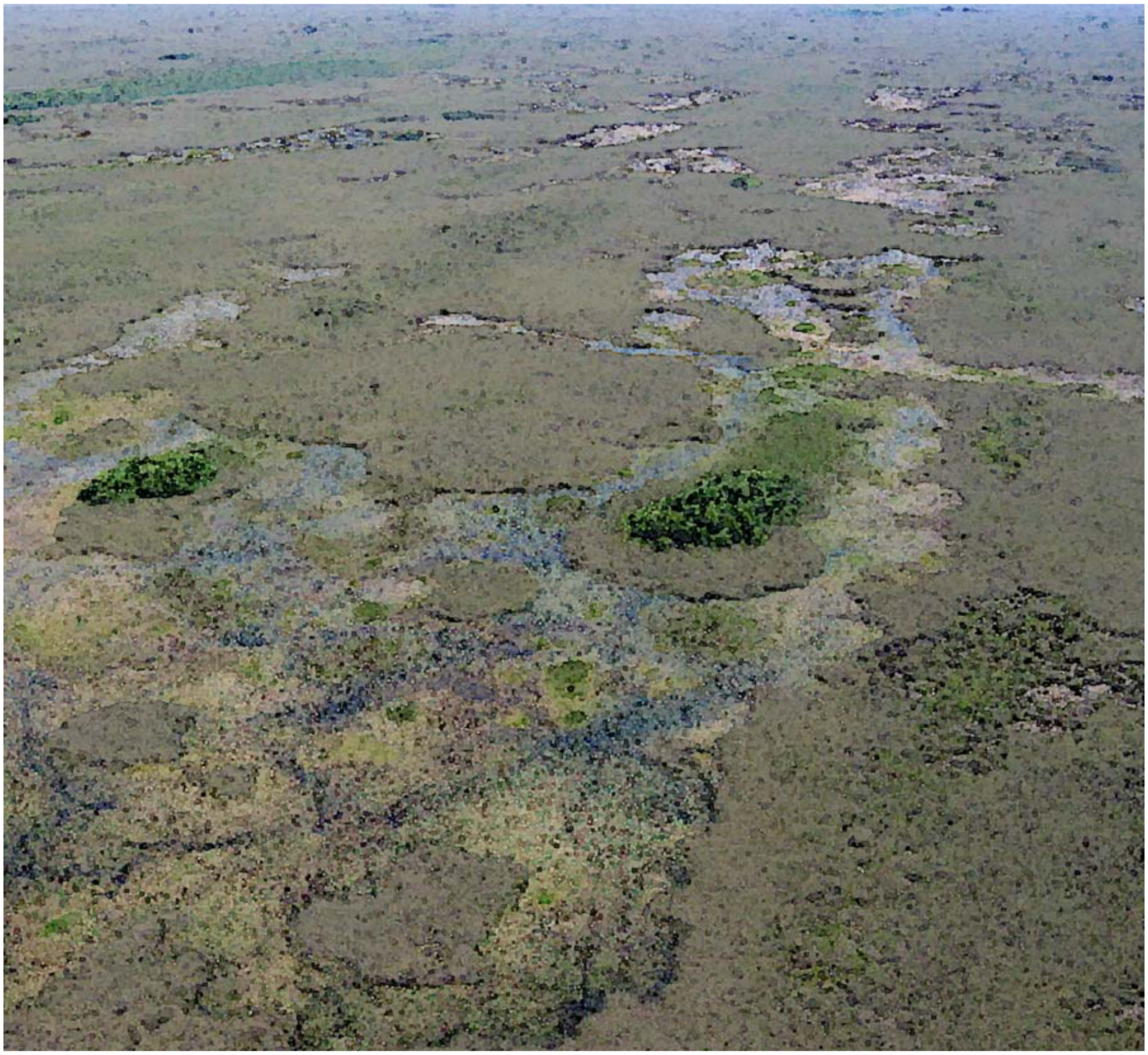
Terrestrial Ecosystem Group

TREE ISLANDS IN THE SHARK SLOUGH LANDSCAPE: INTERACTIONS OF VEGETATION, HYDROLOGY AND SOILS



FINAL REPORT

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Florida International University

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TREE ISLANDS IN THE SHARK SLOUGH LANDSCAPE: INTERACTIONS OF VEGETATION, HYDROLOGY AND SOILS

FINAL REPORT

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Executive Summary

This report presents what we have learned about tree islands of Shark Slough and adjacent marshes of Everglades National Park (ENP), based on ecological studies carried out in these wetlands during the period 2000-2003. The tree islands of Shark Slough share many features with tree islands elsewhere in the Everglades. Their current composition and community structure is determined to a large extent by recent hydrology, as well as by disturbances (fire, freezes, hurricanes, man). Tree islands have historical, cultural, and biological values that are recognized by nearly all parties to the Comprehensive Everglades Restoration Plan (CERP). Maintaining and/or restoring the health of tree islands are major objectives of CERP. Consequently, there is a need within CERP for tools to assess the health of tree islands, and to relate these measures to the hydrologic regime to which they are exposed.

