

Final Report



Assessment of Marsh Vegetation Responses to Hydrological Restoration in Shark Slough, Everglades National Park

Table of Content

Section 1:

Section 2:

Section 3:

Section 4:

Section 5:

Section 6:

Acknowledgments:

Literature Cited:

Appendix 1:

Appendix 2:

Appendix 3:

Appendix 4:

Appendix 5:

Appendix 6:

Home Page

Project Menu

Contact P.I.

Introduction:

Shark Slough is the main artery by which surface water sheetflow passes through the southern Everglades to Florida Bay and the Gulf of Mexico. The nature of water flow in Shark Slough has, over many



centuries, yielded the linear vegetation pattern that epitomizes the Everglades. This pattern consists of a series of slightly elevated strands of dense, tall sawgrass or woody vegetation, separated by lower, more open marsh communities, or “wet prairies”.

Shark Slough vegetation structure and dynamics have been examined by a number of researchers during the last half century (Kolipinski and Higer, 1969; Craighead, 1971; Hofstetter, 1976; Hofstetter and Pearson, 1976; Wade et al., 1980; Gunderson, 1994; Davis et al., 1994; Olmsted and Armentano, 1997). For the most part, changes appear to be regional rather than Slough-wide, with sawgrass invading wet prairies in some places, dying back elsewhere, and being replaced by woody (sometimes non-native) plants in others yet. As Everglades restoration proceeds, a more comprehensive and current view of the Shark Slough landscape is needed, along with a better understanding of the processes by which it has developed and is maintained.

Below we report on research addressing several aspects of Shark Slough landscape ecology, carried out by a group of FIU scientists during 1997-2001. The specific



objectives of the study were: (a) to examine associations between vegetation, hydrology, and soils in Shark Slough, (b) to assess historical changes in vegetation patterns, and (c) to establish a monitoring network that included previously sampled sites near the center of the Slough, as well as peripheral sites that may be more sensitive to future environmental alterations. Our results are organized into the six separate but interdependent documents that follow.

Section 1



Vegetation:Environment Relationships and Water Management in Shark Slough

Section 1:**Introduction****Methods****Data Analysis****Results****Discussion****Introduction:****Section 2:****Section 3:****Section 4:****Section 5:****Section 6:****Figures:**

<u>1.1</u>	<u>1.2</u>	<u>1.3</u>
<u>1.4</u>	<u>1.5</u>	<u>1.6</u>
<u>1.7</u>	<u>1.8</u>	<u>1.9</u>
<u>1.10</u>		

Literature Cited:**Appendix 1:**

Home Page

Project Menu

Contact P.I.

Introduction:

Plans under development for revising water management in South Florida to benefit the Greater Everglades ecosystem (USACOE 1994) represent one of the most ambitious ecological restoration efforts ever attempted. The problems which have motivated this effort include: (a) sharp declines in populations of wading birds and other animals of special concern (Powell et al., 1989; Ogden, 1994; Curnutt et al., 1998); (b) deteriorating conditions in the Florida Bay estuary, the terminal receiving basin for Everglades surface water (Fourqurean and Robblee, 1999); (c) rapid expansion of cattails (*Typha domingensis* Pers.), associated with the outflow of phosphorus-enriched canal water into the Water Conservation Areas (WCA's) and adjacent marshes north of Everglades National Park (Davis, 1991; Craft and Richardson, 1997; Doren et al., 1997; Wu et al., 1997); (d) loss of tree islands due to excessive flooding or fire in some parts of the WCA's (Brandt et al., 2000); (e) expansion of sawgrass at the expense of wet prairie communities (Davis et al., 1994); and (f) the rapid growth of exotic plant and animal populations throughout the Everglades (Schmitz and Brown, 1994; O'Hare and Dalrymple, 1997). With the exception of (e) and (f), the problems listed above are primarily manifested in wetlands peripheral to Shark Slough, the main pathway of surface water drainage through Everglades National Park (ENP). However, as a result of its central location, the Slough's hydrology will be affected by water management measures undertaken to benefit other portions of the Everglades ecosystem. Furthermore, long term alterations in the hydrologic regime of Shark Slough may result in parallel biotic changes, especially in the distribution and abundance of native plant and animal communities.

Hydrologic restoration activities currently being developed follow on the heels of a long sequence of structural, operational, and regulatory changes in water management in South Florida, beginning

well before the creation of ENP in 1947. During the early period of water management, the primary objectives were drainage, flood control and water storage. These goals were achieved through construction and operation of an extensive network of pumps, canals, and levees, which effectively compartmentalized the central Everglades north of US Highway 41 (Figure 1.1). Since congressional passage of Public Law 98-181 in 1983, legally mandated concerns for the restoration and maintenance of natural Everglades ecosystems have stimulated a series of regulatory changes within the existing structural network. However, in the southern Everglades, one management direction has remained consistent during the 1980's and 1990's: the routing of southbound water to the west at Highway 41, away from its primary pre-development flow-way (Light and Dineen, 1994; Van Lent et al., 1999). In this area, concentration of delivery through control structures west of the L-67 levee has eliminated the historic northeast-southwest flow of water in the northern portions of ENP (Figure 1.1). This distribution pattern has served to decrease water level and flooding duration in Northeast Shark Slough, while accounting for wetter conditions in Northern Shark Slough. The spatial pattern of water delivery may have had less hydrologic impact on the more remote southern portions of the Slough. Effects of these management activities on regional vegetation patterns have not been addressed in detail.

From a distance, the vegetation of the Slough appears rather homogeneous, but closer inspection reveals a complex mosaic of marsh assemblages, spotted liberally with distinct wooded parcels called tree islands. Within the marsh, large acreages supporting monodominant stands of the large sedge *Cladium jamaicense* Crantz (sawgrass) are interrupted, sometimes abruptly, by more open communities featuring a relatively rich mixture of smaller aquatic plants and periphyton (an integrated mat community consisting of algae, bacteria, and microheterotrophs). These habitat units are frequently elongated in shape and oriented parallel to the

predominant NE-SW direction of water flow, suggesting a strong functional connection between hydrology and vegetation. Recent investigations (Gunderson, 1989; Olmsted and Armentano, 1997; Busch et al., 1998) documented small differences in mean hydrologic regime among community types, e.g., flooding was usually deeper and more persistent in open marsh types dominated by spikerush (*Eleocharis cellulosa* Torr.) or maidencane (*Panicum hemitomon* Schult.) than sawgrass marsh, which in turn was wetter than forested cover types. However, these conclusions were based on data from a limited number of Shark Slough settings, and quantification of variation in the vegetation:hydrology relationship at the broad landscape scale remains incompletely understood.

