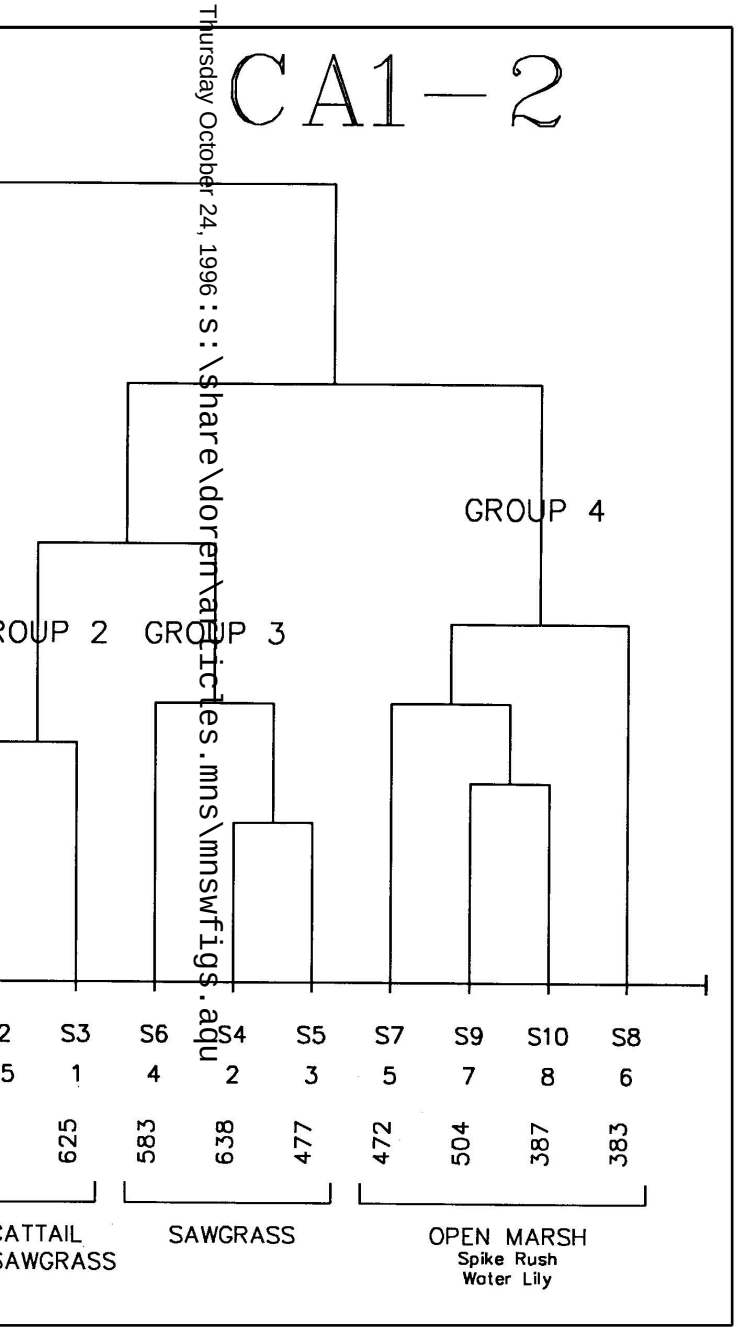
Figure 10. Histogram comparing presence of Typha and Cladium with distance from nutrient source and Total P

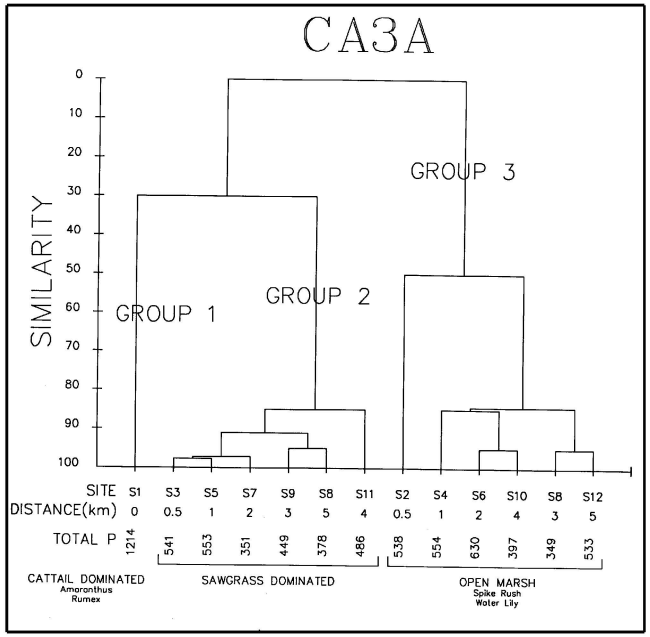
concentrations along Transect CA3A.