Hydrologic Variation Among and Within Tree Islands of Shark Slough

Meso- and micro-scale topographic and vegetative variability within the Everglades create a mosaic of local water elevations, flow vectors and flow rates. The hydrologic regimes impacting three tree island sites were described from topographic surveys conducted in the hardwood hammock (HH), bayhead (BH), and bayhead swamp (BS) forest communities of each site. Water levels were determined from wells installed in these communities and the adjacent marsh. Seasonal patterns of water depths in BS, B, and HH communities in the three tree islands varied substantially from one another. Hourly fluctuations in the water table at individual sites, consisting of a rapid decline during daylight hours, with partial recovery at night, were also observed. The findings suggest that seasonal shifts in water elevation are driven by regulatory releases from the S-12 structures and may be modified substantially by soil permeability, drainage characteristics, and local differences in evapotranspiration.

Vegetation Mapping and Landscape Pattern in Shark Slough

A network of mapping points was established for the purpose of describing and documenting local and regional variations in landscape structure within Shark Slough and adjacent areas. The vegetation, hydrology, directionality of all landscape features (using longest vector length, LVL), and landscape patch shape (using elongation ratio, R_e) for each of 12 regionally distributed sites throughout the slough were determined. The slough's landscape is generally characterized by a mosaic of patches interwoven within a mixed-marsh community matrix; patches vary in size, shape, directionality, vegetation cover, and relative density. The findings show that Shark Slough is a highly complex landscape, whose physiognomy is controlled by local and regional variation in hydrology, topography, and disturbance history. The data also suggest that relatively long-term changes in flow patterns, such as those imposed on NESS marshes, can reduce the ridge-and-slough character of the landscape.

Characterization, Biogeochemistry, Pore Water Chemistry, and Other Aspects of Soils in Tree Islands of Shark Slough

Only a few studies have analyzed soil nutrients (N and P) and their cycling in tree islands. Baseline physical and chemical properties of soils from three tree islands in Shark Slough were established. An attempt to understand the biogeochemistry of nutrient cycling, particularly phosphorus, was also made. In general, soils in the hardwood hammock communities had alkaline pH, low organic matter, abundant carbonate minerals, low nitrogen, and high phosphorus. The mineral composition and the high phosphorous content in hardwood hammock soils are surprising results; several factors may be involved in the accumulation of the high P levels. Pore water nutrient chemistry was also examined to link labile form of nutrients, N and P, to plant uptake. Levels of NH_4-N were lower in hardwood hammocks than adjacent bayheads and marshes. Higher levels of SRP in hardwood hammock soil solution are attributed to solubilization/mineralization/dissolution phenomena

Winter Air Temperatures in Tree Islands and Adjacent Marshes of Shark Slough

Little is known about how contrasting vegetation cover (tree islands *vs.* marshes, for example) within a climatic envelope influences ambient air temperature. Temperature monitoring stations were installed and monitored in the interior of a hardwood hammock and in the adjacent marsh at seven locations in Shark Slough, from December 2002 to March 2003. There was a difference in ambient air temperature between the hammock and marsh environments, apparently related to shading and insulation as a result of canopy cover which is significantly higher in the hammock environment than in the marsh. However, canopy cover alone does not fully explain this difference. The uniformity of winter temperatures within the slough is surprising, given the coastal distribution of many tropical tree species within Florida. Our data indicated that minimum temperatures did not drop as low in the slough proper as in peripheral sites (i.e., CR3, P38, NP205, and T6).