The relationship of hydrology and vegetation in the Everglades is complicated by interactions with other dynamic environmental factors, including soil characteristics and disturbance regime (Duever et al., 1986). For instance, data presented by Olmsted and Armentano (1997) indicate that soils underlying sawgrass marsh were, on average, deeper than soils of spikerush/maidencane communities, though overlap was substantial. Everglades soils are biological entities whose development reflects a balance of accretionary v. degradational processes, i.e., root production, sedimentation, decomposition, and erosion rates; all of these processes may be functionally related to the overlying plant communities (e.g., Craft et al., 1993; Day et al., 1999). These relationships are largely unquantified, but may account for much of the variation in marsh surface topography (and in the depth of the soil profile), with associated feedbacks on hydrology.

In the research reported below, our objectives were: (1) to clarify the associations of hydrology, soil depth, and plant community structure in Shark Slough, focusing especially on regional variation in these relationships, and (2) to evaluate the possible role of water management in creating such variability, if present. Our approach

was to sample vegetation, soils, and water depth at regular intervals along cross-Slough transects, construct a hydrologic record for each point by referencing the nearest water level recorder, then control for local spatial effects and the covariance among soil and hydrologic variables in the analytical phase.

Current water management practices and their antecedents:

Efforts to drain South Florida wetlands began as early as 1850. Rising population and agricultural development throughout central Florida provided the stimulus for state, federal, and privately funded diversion projects whose purposes were drainage, flood protection, and irrigation (McCally, 1999). Beginning with the dredging of the Caloosahatchee River in the 1890's, and continuing with the West Palm Beach, Hillsboro, North New River, and Miami Canals in the early years of the twentieth century, water that had previously overflowed Lake Okeechobee and moved south by sheetflow was instead directed to the coastal estuaries. Construction of the Tamiami Canal (1915-1928) also intercepted and diverted flows to Shark Slough and the Southern Everglades. With the issuance of the 'Comprehensive Report on Central and South Florida for Flood Control and Other Purposes' in 1948, the Army Corps of Engineers initiated the construction of a network of interconnected levees and canals to create water-storage and agricultural areas along the Everglades trough. This network, completed in 1963, compartmentalized the northern Everglades into a patchwork of Water Conservation Areas (WCA's), designed to store water during dry periods and release it to the Southern Everglades when flooding conditions became imminent (Light & Dineen, 1994).

In the first decades after the establishment of ENP in 1947, retention of water in the WCA's clearly conflicted with water supply to the central and southern reaches of Shark Slough. In 1967, the L-67 levee and canal was extended southward in order to direct water

further into the Slough. A side effect of the extension was to prevent water delivered through control structures west of the levee from flowing to Northeast Shark Slough (Walters et al., 1992; Light and Dineen, 1994) (Figure 1.1). Regional disputes over supply responsibilities to ENP led to congressional action in 1970, whereby a minimum annual delivery was guaranteed. During the 1970's, minimum deliveries were generally achieved by increasing flows during the wet season, while dry season flows remained low.

Until 1983 water releases from the WCA's into ENP were solely through four control structures located along the Tamiami Canal, west of the L-67 levee. Both the Experimental Water Deliveries Program (1983) and the Modified Water Deliveries Program (1989) attempted to reproduce the natural timing and distribution of precipitation inflow to Shark Slough by balancing flows to Northern and Northeastern Shark Slough. However, regulations for both programs required moderate conditions in order to achieve target deliveries to the two areas. Currently, the Modified Water Deliveries Program anticipates a 45-55% split of flow between structures west and east of the L-67 levee, respectively. However, during wet years, regulations call for the closing of the eastern structures to prevent flooding in adjacent areas, and 100% of flow is released through the western structures (Van Lent et al., 1999).

Methods:

Vegetation and environmental sampling:

Five transects were established to examine the variability in vegetation, hydrology, and soils along the length of Shark Slough in Everglades National Park (Figure 1.1, Table 1.1). Transects were oriented perpendicular to the apparent direction of water flow, and ranged in length from 4 to 12 km. Three transects were effectively divided into eastern and western portions, because they were interrupted for at least 1 km by impassable terrain or disturbance

associated with a canal or airboat trail. Sampling stations were established every 100 meters along each transect. To address smaller-scale variation, each km of transect also included a 200-meter section that was sampled at 20-meter intervals. In all, 569 points were sampled. Vegetation sampling was conducted when water levels were high in Shark Slough, i.e., during the periods November 1998 - January 1999 and July 1999 - December 1999. Sampling within individual transects was generally completed within six weeks or less.

Table 1.1. Transect and plot layout in four Shark Slough (SS) hydrologic regions.

Region	Transect	Transect Length (km)	Number of Plots
Northeast SS	1	4.0	73
	2E	1.4	22
Northern SS	2W	5.0	91
	3	6.0	110
Central SS	4E	3.0	55
	4W	4.0	73
Southern SS	5E	4.6	87
	5W	3.3	58

A nested plot design was chosen for quantitative vegetation sampling, because of the range of plant growth forms present in the Slough. At each station, a PVC tube driven into the sediment marked the SE corner of both a 10 x 10 meter tree plot and a 5 x 5 meter shrub/herb plot. In the former, we measured the DBH, crown length and width of each tree (defined as woody stems ≥ 5 cm DBH), then calculated species cover assuming elliptical crown form. In the latter, we estimated the cover class of each species of shrub (vines

and woody stems ³ 1m height and < 5cm DBH), using the following categories: < 1%, 1-4%, 4-16%, 16-33%, 33-66%, and > 66%. Species cover class of herbs and woody plants < 1 m height was estimated in similar fashion in three randomly located 1-m² subplots within the 5 x 5 m plot. Plot averages were calculated using the midpoints of the cover classes. Species present in the plot but not found in any of the subplots were assigned a mean cover of 0.01%. Data analysis was based on the total of tree, shrub, and herb stratum estimates for each species.

In addition to the quantitative observations described above, we also characterized vegetation cover every five meters along the transects, based on a visual assessment of several broad structural and compositional attributes. We assigned each point to one of six cover types defined in Table 1.2: spikerush marsh, sparse sawgrass, tall sawgrass, bayhead swamp, cattail marsh, and dead sawgrass/open water. The first four of these units were equivalent to types described by Olmsted and Armentano (1997).

Table 1.2 Criteria used to distinguish major cover types in Shark Slough.

Vegetation Type	Criteria
Spikerush Marsh	Dominant species <i>E. cellulosa</i> , <i>P. hemitomon</i> , or <i>P. geminatum</i> ; canopy height < 1.5 meters.
Sparse Sawgrass	Dominant species <i>C. jamaicense</i> ; canopy height < 2 meters.
Tall Sawgrass	Dominant species <i>C. jamaicense</i> ; canopy height 2 meters or more.
Bayhead Swamp	Woody vegetation dominant or co-dominant with <i>C. jamaicensis</i> .
Cattail Marsh	Dominant species <i>Typha domingensis</i> ; canopy height 2 meters or more
Dead Sawgrass - Open Water	Total live vegetation cover < 20%; evidence of large dead culms of <i>C. jamaicense</i>

Concurrent with vegetation sampling, soil depth was measured at the SE corner of each plot and at the three herb subplots. Soils were

probed to bedrock with a 1 cm diameter aluminum rod, and mean depth was calculated from the four measured values. Water depths were likewise recorded during vegetation sampling at the same four locations. Referencing the average of these values to the datum for the same day at the nearest longterm water recorder, daily water level at each plot was estimated for the period January 1, 1990 - December 31, 1999; these data were used to calculate hydroperiod (number of days per year when the surface was inundated), mean water depth (average of all days when water was above the surface), and maximum water depth (highest 30-day running mean) for each year during the decade.