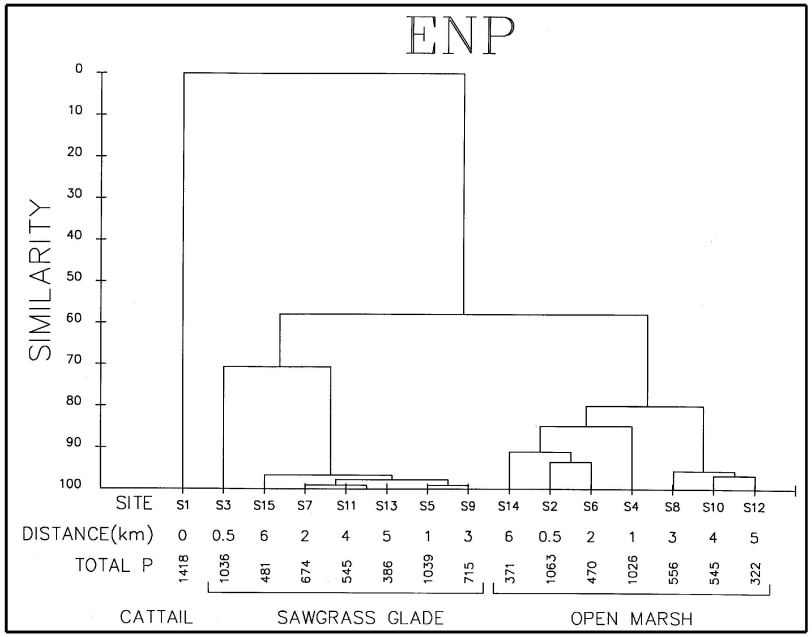
Figure 11. Dendrogram of Transect ENP delineating among and within group species similarity along the transect with distance from the 0.0 km point and Total Soil P in $\mu g.g^{-1}$ at each sampling location.

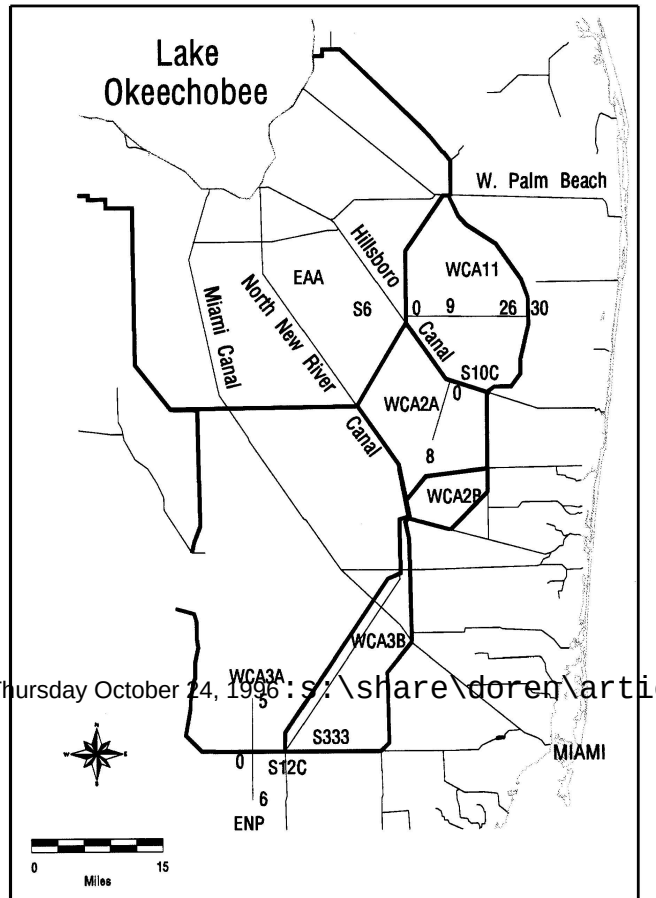
Figure 12. Histogram comparing presence of Typha and Cladium with distance from nutrient source and Total P concentrations along Transect ENP.