Sediments, Stratigraphy, and Aspects of Succession, Chronology, and Major Prehistoric Disturbance in the Principal Type of Large Tree Island in Shark Slough

Basically unknown were the sediment stratigraphy, the succession giving rise to woody vegetation, and the predrainage (natural) and postdrainage history of disturbance. Mixed organic and residual-mineral sediments underlie hammock heads and evidence archeological disturbance. Bayhead tails were emphasized and contained typical fibrous peats along with little-understood mucky sediments having abundant fine-grained organic and mineral matter, plus a distinct mineral layer thought to be ash. An external source is implied for the fine mineral matter and suggests a role of flow. A subpeat marl layer shows that marshes once occupied bayhead locales, and fossil pollen from the peat and muck indicate marsh occurred for much of that period as well, including waterlily marsh. The bayhead forest arrived late in the wetland era. Severe disturbance by natural peat fire is implied by the apparent ash and is reflected in the pollen findings. Recent shifts in tree island vegetation are shown, but these may predate regional drainage. Nonpollen microfossils are consistent with phosphorus enrichment in the tree island era.

Vegetation Structure and Composition in Relation to the Hydrological and Soil Environments in Tree Islands of Shark Slough

A total of 128 species were identified from three tree islands in Shark Slough. Species richness was higher in bayhead and bayhead swamps than in hardwood hammocks and tall sawgrass marsh, and was directly related to size of tree island. Vegetation composition and structure was influenced by a strong elevation gradient and correlated environmental variables. Hydrological variables and certain soil characteristics were strongly correlated with elevation. Hydrology was the strongest gradient influencing vegetation composition. Canopy height and productivity decreased with an increase in mean water level. Soil depth and total carbonate were important in determining differences in vegetation composition among tree island sites. Differences in tree size class distribution among species, especially in bayhead and bayhead swamps, revealed that vegetation in those forests would change in a few years. Ranking of woody species in terms of their flood tolerance did not differ among sites. Seedlings of a few tree species had higher hydroperiod optima than mature trees of the same species.

Note and Observations on the Use of Tree Island Habitat by Wildlife

Few studies have documented wildlife in Everglades tree islands. An annotated list of wildlife species was created from anecdotal information derived from three years of observations in three tree islands in Shark Slough. Lists of the animal species observed, and the tree island forest communities they were associated with, were recorded for the classes Amphibia (1 sp.), Arachnida (1 sp.), Aves (13 spp.), Insecta (5 spp.), Mammalia (2 spp.), and Reptilia (9 spp.). Tree islands of the slough are an important habitat resource for the wildlife of the Everglades, providing ground, food, roosting, and a nesting sites for many animals species. Biologists, resource managers, and policy makers must take into account how the restoration effort might impact the wildlife that appears tightly bound to the tree island habitat.

Responses of Tree Island Tree Species to Simulated Hydrologic Regimes: A Shadehouse Study

Seven swamp and five upland tree species common to Everglades tree islands were subjected to three hydrologic regimes (high, low, and no flood) under controlled conditions for 25 weeks, and assessed for growth and physiological responses. Soil inundation under the high flood treatment resulted in reduced tree growth that was more pronounced and occurred earlier in mesic forest species than in swamp forest species. Physiological responses differed less among species, although stomatal conductance was a better predictor of the effects of flood stress on growth. Some swamp species appeared to be better adapted to rising water levels than others. The highest mortalities and lowest growth were observed in the upland species. The moist soil conditions simulated by the low flood treatment resulted in greater growth in most species compared to high flood. The arrangement of species according to their responses to experimental flooding roughly paralleled their spatial distribution in the marsh landscape.

Tree Islands as Elements in the "Ridge and Slough" Mosaic (Conclusion)

Shark Slough tree islands have been influenced by the same uneven environmental history that has affected other Everglades wetland communities. Vegetation patterning within these tree islands resembles patterns in the marshes that surround them; species composition is largely arranged along a single strong gradient represented in this study by hydrologic measures. Hydrology is in fact one aspect of a multi-factorial environmental complex that includes nutrient availability, canopy openness, and possibly temperature and other climatic variables. Paleoecologically, these tree islands are the product of a non-linear, successional process subject to long-term climatic variation and significant local and regional disturbances. Within the landscape, tree islands play many important functional roles (e.g., by providing wildlife habitat). Because tree islands are very much a part of the ridge and slough landscape of Shark Slough, they can probably best be protected by managing for the health of the landscape as a whole.

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Introduction

In this document, we recount what we have learned about tree islands of Shark Slough and adjacent marshes of Everglades National Park (ENP), based on ecological studies carried out in these wetlands during the period 2000-2003. As we apply it, the term *tree island* refers to a forest that has arisen naturally within a lower, shrub-dominated or herbaceous vegetation matrix that surrounds it on four sides. In the Everglades, this definition distinguishes tree islands from true *islands*, which are surrounded by water; *riverine forests*, which are linear features that line current or historical watercourses and connect to larger water bodies or their fringing forests; the *fringing forests* themselves; or *forest fragments* that have been isolated by human alterations to the surrounding landscape. A broader definition of tree island could also include the closely related broadleaved forest inclusions in the pine forests of Long Pine Key, the Miami Rock Ridge, or the Florida Keys, which are commonly referred to as *hammocks*, as well as artificially-created tree islands associated with ecosystem restoration.