The assumption on which estimates of the above hydrologic parameters are based is that daily change in water level is equal at the reference recorder and at all plots along a transect. Comparison of water levels along the transects and at the reference recorders for two days in October 1999 and February 2000 - a recession period when water remained well above the surface throughout the Slough - indicated that the 95% confidence limits for daily estimates were approximately ± 1 cm. However, the assumption of equal change along the transect is violated when water at the recorder recedes below the soil surface, after which its level changes more rapidly than at any still-flooded plots, because water occupies pore spaces only. Therefore, during periods when water level dropped below the surface at the water level recorder, we assumed that water level at the flooded plots fell at a rate of 0.5 cm/day until reaching the surface; and rose, ahead of the water surface at the recorder, at the same rate. The above rate is a reasonable maximum, based on inspection of recorded recession rates at several recorders, supported by estimates of daily evapotranspiration in the Everglades (German, 2000; Gunderson and Stenberg, unpublished manuscript) and an emergent aquatic macrophyte-dominated wetland in Central Florida (Dolan et al., 1984). The situation described above constituted a minor proportion of the data base, because most of the water level recorders

were situated in open slough conditions where water depths rarely dropped below the soil surface.

Data analysis:

We examined compositional variation in Shark Slough vegetation and its environmental correlates through ordination and other multivariate analytical techniques, using data from all five transects. To downweight the effects of very abundant species, a square root transformation was applied to the cover percentages, and the transformed data were relativized within plots. A site-by-site dissimilarity matrix was created based on the Bray Curtis metric, and the data were ordinated with the non-metric multidimensional scaling (NMS) algorithm in PC-ORD version 4.10 (McCune and Mefford, 1999). The site ordination was examined with respect to the distribution of (a) the three hydrologic variables, (b) soil depth, and (c) the vegetation categories defined in Table 1.2. To test the strength of the relationships between plant species composition and the environmental variables while accounting for spatial structure, we applied partial Mantel tests, using the R-Package program (Legendre, et al. 1996-99).

In addition to the ordination approach described above, in which vegetation was treated as a continuous variable, we also tested for differences in hydrologic and edaphic measures among discrete vegetation and management units, using two-way, Model 1 analysis of variance. Four management units were defined (Table 1.1, Figure 1.1). Northeast Shark Slough (NESS), which included the water-deprived marshes east of the L-67 levee, was represented by Transect 1 and the east end of Transect 2. Northern Shark Slough (NSS), the water-enhanced wetlands immediately west of the L-67 levee, were represented by points along Transect 3 and the west side of Transect 2. Central Shark (CSS) was represented by Transect 4, and Southern Shark Slough (SSS) by Transect 5. Only plots characterized as

spikerush marsh, sparse sawgrass, or tall sawgrass were considered in the analysis of variance, because the other cover types were not sufficiently well-represented throughout the study area. Soil depth, hydroperiod, mean water depth, and maximum water depth were the environmental variables analyzed. We analyzed data from 1991 and 1997, which were dry and average water years, respectively, in comparison to other years in the 1990's.

Results:

Based on characterization of points at five-meter intervals along each transect, rank abundances of the three major marsh cover types were identical in the four regions: sparse sawgrass > spikerush marsh > tall sawgrass (Figure 1.2). However, regional trends in the relative abundance of individual communities were noteworthy. Vegetation in NESS and SSS was relatively uniform, with Sparse Sawgrass occupying more than 60% of the landscape. Dominance was more evenly distributed among cover types in NSS and CSS, where open spikerush marsh covered nearly one-third of the surface. Tall sawgrass was least abundant in the two southern regions, and never exceeded 20%. Bayhead swamp, dead sawgrass/open water, and cattail marsh were minor components in the three southern regions.

Analysis of the compositional data within transects indicated considerable small-scale spatial structure in marsh vegetation. Typically, mean Bray-Curtis dissimilarities for pairs of points 1, 2, 20, and 40 meters apart were considerably smaller than those for points further apart. Hydrology and soil depth likewise exhibited spatial patterning. To eliminate redundancy associated with spatial structure, ordination of the vegetation data was therefore based on points separated by 200 meters or more. The two-axis NMS site ordination derived from these data (Figure 1.3) was characterized by a low stress value (13.1), and explained about 96% of the total variation in the dissimilarity matrix. Plots within four major

vegetation units (spikerush marsh, sparse sawgrass, tall sawgrass, bayhead swamp) occupied distinct positions in the ordination, with small areas of overlap between tall and sparse sawgrass, and between the latter and spikerush marsh. The positions of individual species within the ordination, calculated from abundance-weighted distributions among sites, are informative with respect to the ecological niches of minor species. For instance, *Crinum americanum* L., *Peltandra virginica* (L.) Schott & Endl., and *Justicia angusta* (Chapm.) Small were associated with denser sawgrass strands, while *Rhynchospora tracyi* Britt., *Nymphoides aquatica* (J. F. Gmel.) Kuntze, *P. geminatum* and *Sagittaria lancifolia* L., were more characteristic of more open spikerush marsh.

Superimposing contour plots based on calculated hydroperiods, maximum water depths, or average water depths for each point on the ordination (Figures 1.4 - 1.6) suggests that hydrology bears a strong influence on the Shark Slough habitat mosaic. During 1991, a dry year, spikerush marsh and sparse sawgrass were generally inundated for nine months or more, with maximum water depths of at least 40 cm, and average water depths of 25 cm or more. Tall sawgrass sites were inundated for 6-10 months and bayhead swamp for 2-6 months, with concomitantly lower water depths (Appendix 1). In 1997, a year in which water levels were about average for the decade, all points were inundated for at least eleven months except in bayhead swamp (range: 4-8 months). Dead sawgrass/open water was found at points intermediate in hydroperiod between tall sawgrass and bayhead swamp.

Application of partial Mantel tests to control for spatial effects within regions further supported the correlation of hydrology and plant species composition. Except in NESS, all three hydrologic parameters were strongly correlated with vegetation when spatial effects were removed (Table 1.3: Analysis 1). In contrast, significant Mantel associations between soil depth and vegetation were observed

in CSS and SSS only. The relative weakness of the soil:vegetation relationship is also evident when soil depths are superimposed on the NMS ordination, without accounting for region (Figure 1.7).