Figure 13. Histogram comparing presence of Typha and periphyton with distance from nutrient source and Total P concentrations along Transect ENP.

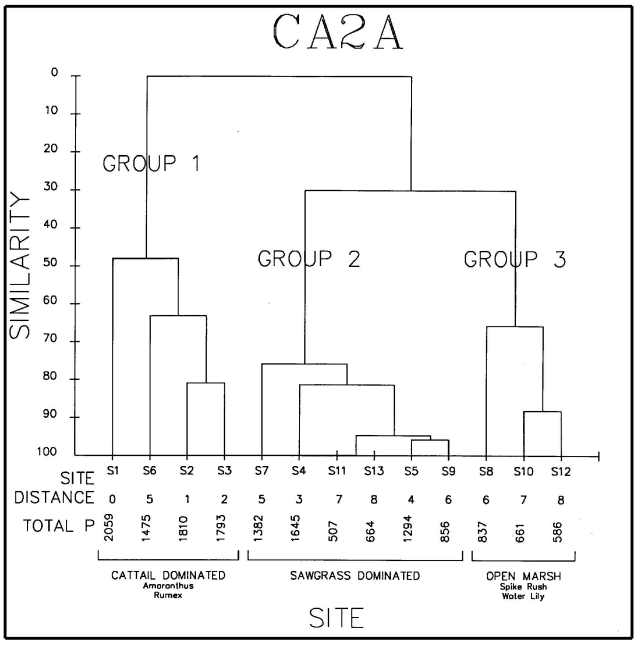

CA1-2
Thursday October 24, 1996 :s:\share\doreen\articles.mns\mnswfigs.aqu
GROUP 4
ROUP 2
GROUP 3
2
S3
S6
S4
S5
S7
S9
S10
S8
5
1
4
2
3
5
7
8
6
625
583
638
477
472
504
387
383
CATTAIL
SAWGRASS
SAWGRASS
OPEN MARSH
Spike Rush
Water Lily


CA3A
SIMILARITY
0
10
20
30
40
50
60
70
80
90
100
GROUP 1
GROUP 2
GROUP 3
SITE S1 S3 S5 S7 S9 S8 S11 S2 S4 S6 S10 S8 S12
DISTANCE(km) 0 0.5 1 2 3 5 4 0.5 1 2 4 3 5
TOTAL P 1214 541 553 351 449 378 486 538 554 630 397 349 533
CATTAIL DOMINATED
Amoronthus
Rumex
SAWGRASS DOMINATED
OPEN MARSH
Spike Rush
Water Lily


ENP
SIMILARITY
0
10
20
30
40
50
60
70
80
90
100
SITE S1 S3 S15 S7 S11 S13 S5 S9 S14 S2 S6 S4 S8 S10 S12
DISTANCE(km) 0 0.5 6 2 4 5 1 3 6 0.5 2 1 3 4 5
TOTAL P 1418 1036 481 674 545 386 1039 715 371 1063 470 1026 556 545 322
CATTAIL
SAWGRASS GLADE
OPEN MARSH



Thursday October 24, 1996 :s:\share\doren\articles.mns\mnswfigs.aqu


CA2A
SIMILARITY
0
10
20
30
40
50
60
70
80
90
100
GROUP 1
GROUP 2
GROUP 3
SITE S1 S6 S2 S3 S7 S4 S11 S13 S5 S9 S8 S10 S12
DISTANCE 0 5 1 2 5 3 7 8 4 6 6 7 8
TOTAL P 2059 1475 1810 1793 1382 1645 507 664 1294 856 837 661 586
CATTAIL DOMINATED
Amaranthus
Rumex
SAWGRASS DOMINATED
OPEN MARSH
Spike Rush
Water Lily
SITE