The tree islands of Shark Slough share many features with tree islands elsewhere in the Everglades. Their geomorphology is shaped by a history that stretches back thousands of years, while their current composition and community structure is determined to a large extent by recent hydrology. Disturbances also play a large role in their ecology. They are impacted frequently by hurricanes and less often by fire, because of a humid microclimate and low flammability in comparison to adjacent marshes. However, the organic soil lost to a single fire may take many centuries to be replaced. By sequestering and storing nutrients, they play an important role in the cycling of N, P, and other elements in the Shark Slough ecosystem. Finally, these forest patches enhance the diversity of the broader grassland landscape, concurrently providing upland, forested refuges for many animal species during different stages of their life cycle.

In comparison to similar forests, Shark Slough tree islands are not extremely rich in tree species. The small upland portions of the islands are often dominated by three or four tree species, with a few other taxa scattered about in low abundance. In comparison, hardwood hammocks in the Rocky Glades or eastern Big Cypress National Preserve typically support twice as many tree species, and hammocks of similar size in the Florida Keys are even more species-rich. Clearly, factors such as the isolation of the Shark Slough sites and biogeographic patterns within the pool of available tropical species limit diversity in Shark Slough hammocks. Similarly, tree species diversity in Shark Slough bayheads is low in comparison to some bottomland forests in the southeastern US. Bayheads in the southern Everglades typically contain seven or eight ubiquitous trees, most of them temperate in origin. In more open bayhead-swamp communities, this level of diversity is greatly enhanced by a rich herbaceous flora. Though plant diversity in Shark Slough tree islands is unexceptional, the bio-complexity of the larger islands, with a small, raised tropical forest embedded within the head of a teardrop-shaped, temperate wet forest, is quite notable.

Maintaining and/or restoring the health of tree islands are major objectives of the Comprehensive Everglades Restoration Plan (CERP). Tree islands have historical, cultural, and biological values that are recognized by nearly all parties to CERP. Prolonged periods of high water may adversely affect the condition of tree islands via death or dieback in flood-intolerant species (Guerra 1996, Jones et al. 1997). Similarly, persistent low water may create conditions of extreme fire risk, during which tree islands may be catastrophically damaged. Because of the uneven distribution of water in the regulated and compartmentalized Everglades ecosystem, flooding has been a larger problem in the northern Everglades, while fire induced by low water is of more concern in ENP. Consequently, there is a need within CERP for tools to assess the health of tree islands, and to relate these measures to the hydrologic regime to which they are exposed.

In the pages that follow, we describe, the physical nature and origin of Shark Slough tree islands in five chapters (Hydrologic Variation, Vegetation Mapping, Soils, Temperature Patterns, and Paleoecology), the biological character of the islands in a second set of two chapters (Vegetation and Environment, Wildlife Usage), and an experimental approach in one chapter (Shadehouse Study). In the final chapter, we integrate these results and present recommendations for maintaining and monitoring tree island health as the restoration effort unfolds.

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Physical Nature and Origin

1

Hydrologic Variation Among and Within Tree Islands of Shark Slough

Dave L. Reed and Michael S. Ross

Introduction

Shark Slough hydropatterns are affected by surface water delivery, local precipitation, and groundwater transport. These factors are interdependent and locally defined; water channels and pools across flow vectors that are further shaped by variable elevation, vegetation pattern, and anthropogenic structures present in the slough. Generally, the annual hydrologic cycle is comprised of a sinusoidal surface water elevation oscillation. This annual cycle can be divided into wet and dry seasons, from May to October and November to April, respectively. Maximum water elevations are usually reached in October, after which evapotranspiration and drainage (both natural outflows and anthropogenic diversions) gradually drive the system toward annual minimum levels around May. Evapotranspiration occurs at an average rate of 0.5 cm per day, though local variation in drainage and evapotranspiration may accelerate water elevation declines (Gunderson and Stenberg 1989, German 1996). Despite the generally uniform water elevation inherent in Everglades sheet flow, the meso- and micro-scale topographic and vegetative variability described above create a mosaic of local water elevations, flow vectors and flow rates.