Partial Mantel tests were also applied to explore associations among environmental variables. The three hydrological parameters were highly inter-correlated (Table 3: Analysis 3), but the strength of their relationships with soil depth were region-specific, with 1-3 significant associations per region (Table 1.3: Analysis 2).

Table 1.3. P-values for partial Mantel statistics, indicating strength of association among plant species composition, soil depth, and three hydrologic variables in four regions, after removing effect of spatial contiguity among sampling points.

	Independent Variable Tested	Northeast SS (95)^f	Northern SS (114)	Central SS (114)	Southern SS (113)
Analysis 1 ^a	Hydroperiod ^d	0.113	0.001	0.001	0.007
	Mean Depth ^e	0.085	0.001	0.001	0.002
	Max Depth ^e	0.087	0.001	0.001	0.002
Analysis 2 ^b	Soil	0.336	0.235	0.008	0.037
	Hydroperiod	0.026	0.040	0.020	0.140
	Mean Depth	0.009	0.110	0.067	0.026
Analysis 3 ^c	Max Depth	0.011	0.030	0.015	0.056
	Mean Depth	0.001	0.001	0.001	0.001
	Max Depth	0.001	0.001	0.001	0.001

^aassociations of species composition with environmental variables

^bassociations of soil depth with three hydrologic variables

- ^cassociations among three hydrological parameters
- ^dhydroperiod data is based on dry year (1991)
- ^emean and maximum water depth are based on an average water year (1997)
- ^fsample size.

The analysis of variance indicated highly significant effects of both cover type and region on all three hydrologic variables in both years, 1991 and 1997 (Table 1.4). Interaction effects were mostly non-significant, except for hydroperiod in 1997, when most of the non-forested portions of the Slough were continuously inundated with the exception of several tall sawgrass strands in CSS (Figure 1.8). Inter-regional differences were explored further by applying multiple comparison tests (Tukey's HSD) to sparse sawgrass locations, which were abundant in all four regions. Differences between regions varied with year and with hydrologic variable. In general, hydroperiod was longest and water level was deepest in NSS, while CSS and SSS were characterized by shorter hydroperiod and shallower water. Differences among regions were comparable in magnitude to differences among cover types within a single region. For instance, in 1991, when mean hydroperiod for spikerush marsh consistently exceeded that of tall sawgrass in the same region by 10-60 days, tall sawgrass sites in NSS had a longer mean hydroperiod than spikerush marsh in any of the other regions (Figure 1.8).

Two-way analysis of variance showed significant effects of both cover type and region on soil depth also (Table 1.4). Soil depth in tall sawgrass was 10 to 31 cm deeper than in spikerush marsh and sparse sawgrass, depending on region. Multiple comparison tests among regions were applied to the widely distributed sparse sawgrass type alone. They indicated that soil depth in NESS exceeded that in NSS, but other regional differences were non-significant (Figure 1.9).

Table 1.4. P-values for two-way analyses of variance, testing fixed effects of region and cover type on soil depth and three hydrologic variables in dry and average water years (1991 and 1997, respectively).

Effect	Hydroperiod		Mean Water Depth		Maximum Water Depth		Soil Depth
	1991	1997	1991	1997	1991	1997	
Region	<	<	<	<	<	<	
Cover	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	
Type	<	0.0072	<	<	<	<	0.0456
Region x	0.0001		0.0002	0.0001	0.0001	0.0001	0.0007
Cover	0.2199	<	0.4012	0.4153	0.3354	0.3303	
Type		0.0001					0.3854

Discussion:

The results described above support the contention, expressed most comprehensively by Olmsted and Armentano (1997), that Shark Slough plant communities are comprised of several widespread and distinct cover types, arranged roughly along a hydrologic gradient. Owing to the extensive nature of the current data, our analyses go a step further in (a) assessing the strength of relationships among vegetation, hydrology, and soil depth, and (b) defining the range of temporal and spatial variation in hydrology and soils within the major cover types, both for the Slough as a whole and for individual management units within it. Examination of broad spatial variation indicates that water management has contributed to regional hydrologic differences that are large in comparison to those that distinguish cover types in a local area within a single year. Given the observed strength of the vegetation:hydrology association, management that artificially maintains such regional patterns in hydroperiod and water depth on a longterm basis is likely to have

important effects on the structure of Everglades plant communities.

Vegetation:environment relationships:

Our examination of vegetation:environment relationships consisted of graphical descriptions of Slough-wide patterns, and statistical analyses that also accounted for regional effects. Statistics included both continuous and categorical approaches; both appear to be justified, based on the clustering within the vegetation ordination (Figure 1.2) of sites assigned to specific wetland community types according to the criteria of Olmsted and Armentano (1997).

A strong association of vegetation with hydrology was evident in our data, whether viewed for Shark Slough in its entirety (Figures 1.4-1.6) or within individual subsections of the marsh (three of four regions in Table 1.3). Outside of the forested areas (Appendix 1), sawgrass-dominated marsh is most common where hydroperiod is shortest and water depth shallowest, and more open spikerush marsh is characteristic of more hydric conditions. Dramatic contrasts in vegetation are typically associated with slight differences in hydrologic regime, e.g., 5-10 cm water depth or 10-60 days annual inundation (Figures 1.4-1.6 & 1.8). The role of hydrologic variables in distinguishing among a broad range of South Florida wetland communities has been noted by many authors (e.g., Davis, 1943; Loveless, 1959; Craighead, 1971; Duever et al., 1986), but the predominant mechanism that drives fine-scale patterning within the narrower range of Shark Slough marshes is a less settled issue. Sampling a set of nine relatively wet Shark Slough sites quarterly over a 10-year period, Busch et al. (1998) attributed the observed variability in species composition primarily to spatial and temporal variation in hydrologic conditions, and secondarily to the effects of a recent hurricane. Olmsted and Armentano (1997) demonstrated that wetland community types were distributed in a predictable elevation (hence, water depth and hydroperiod) sequence along three Shark Slough transects, with modest (± 15 cm) differences distinguishing

tall sawgrass and spikerush marsh. Gunderson (1989) noted an imperfect correlation between cover type and several hydrologic metrics in the vicinity of five longterm Shark Slough water level recorders, which he attributed to factors such as fire history (cf. Herndon, 1991), soil characteristics, and seed availability. Our results therefore tend to support earlier conclusions regarding Shark Slough marshes, i.e., though other factors may be involved, hydroperiod and water depth variables are important determinants of marsh community composition and structure.