Our work was concentrated at three tree island sites. Satinleaf Hammock (SL) is located 1 km south of the Shark Valley observation tower in the northwestern portion of Shark Slough, ENP. Gumbo Limbo Hammock (GL) is situated near the center of the slough, and Black Hammock (BL) is located near the eastern edge of the slough at the terminus of the former L-67 extension levee (Figure 1-1). Local average marsh soil elevations for SL, GL, and BL are 1.34, 1.14 and 1.4 m (amsl), respectively, and average marsh bedrock elevations for SL, GL, and BL are 0.84, 0.26 and 0.92 m, respectively. Thus, soil depths, which are shallower along the eastern and western fringes of the slough and deeper in its center, moderate but do not entirely obscure the bedrock trough underlying Shark Slough.

The hydrologic regimes impacting SL, GL, and BL are strongly affected not only by the physiographic positions of these sites within the slough, but also by their proximity to water control structures. Water delivery structure S-12B is located less than a kilometer west of the Shark Valley tram road and 10 km west of the former L-67 extension levee. Structures S-12C and S-12D are located 5 and 0.5 km west of the former levee, respectively. Finally, the S-333 pumping station, which directs water into Northeast Shark Slough (NESS), is located 0.5 km east of the former levee. In particular, the southerly flow of water delivered by structure S-12D and pumping station S-333 result in increased volume being channeled to the area of BL, compounded in part by the former levee, which likely continues to channel water south to its terminus.

Local variation in water elevation may be inferred from hourly stage measurements at Everglades National Park (ENP) and U.S. Geological Survey (USGS) water depth recorders distributed throughout the slough. For some of our purposes, however, these recorders may be too distant to adequately represent the local water table within the tree islands. Moreover, local variation in soil depth and bedrock elevation may create important variation in the water table within each tree island. For these reasons, we established our own water recorder network in each tree island, and tied these measurements into the nearest long-term recorder.

Materials and Methods

Topographic Surveys

In order to describe the local hydrologic regime throughout the three study tree islands, it was necessary to determine ground elevations. We established a network of four transects in each island. One transect followed the long axis of the tree island, and the others crossed the island at right angles to the first, in the "head" and at two locations within the "tail." Along these transects, surface elevation was determined at ten meter intervals (five meter intervals within and immediately adjacent to the hardwood hammock) by surveying via auto-level from a benchmark of known elevation. Temporary benchmarks were established along the transects, and elevation differences between adjacent benchmarks were determined from at least two positions, such that the two estimates did not differ by more than 1 mm. Surface elevations were then determined by difference with the nearest benchmark We also established semi-permanent benchmarks at the ends of each transect, at transect intersections, and adjacent to each well (see below) by pounding a 0.25 inch diameter rebar into the limestone bedrock with a sledge hammer until it was solidly fixed. Since the vegetation plots representing the hardwood hammock, bayhead, and bayhead swamp forest communities were located adjacent to the transect intersections, it was a simple matter to survey to the centers and corners of each sampling cell in the plots from the semi-permanent benchmarks. At each surveyed location, soil depth was determined by probing to bedrock with a metal rod.

Hydrologic Variation Among and Within Shark Slough Tree Islands

Wells were installed in April of 2003 in bayhead (B), bayhead swamp (BS) and marsh (M) communities in and adjacent to each tree island. An additional well was established in the hardwood hammock (HH) in SL. Each well consisted of a two inch screened PVC pipe, driven to the bedrock and capped at the base in order to prevent groundwater intrusion. The BS well in BL was exceptional in not reaching bedrock, despite being driven to a depth of 3 m. Soil cores three inches in diameter were used as pilot holes for the two inch wells, and sand was poured around the walls to prevent muck intrusion into the well. Water depth sensors (piezoresistors) were lowered to within 20 cm of the base of the well and cables were extended from the sensor to a circuit box installed at approximately breast height for data acquisition. Prior to installation in the field, each sensor was calibrated to 0.5-1.0 cm accuracy in the lab. Reference benchmarks were surveyed for elevation and sensor elevations were calculated in order to provide water elevation (amsl). Data were recorded in intervals of 30 minutes by a HOBO H8 datalogger (Onset Computer Corporation, Bourne, MA, USA).