One ecosystem process that may affect vegetation directly or through its interaction with hydrology is soil development. In the southern Everglades, surface topography may result from local variation in soil accretion rates, which are themselves based on the balance of biological and physical processes. Soil depth was not strongly associated with vegetation over the Slough as a whole (Figure 1.7), but clear associations of soil depth and vegetation were observed in two of four regions, and soil and hydrologic variables were generally associated at the regional level (Table 1.3). Marsh soils were deepest in the tall sawgrass type (Figure 1.9), which is characterized by relatively low water (Figure 1.8). Similar results were reported by Olmsted and Armentano (1997), who noted a statistically non-significant tendency toward deeper soils in tall sawgrass than in neighboring plant communities.

The observed interactions between vegetation, hydrology, and soil depth suggest the simple model illustrated in Figure 1.10. The model postulates that hydrology's influence on soil depth is primarily indirect, through its influence on fire and vegetation. Wu et al. (1996) modeled the effects of hydrology (as well as vegetation) on the frequency and nature of Everglades fires, which modify the surface and reduce soil depth by removing accumulated organic matter (cf. Arabas, 2000). The pathway through vegetation may involve differential belowground production:decomposition and/or resistance

to surface water sheetflow, e.g., in tall sawgrass (deep soils) cf spikerush marsh (shallow soils). Daoust and Childers (1998) found net aboveground primary production to be about seven times higher in sawgrass than adjacent spikerush marsh in the southern Everglades. Root production was not estimated, but may also be relatively high in sawgrass marsh. Rejmankova et al. (1996) observed that *Cladium jamaicense* decomposed much more slowly than *Eleocharis cellulosa* under several hydrologic conditions in Yucatan Peninsula marshes. Vegetation-related differences in flow resistance among Shark Slough habitats are complex and not yet completely understood, varying with macrophyte density, periphyton structure, flow rate, and position in the water column (Carter et al., 1999). Nevertheless, it is reasonable to expect that the taller, denser tall sawgrass community would be more resistant to flow under many conditions, including extreme high water conditions when erosion and redeposition processes may be most significant. A net transport from spikerush marsh to tall sawgrass would result, enhancing soil accretion further in the latter type. It is notable that, within the range of the model, the productivity and sedimentation trends cited above would elicit a positive feedback loop, accentuating variability in surface topography, hydroperiod, and water depth until fire or other disturbances intervened. In contrast, a hydrologic mechanism cited by Craft and Richardson (1993) to explain patterns of soil accretion in their northern Everglades study area, i.e., slower decomposition in wetter sites due to anaerobic conditions, would tend to reduce surface variability.

The above discussion concerns processes that result in small-scale topographic variation within regions. However, inter-regional variation in soil depth (Figure 1.8) may be more a function of bedrock topography than of soil development. Soils in Shark Slough develop on uneven limestone bedrock, with micro-karst features prominent at the local scale. Regionally, the Slough occupies a slightly inclined bedrock trough bounded by the Miami Rock Ridge

on the east and the modestly elevated Big Cypress swamp on the west. Within it, limestone outcroppings and narrow ridges oriented perpendicular to the predominant direction of flow (“rock reefs”; Froehlich 1973) alternate with more extensive areas of lower bedrock. One bedrock depression occurs in the western portion of NESS, where all cover types are underlain by peat soils of more than 1 meter depth (Leighty et al., 1958). Conversely, sections of NSS and smaller portions of NESS and CSS are characterized by frequent bedrock outcrops.

Regional variation and water management effects:

In light of the strong association between vegetation and hydrology discussed above, how are the observed differences in hydrology among regions within the same cover type to be interpreted? These regional patterns may be summarized as follows: (1) NSS, directly below the primary water delivery points from the Water Conservation Areas, experienced the longest hydroperiods and deepest water levels during 1990-99; (2) More remote areas in CSS and SSS were characterized by shorter hydroperiods and shallower waters over the same period; but (3) the relative hydrologic positions of the major cover types were preserved throughout all regions (Table 1.4, Figure 1.8). The finding of strong regional variation may be taken as evidence of some degree of imbalance between existing vegetation pattern and recent hydrology. This imbalance is also suggested by the nature of the current vegetation mosaic (Figure 1.2). For instance, if current vegetation patterns were in equilibrium with hydrology of the last decade, then CSS would more closely resemble the monotonous sawgrass marsh of NESS and SSS than the more heterogeneous mixture of spikerush-and sawgrass-dominated communities of NSS, as it currently does.

The less-than-perfect concordance of vegetation with recent water level and hydroperiod may reflect a lag in response, and/or the influence of interacting environmental factors, especially fire (Figure

1.10). Little is currently known about the time frame of vegetation response to altered hydrology in the Everglades. Busch et al. (1998) observed annual variation in plant species composition in several Shark Slough wet prairies. Though these small changes did appear to be related to year-to-year variation in water level, they did not result in consistent changes in community type over the ten years of study. Based on an analysis of pairs of aerial photographs encompassing a 15-21 year period from the mid-1960's to the mid-1980's, Davis et al. (1994) documented a general increase in sawgrass marshes at the expense of open slough habitats in portions of Shark Slough and the Water Conservation Areas. However, no attempt was made to relate vegetation changes to hydrology at a local scale. In some cases, the response time of vegetation change to important forcing factors varies with the spatial scale considered. For instance, Williams et al. (1999) found that small-scale effects of salt water intrusion in coastal forests (elimination of tree regeneration) sometimes preceded coarse-scale effects (death of established trees) by many decades. Only the latter would have been detectable on aerial photos. In Shark Slough, when fire is followed by a rapid rise in water level, extensive areas of sawgrass marsh may change to open water habitat within a matter of weeks (Herndon, 1991), but reinvasion by sawgrass may be exceedingly slow (Herndon, unpublished manuscript). In contrast, the open water areas we encountered in southern Shark Slough (Figure 1.3) represent a late stage in a recurring phenomenon Wade et al. (1980) termed "sawgrass decadence". The cause of sawgrass decadence, the successional sequence that typically follows it, and the role of fire or hydrology in the process are currently unknown (Olmsted and Armentano, 1997).

The regional differences in hydrology documented in Figure 1.8 are those of a closely managed wetland ecosystem, rigidly compartmentalized at the upstream end but open downstream. Within these regions, we found clear and consistent differences in the hydrologic regime of the three major marsh cover types, in the

direction expected based on the existing literature, i.e., hydroperiod and water depth increased in the order tall sawgrass marsh < sparse sawgrass marsh < spikerush marsh. Locally, these differences were quite subtle; mean annual values for the two water depth parameters typically varied less than 15 cm among types, and hydroperiod by 60 days or less. This narrow range is relevant in assessing the impact of inter-regional variation in hydrology, whose magnitude equaled or exceeded that attributable to cover type within a region. If hydroperiod or water depth are important influences on vegetation pattern within regions, as our data and others' suggest, it is likely that a continuation of current water management practices will eventually result in large scale changes in vegetation pattern, with possible feedbacks on soil development and fire regime. In other words, hydrologic compartmentalization will inevitably result in a regionalization of Shark Slough ecosystems. Current restoration plans are intended to mitigate such undesirable effects in this pivotal portion of the Florida Everglades.