Plot Hydrology

Elevation surveys were extended from several benchmarks established within each tree island to the four corners and center of each sampling cell. Calculation of the hydrology of each cell was based on an average of all five elevations per cell. Cell elevation was subtracted from water elevation at the recorder to derive local hydrologic regime. Annual and monthly hydroperiod were calculated, as well as average distance to water table from the soil surface. The latter measure may serve as an indicator of soil wetness and/or redox condition in areas of higher elevation, where annual period of inundation lasts only a few months and aerobic conditions persist. Gaps in site records were extrapolated from regressions with nearby recorders within the tree island, or, in several cases, with the closest ENP or USGS recorder. Regressions among recorders were developed for wet and dry seasons separately. Analysis of variance was used to assess among-island differences in hydroperiod and average water depth. Bonferroni post-hoc comparisons were applied when an island effect was identified.

Results

Tree Island Physiography

Surface and bedrock elevations along the central axis of the three study tree islands are presented in Figure 1-2. The “heads” of the tree islands rose sharply above the surrounding landscape; in all three sites, relief between the highest point in the tree island and the marsh on the upstream side (left side of figure) was about 1 m. Downstream from the tree island “head”, the topographic gradient was gradual (GL, Figure 1-2C) or essentially unnoticeable (SL and BL, Figure 1-2A,B). Surface elevation varied less than bedrock elevation, because soils on the highest elevations (typically 50 cm or so in depth) were shallower than soils in the tails of the tree islands. This was especially true in GL, where soils in the tail were generally 1 m or more in depth. At nearly 1.5 m, the bedrock rise at GL was considerably steeper than at SL or BL.

Hydrologic Variation Among and Within Shark Slough Tree Islands

In order to extrapolate historic conditions at the three tree island sites, we analyzed data collected from water level recorders at hydrological monitoring stations G620, NP203, and P33, which were those closest to SL, GL, and BL, respectively. Relative differences among these sites over the period 1989 to 2003 were similar to those suggested by our own records within the tree islands during 2003. Over the last decade and half, G620 exhibited the greatest range in water level, consistently attaining maximum water elevations 5-10 cm greater than P33 and NP203 during the wet season (Figure 1-3). This pattern typically diminished by December and resumed by July of the following year. Wet season water levels at P33 and NP203 deviated by less than 2 cm from one another. In contrast to wet season patterns, hydropatterns during the dry season varied with mean annual water elevations. For example, during 1990-1991 and 2001-2002, when water elevations averaged over all three recorders were relatively low (i.e., 122 and 142 cm, respectively), G620 water level receded much further than the other two sites. It is notable that the latter two years marked the beginning of regulation of the S-12 structures by IOP rules. In contrast, during 1993-2000, a period when the annual average water level across all sites was relatively high at 157 cm, dry season minima for G620 were at or above those at P33, and NP203 levels were lowest of the three locations in every year. Water elevation at recorder P33 remained at or above NP203 throughout the period, regardless of season or year, with a few days of exception in 1990, 1991, 2001, and 2002.

Records from the three park reference recorders described above represent the hydrology near but not within the tree islands themselves. All are situated in the open marsh at variable distances from the head of islands: 1.1 km (G620 to SL), 0.8 km (NP203 to GL), and 1.5 km (P33 to BL). Local water level averages for 2003 (based on three water level recorders at GL and BL, and four at SL) are tracked through the annual cycle in Figure 1-4A, and relative differences among islands are highlighted by month in Figure 1-4B. Among-site patterns from these data resembled those from the ENP recorders. GL water level was lowest, and SL was high with maximum seasonal variation, and BL was at its highest during the dry season. On an annual basis, water levels were about as high at BL as SL; such high water levels were not evident at P33 (Figure 1-3), perhaps because it is further from the outfall of the L-67 extension canal than BL.

Local differences from ENP recorders were most evident at SL, where two years of data were available. At this site, wet season levels within the tree island were higher than at G620 during the peak of both wet seasons and during the dry season of 2002 (Figure 1-5). Coefficients of variation from regressions relating SL site water elevations with that of G620, both within quarters and across the entire year, are presented in Table 1-1. Site differences within SL are evidenced in the disparity between periods of rapid wetting and drying (June-August and December-February, respectively), and mid-wet and mid–dry season periods (September-November and March-May, respectively); correlations were highest during the former. We suspect that during these periods of rapid transition, local differences among sites are overshadowed by strong environmental gradients created by the initiation or cessation of water delivery.

Table 1-1. Quarterly stage data regression R^2 between each SL site well and recorder G620, for 2002-2003. All comparisons are significant to $p<0.01$.