Section 2

Characteristics of Shark Slough Soils

Section 2:**Introduction****Methods****Results****Introduction:****Section 1:****Section 3:****Section 4:****Section 5:****Section 6:****Figures:**

<u>2.1</u>	<u>2.3</u>
<u>2.2</u>	<u>2.4</u>

Literature Cited:**Appendix 2:****Appendix 3:****Home Page****Project Menu**

Introduction:

Shark Slough soils are relevant to considerations of the current vegetation mosaic for several reasons. Most importantly, they serve as media for plant growth and the storage and exchange of nutrients. Second, their structural profiles provide records of site history, although these records may be obscured by diagenetic processes that ensue after sediment deposition. In this document we describe the physical and chemical nature of Shark Slough soils, and how they vary regionally and with vegetation type.

Methods:

In January 2000, we collected composite soil samples from selected Shark Slough sites representing each of the six transects and two sites near the mangrove ecotone north of Mahogany Hammock (P38A & B) (Figure 2.1). Soil properties were determined by field examination and by laboratory methods on selected soils at different depths. During three days of field sampling, several 6" diameter soil cores were taken to bedrock, physically examined for general profile description. Samples were taken from selected depths (usually 3 samples per site representing typical profiles), and brought to the laboratory to determine physicochemical and biological properties. Soil were homogenized in the collection bag and refrigerated until further analysis. A subsample from each bag was transferred to a plastic sample cup, weigh wet (g) and measured for sample volume (cm³). These samples were analyzed for dry weight (80°C), sample bulk density (g dry cm⁻³), fractional water content, total C, inorganic C, organic C, organic Matter content, total N and P. Another set of sub-samples from the bag was diluted with distilled, deionized water to a nominal 1:1 dilution and homogenized in a blender for 90 seconds. The pH of the soil slurries were recorded. A known weight of approximately 4 g each are added to 20 mL GC vials for the determination of microbial respiration (CO₂/CH₄ production). A known volume of approximately 100 cc each are processed for root

Appendix 3 outline several physicochemical properties of the soils sampled along all six transects. These soils ranged in pH from 6.3 to 8.1; for the most part, relatively acid soils were those with high organic matter content (Figure 2.3D). Total nitrogen ranged from 0.2% to 4.2%, and total phosphorus from 40 to 780 ppm. Nitrogen was almost entirely associated with organic matter content while phosphorus was not (Figures 2.3A and 2.3B, respectively). Consequently, N:P ratios (range 3-380) generally increased from predominantly marl to peat soils (Figure 2.3C). Respiration rates > 0.10 mm/hr/g were generally restricted to peat soils (Figure 2.4A); however, total phosphorus was unrelated to soil respiration (Figure 2.4B). The lone tropical hardwood hammock (tree island) location (Transect 2, Vulture Hammock) was a distinct outlier. The surface soil layer in this site had the highest phosphorus content, the lowest N:P ratio, and the highest pH encountered, despite an unexceptional organic matter content of 20%. Several mechanisms may be postulated for high phosphorus concentrations in Everglades tree islands, including position with respect to pathways of surface water flow, high productivity and efficient recycling, and attraction for wildlife, especially birds.



Section 3

Pore Water Chemistry and Plant Nutrient Content

Section 3:

Introduction

Methods

Results

Discussion

Introduction:

Section 1:

Section 2:

Section 4:

Section 5:

Section 6:

Figures: 2.1 & 3.1

Literature Cited:

Appendix 4:

Appendix 5:

Home Page

Project Menu

Contact P.I.

Introduction:

Pore water or soil interstitial water physicochemical properties provide important information regarding nutrient availability to plants. Pore water chemistry has been described from the Water Conservation Areas and northern Everglades, but research linking soil physicochemical characteristics, pore water properties, and plant nutrient uptake by the plant communities in the southern Everglades is lacking. In this section, we relate pore water chemistry to the nutrient content of sawgrass (*Cladium jamaicense*) and spikerush (*Eleocharis cellulosa*) from selected locations along the Shark Slough transects described in Section 1.

Methods:

Soil interstitial (pore) water was collected by inserting a permanent sampling device (sipper) into intact soils at selected locations along six transects and two sites (P38A & B) near the mangrove ecotone north of Mahogany Hammock (Figure 2.1). Sippers consisted of a filter (pore size 60 mm, Porex 6810, Interstate Specialty Products) held on to a male slip connector with Teflon tape. The slip connector was attached to a hollow Tygon tube approximately 50 cm in length, the distal end of which was connected to a capped female luer fitting. The filter was inserted into the soil to a depth of 10 cm with an insertion tool. A large syringe (140 mL) was connected to the female luer fitting, suction was applied, and approximately 110 mL of soil solution was withdrawn. Approximately 30 mL sample was filtered through a syringe filter (Whatman GF/F, pore size 0.45 mm) into a 30 mL polyethylene sample bottle. The remaining 80 mL sample was transferred into a 125 mL polyethylene sample bottle. Samples were stored in a cooler box until being returned to the laboratory. Soil pore water samples were either analyzed immediately (<24 h) or stored frozen until analysis (<30 d).

The unfiltered samples were analyzed for pH using a Ag/AgCl

along Transect 1. In contrast, DOC concentrations did not increase toward the south. It is clear that significant quantities of particulate organic carbon (POC: TOC minus DOC) are present in Shark Slough pore water samples. A detailed analysis of soil organic matter, TOC, POC, and DOC is warranted to interpret the existing dataset.

Significant amounts of nitrogen were measured in unfiltered samples (TN) compared to phosphorus (TP). TN ranged from 1.1 to 6.0 mg L⁻¹, whereas TP was about two orders of magnitude lower (range: 9.6 to 69.1 mg L⁻¹). Expressed as a molar ratio, N:P for all sample locations was 462:1; transect means ranged from 319:1 (Transect 1) to 622:1 (Transect 3). The high ratios in Shark Slough pore water suggest that phosphorus limitation is probably quite extreme for organisms throughout the wetland food chain (Bedford et al. 1999).

Analysis of nitrogen speciation in filtered samples indicated that inorganic forms, especially NH₄-N, predominate in Everglades pore water. Concentrations of NH₄-N exceeded 2000 mg L⁻¹ at all but two sampling locations, and the total of the three inorganic forms represented an average of 71% of TN across all samples. The accumulation of ammonium does not in itself present a problem, since this form of nitrogen is preferentially utilized by most plants and microorganisms (Paul and Clark, 1996). High soil pH and low phosphorus availability are factors that may inhibit nitrification, thereby causing ammonium to accumulate (Jayachandran et al., 2001 (in prep)). Under certain conditions, unknown organic compounds or elevated salinity may also inhibit nitrification (McClung and Frankenberger, 1985). Nitrate rarely accumulates to high levels in undisturbed ecosystems.

Unlike nitrogen, inorganic phosphorus forms (i.e., SRP) represent a very small proportion (mean 6.4%) of the limited pool of phosphorus in Shark Slough pore water. With the exception of a single Transect 6 location (m 2300), SRP was less than 5 mg L⁻¹.

Table 3.1: Mean nutrient content of *C. jamaicense* and *E. cellulosa* leaves in four broad habitat types. Standard errors are enclosed in parentheses.

Species	Habitat	# of Sites	N (%)	P (%)	N:P (molar ratio)
<i>C. jamaicense</i>	Spikerush Marsh	9	0.72 (0.04)	0.023 (0.001)	69.5 (5.0)
	Sparse Sawgrass	13	0.68 (0.03)	0.024 (0.001)	65.2 (3.6)
	Tall Sawgrass	7	0.54 (0.03)	0.026 (0.001)	47.9 (5.4)
	Bayhead Forest	1	0.47 (--)	0.027 (--)	38.5 (--)
<i>E. Cellulosa</i>	Spikerush Marsh	13	0.77 (0.04)	0.038 (0.003)	48.7 (2.2)
	Sparse Sawgrass	11	0.73 (0.03)	0.037 (0.003)	44.9 (2.5)
	Tall Sawgrass	4	0.70 (0.05)	0.033 (0.002)	46.2 (1.8)

Table 3.2: Mean nutrient content of pore water in four broad habitat types. Standard errors are enclosed in parentheses.

Habitat Type	# of Sites	N (µg/L)	P (µg/L)	N:P (molar ratio)
Spikerush Marsh	12	4132 (522)	16.3 (2.9)	697.7 (112.0)
Sparse Sawgrass	13	3072 (324)	24.9 (4.3)	346.3 (58.5)
Tall Sawgrass	7	2543 (394)	30.9 (8.0)	269.0 (86.5)
Bayhead Forest	1	3191 (--)	30 (--)	235.3 (--)

Section 5



Temporal Changes in the Vegetation Structure of Shark Slough During the Last Two Decades

Section 5:**Introduction****Methods****Results****Discussion****Conclusion****Introduction:****Section 1:****Section 2:****Section 3:****Section 4:****Section 6:****Figures:**

<u>1.1</u>	<u>4.1</u>
<u>5.1</u>	

Literature Cited:**Appendix 6:****Home Page**

Introduction:

The vegetation and physiography of Shark Slough have been described by many observers during the last century or so (e.g., Willoughby, 1898; Small, 1923 & 1927; Harper 1927; Davis, 1943; Craighead, 1971; Gunderson, 1994; Davis et al., 1994). In general, the vegetation of the Slough consists of a mosaic of mixed-species patches of several more or less distinct types (Table 4.1), interwoven by monotypic stands of sawgrass (*Cladium jamaicense*) which in places exceeds two meters in height. The boundaries between these units are generally abrupt and are controlled by topography, hydrology, soil depth, and fire, to name a few (Davis, 1943; Craighead, 1971; Herndon et al., 1991). These boundaries can change through time (Herndon, unpublished manuscript), but controls on the rates of change are not well understood.

Early accounts of the Everglades marsh were descriptive and botanical in emphasis (Willoughby, 1898; Small 1923 & 1927; Harper, 1927; Davis, 1943). More recent studies have focused on the physical factors driving changes in plant species

presented in Table 5.1, we assigned each point to one of the following seven cover types: Dead Sawgrass, Tall Sawgrass, Sparse Sawgrass, Spikerush-Sawgrass Mosaic, Spikerush Marsh, Bayheads, and Cattails. Data collected from Transects 3, 4, and 5-which correspond to the same areas mapped in Olmsted and Armentano (1997) (Figure 1.1, Appendix 6)-were used to test for temporal changes in the landscape structure of Shark Slough during the last two decades.

We used Arc-View 3.1 to overlay the above data on each of the three vegetation maps presented in Olmsted and Armentano (1997) (Appendix 6). Then, using the Spatial Analysis utility in Arc-View 3.1, we compared the cover types determined in 1980 (Olmsted and Armentano, 1997) and in 2000 (our point assignments). The distance of overlap between the two surveys were ca. 6.4, 8.0 and 11.9 km for Transects 3, 4, and 5, or approximately 1,282, 1,601, and 2,376 paired observations, respectively.

Table 5.1: Description of cover types.

Cover Type	Criteria
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communities increased during the interval 1980-2000, while Sparse Sawgrass and especially Tall Sawgrass decreased in extent across the three transects (Table 5.2). Bayheads were more extensive in the 2000 survey; however, this apparent increase may be attributable to the sampling method, since this cover type represented a very small proportion of the entire transect length in both years (Table 5.2).

The marsh community we examined in 2000 was organized along a latitudinal gradient. Whereas greatest temporal changes were generally observed in the southernmost transect (Transect 5), the changes cited above were observed to varying degree in all transects (Table 5.2). The amount of Dead Sawgrass and Spikerush-Sawgrass Mosaic increased from Transect 3 to Transect 5-from north to south and from highest elevation to lowest-while Tall Sawgrass and Sparse Sawgrass communities decreased across the same range. Unlike the other types, the spatial distribution of Spikerush Marsh in Shark Slough was relatively uniform in 2000, despite an increase in abundance across all transects during the previous two decades.

1992), mean surface water levels in Shark Slough have exhibited a general increase since the mid-1960's (Figure 5.1). Based on what is currently known about the hydrologic regime that characterizes different Shark Slough plant communities (e.g., Ross et al., 2000; Olmsted and Armentano 1997; Gunderson 1989); Herndon, unpublished document), one would predict that persistently high water levels might lead to the replacement of shorter hydroperiod sawgrass marsh by long hydroperiod types such as Spikerush Marsh. In fact, this is what the data summarized in Table 5.2 indicates, i.e., Spikerush Marsh and Spikerush-Sawgrass Mosaic increased in all three transects, primarily at the expense of the two major sawgrass types. However, with data limited to two vegetation surveys separated by 20 years, it is not possible to determine when and over how long a period these changes in landscape pattern took place, or even whether hydrologic variability was the primary driving force behind it.

Hofstetter (1976) made the following observations about the sawgrass marshes of Everglades National Park in the early 1970's, following several years of high water: 1) a decrease

hydrologic regime of Shark Slough, and rapid response of vegetation to it. We base these hypotheses on the observation that every reported increase in the relative abundance of sawgrass in the Slough coincided with or closely followed periods of below-average water level (e.g., Wade et al., 1980; Davis et al., 1994; Olmsted & Armentano, 1997). Conversely, every increase in the relative abundance of Spikerush Marsh coincided with or followed periods when annual mean surface water elevation was high (e.g., Hofstetter, 1976 and this study). Based on the hydrograph presented in Figure 5.1, it is quite likely that the dominance of sawgrass among the plant communities of Shark Slough has changed markedly several times during the 1980-2000 period considered in this study.