Site	Annual	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov
Hardwood Hammock (HH)	0.9752	**0.9637**	0.8071	**0.9593**	0.7279
Bayhead (B)	0.9826	**0.9635**	0.9391	**0.9772**	0.9629
Bayhead Swamp (BS)	0.9713	0.8459	**0.9496**	0.9385	**0.9726**
Marsh (M)	0.8277	**0.8398**	0.8035	**0.8985**	NA

Within SL, where our data are most complete, water levels at the HH, BS, and M recorders were very similar when averaged over the whole year, while the average water table at B was somewhat lower than at the other sites (Figure 1-5). Seasonal variation in the relative elevation of the water table at these four locations was small and inconsistent. In both BL and GL (data not shown), the water table was highest at B, followed by BS and M during most of the year, except during April through May. The higher water elevations at B were most pronounced at

GL, where the average difference between it and the other sites was 3 cm; in BL, differences between B and the two other sites were typically 0-1 cm.

From the point of view of the vegetation occupying each site, water depth is more relevant than the elevation of the water table. In general, sites of similar vegetation experienced similar hydrology (Figure 1-6). The single exception was the M site at BL, where water depths after July 2003 were more similar to BS sites than to M sites in SL and GL.

ANOVA was used to assess Site and Island effects on hydrology for the period December 2002 to November 2003. Significant main effects and interactions were observed. Subsequent one-way ANOVA indicated significant among-island differences for water depth in bayhead ($p=0.009$), bayhead swamp ($p=0.001$), and hardwood hammock environments ($p<0.001$, applying average water levels from B, BS, and M to HH elevations in GL and BL). Means and results of post hoc comparisons among islands are shown in Table 1-2. Among BS communities, mean water depth in GL significantly exceeded BL, which in turn exceeded SL. Water depths for B followed a similar inter-island pattern, though the difference between BL and SL was non-significant. No HH sites were inundated during 2003, but the water table was further from the surface at BL than at either SL or GL. BS sites experienced hydroperiods of 241-352 days in 2003, with SL exhibiting by far the shortest period of flooding. Hydroperiods for B were much more narrowly grouped, varying from 180 days at SL to 212 days at BL.

Seasonal patterns of water depths in BS, B, and HH communities in the three tree islands varied substantially from one another, in general mimicking the variation exhibited at the nearest ENP recorders and their respective positions within Shark Slough. These patterns are summarized in Figure 1-7. During the months of December through February, B water depths in GL were intermediate between those recorded in B sites in BL and SL. After this transitional period, when water levels throughout Shark Slough declined rapidly, GL B became the driest of the three sites through November. Conversely, SL B was the driest site during December- February, and gradually became the wettest of the three sites by July and continuing through November.

BS sites were affected by seasonal water elevations differently than both the B and HH sites. GL remained consistently 10-15 cm deeper than SL from December through July, after which it was 5 cm deeper or less. The BL BS site experienced deeper water than both SL and GL during the dry season (February-April), and gradually shifted to being the driest site by November. HH sites never became inundated (in BL and GL, water level was estimated from averages of all wells within the tree island). The BL HH site remained well below the other two sites during the wet season and negative depths continued to be at or below those of the other tree islands. In comparison to the other hardwood hammocks, water levels were closest to the surface in GL HH from December through July, after which levels there were similar to SL.

Diurnal Fluctuations in Water Level

In addition to seasonal variation, we also noted hourly fluctuations in the water table at individual sites. The pattern of these fluctuations consists of a rapid decline during daylight hours, with partial recovery at night. The daylight decline suggests involvement of a sunlight-driven process (i.e., stomatally regulated transpiration from the tree island canopy). The nighttime recovery suggests resupply from areas of higher water potential, either from upstream in the watershed or from adjacent areas in which drawdown was less during the day. These patterns do not occur throughout the year. Generally, they are initiated once water elevations drop to near or below local soil elevations, during the March-May dry-down period, depending on annual hydrologic conditions. Daily reduction in the water table is followed by a rise of some fraction - usually less than three quarters - of the daytime decline (Figure 1-8). Diurnal recovery occurs in three stages: the first, initiated by a drop in the water table caused by evapotranspiration (ET), may last for as long as 7 hours; in the second stage, the daily nadir is reached and remains static for up to 8 hours; in the third, recovery stage, the water table approaches its level of the previous morning.

Table 1-2. Bonferroni post hoc comparisons of individual sites across tree islands for water depth and hydroperiod. Negative water depths represent subsoil levels. Site mean soil elevations are also shown. Tree islands: BL, Black; GL, Gumbo Limbo; SL, Satinleaf. Sites: B, bayhead; BS, bayhead swamp; HH, hardwood hammock.