Finally, our finding that a structural change occurred in Shark Slough during the last two decades assumes that the maps presented in Olmsted and Armentano (1997) are an actual representation of the vegetation structure of Shark Slough during the period that the photo was taken (1971) and the groundtruthing conducted (1981). Although there is no way of verifying the accuracy

and make ecologically sound water management decisions knowing in advance what the effects will be on the marsh communities of Shark Slough. This hydrology:vegetation relationship demonstrates how closely bonded the hydrophilic communities of the Slough are to one another and to the physical environment, particularly hydrology.



Section 6

Landscape Structure in Shark Slough

Section 6:**Introduction****Methods****Results****Discussion****Conclusion****Introduction:****Section 1:****Section 2:****Section 3:****Section 4:****Section 5:****Figures:**

<u>1.1</u>	<u>1.4</u>
<u>1.5</u>	<u>1.6</u>
<u>5.1</u>	<u>6.1</u>
<u>6.2</u>	

Literature Cited:

Introduction:

In Section 1 we examined the interrelationships of hydrology and soils with Shark Slough vegetation. In Sections 4 and 5 we summarized geographic variation in the relative abundance of marsh cover types today, and compared them to patterns evident in a similar study concluded in 1980. In this section, we describe the vegetation briefly from a landscape perspective, one that asserts that the Everglades landscape has emergent properties that are not entirely expressed by the characteristics of its constituent local ecosystems.

Methods:

The data consist of a field survey of the identity and extent of habitat patches intercepted by five transects distributed from north to south in the ENP portions of Shark Slough (Figure 1.1). The transects ranged in length from 4-12 km, and were oriented perpendicular to the apparent direction of water flow, which is generally to the southwest. In November - December 2000 we drove an airboat along the transect, noting which of the seven habitat types defined in Table 4.2 best described a five meter-wide band surrounding the transect. The position of every cover type transition was determined by differential GPS to the nearest five meters.

Data analysis focused on the size structure of patches within the habitat mosaic, especially in variation among cover types or regions (as defined in Section 1). It is important to recognize that the orientation of the transects meant that, to the extent that habitat units were aligned parallel to the flow of water, our measurements reflected their shortest dimension. Though anisotropy (directionality) in landscape features was not addressed in this study, the shape, size and orientation of Everglades tree islands has been a subject of recent research attention (Brandt et al. 2000).

In order to describe structural diversity in the Shark Slough

Landscape diversity (H') was much lower in Northeast Shark Slough (NESS) than in the other three regions (Table 6.1). This was a result of a low evenness among cover types in NESS (Table 4.3), because the richness component of diversity was equal in the four regions (seven cover types present in each).

Table 6.1: Landscape diversity matrices in four regions of Shark Slough. Calculations of P and H' are described in ext.

Region	Transect Length (km)	Patch Density (#/km)	Mean Contrast Among Patches ($D_{x\text{-bar}}$)	Patch Index (P)	Landscape Diversity (H')
Northeast	5.47	30.7	1.40	21.6	0.96
Northern	10.94	39.9	1.39	27.4	1.50
Central	8.29	35.1	1.32	22.7	1.56
Southern	12.24	32.4	1.18	19.0	1.46

Regional patterns in patch size structure are illustrated in Figure 5.1. Patches 50 meters across or smaller accounted for 50-70% of total marsh area in each region, and the largest uninterrupted patches were less than 250 meters wide. Small patches were most characteristic of Northern Shark Slough (NSS), and large patches were most prevalent in NESS.

Not surprisingly, the above differences in landscape structure were reflected in the patchiness statistics (Table 6.1). NSS was characterized by the highest patch density ($\sim 40/\text{km}$) and P index of the four regions. Patch density was lowest in NESS ($\sim 30/\text{km}$), but, because of low contrast among patches, Southern Shark Slough exhibited the lowest P. Central Shark Slough was intermediate in both patchiness measures.

Shark Slough cover types did not differ greatly in patch size distribution (Figure 6.2). There was no obvious relationship between

al. 1999) distinguished 3-5 cover types, with patch density of 2-5 patches/km, in Northern, Central, and Southern Shark Slough. On the basis of 1:16,600 aerial photos, Olmsted and Armentano (1997) mapped Shark Slough vegetation in much greater detail. However, detailed as they were, their maps identified only 8-11 patches/km in the above regions, where our field observations yielded patch densities of 33-37 patches/km.

Following Romme (1982), we used the familiar Shannon-Wiener H' to index landscape diversity. Since cover types are not as unambiguous as species, use of this index is especially sensitive to the scale effects discussed above. Nevertheless, H' may be useful in monitoring temporal changes or in describing spatial variation within a broad study area. H' depends on both richness and evenness, but in Shark Slough inter-regional differences were related to the evenness component of diversity. Four of the cover types (Cattails, Dead Sawgrass, Tall Sawgrass, and Bayheads) were always minor elements whose abundance probably did not affect H' greatly. The relatively low landscape diversity observed in Northeast Shark Slough (Table 6.1) is the result of a predominance in that region of Sparse Sawgrass over the other two major marsh cover types, Spikerush Marsh and Sawgrass-Spikerush Mosaic. NESS was once near the center of Shark Slough, but sheet flow through the area was interrupted with the construction of Tamiami Trail, and has never been adequately reestablished. The possible role of sheet flow in maintaining a mixture of marsh types and therefore high landscape diversity is an open question.

H' indexes the number and relative abundance of community types, but does not address how these types are distributed in the marsh. To express this spatial component of diversity, we again borrowed an index previously applied by Romme (1982) to the forest mosaic in Yellowstone National Park. The patchiness index P is highest when the landscape is dissected into many small structural or

landscape.

Data summarized in Table 6.1 illustrates the highly dissected nature of the Shark Slough marsh, with 30-40 patches crossed per kilometer of transect. However, adjacent units tend not to be too dissimilar in structure (mean dissimilarity ($D_{x\text{-bar}}$), 1.18-1.40; Table 6.1). Based on the above discussion, this combination may indicate a landscape in which the primary control on vegetation is hydrologic, and disturbance plays a secondary (but critical) role. One disturbance whose influence may be detected in the Shark Slough landscape is the recent sawgrass dieoff episode that was described in Sections 1, 4 and 5 of this report. Since sawgrass dieoff takes place almost exclusively in Tall Sawgrass, it is possible to compare current patch density and contrast to that of a hypothetical pre-dieoff landscape in which Tall Sawgrass occupies current Dead Sawgrass patches. Dieoff had the following effects:

NESS: Increased patch density by 2%, Increased patch contrast by 4%

NSS: Increased patch density by 6%, Increased patch contrast by 6%

CSS: Patch density unchanged, patch contrast increased by 14%

SSS: Patch density unchanged, patch contrast decreased by 2%