Tree Island	Depth (cm)			Hydroperiod (days)		
	SL	GL	BL	SL	GL	BL
BS mean	16.1	25.1	20.0	241	351	352
SL	-	**0.000**	0.046	-	**0**	**0**
GL	**0.000**	-	**0.006**	**0**	-	1
BL	0.046	**0.006**	-	**0**	1	-
B mean	3.5	-0.3	5.5	180	187	212
SL	-	**0.014**	0.371	-	0.388	**0.000**
GL	**0.014**	-	**0.000**	0.388	-	**0.000**
BL	0.371	**0.000**	-	**0.000**	**0.000**	-
HH mean	-60.0	-56.7	-69.5	HH mean is zero; no inundation		
SL	-	0.622	**0.006**			
GL	0.622	-	**0.000**			
BL	**0.006**	**0.000**	-			

Mean Site Soil Elevation (cm)

	SL	GL	BL
BS	146	124	144
B	158	150	157
HH	222	206	234

Water loss during the first stage can lower the water table by as much as 3 cm, at a maximum rate of 0.7 cm per hour. Such rates were observed in SL B once water elevation dropped below 130 cm in the spring. ET rates observed in the stage record are generally constant through daylight hours, though water loss rates may subside somewhat during midday, then resume briefly. Once the daily nadir is reached at 2-4 PM, the second stage lasts for 5 hours on average for the BS, B, and HH, through about 9 PM. Recovery may occur in two stages, after which water levels remain static until approximately 8 AM, and the next day's fluctuation is initiated.

A diurnal recovery pattern occurred in SL HH when the water table was as high as 146 cm (amsl). In SL B and BS sites, the diurnal recovery pattern was only evident when water level dipped below 142 cm, which is below the mean soil surface in both sites. At GL, data were not available for low water periods when diurnal recovery patterns may have been evident. In BL, the BS and M sites did not exhibit diurnal recovery, but water level records from B showed a daytime step-down pattern, with subtle recovery, that resembled fluctuation at SL M. These subtle recovery patterns include a sharp decline in the stage record at a rate of 0.4 cm per hour, but less than 0.9 cm per day (Figure 1-9). Partial recovery in SL M and BL B sites consists of a slight increase, at a rate of 0.05 cm per day. The overall average daily decline in the water table (based on average daily maximum) associated with the recovery patterns described in the last two paragraphs are similar: 0.7 cm per day at SL M and BL B, and 0.6-0.7 cm per day at SL BS, B, and HH.

Diurnal fluctuations in the tree islands are inversely related to the sinusoidal oscillations of measured air temperatures (Figure 1-10A). Experimental calibration of pressure sensors in the laboratory were performed to determine whether temperature effects on the pressure sensors could have been responsible for the diurnal water patterns discussed above. A previously calibrated water level sensor was submerged in 50 cm of water at room temperature in a 3 mm thick-walled, 2 inch clear PVC tube, and voltages were measured. The tube was placed in a 50 cm deep bucket of ice for 20 minutes, and voltage and temperature were recorded. The tube was then removed from the ice, returned to the original container for 30 minutes, and voltages and temperature measured again. The tube was subsequently placed in a hot water bath for 20 minutes, and voltage and temperature were again measured. Finally, the sensor was once again placed in the original room temperature, 50 cm deep bath, and remeasured. All voltage measurements were averaged over 3 minutes, measuring once per minute. The results obtained are tabulated below:

Temperature ºC	Voltage	Predicted Depth (cm)
24	0.0953	49.885
15	0.0885	46.825
24	0.0948	49.66
34	0.103	53.35
24	0.0957	50.065

The positive linear relationship between voltage (i.e., water depth) and temperature is illustrated in Figure 1-10B. Increased temperature causes voltage output to increase slightly and conversely, decreased temperature causes a decrease in voltage output. The circuit used in this temperature calibration had a calibrated equation for predicted water depth:

$$\text{depth (cm)} = 450^*(\text{Voltage}) + 7.$$

This relationship suggests that water temperature variation in the wells of ±10 degrees °C can shift predicted output ±3 cm, which is a shift of the same order as those illustrated in Figure 1-8. However, like the air temperature record provided in Figure 1-10A, water temperatures are almost certainly higher during the day than the night (though their range may not be nearly as wide). Thus, with a constant water table, the diurnal temperature fluctuation would cause an increase in predicted water level during the day and a decrease at night. Clearly, correcting for the temperature sensitivity of the sensors would not eliminate the diurnal drop-and-partial-recovery pattern we have described, but would instead accentuate it.

Discussion

Most of the inter-annual differences in water level among our three tree islands are attributable to changes in regulation of Tamiami Canal delivery structures during the period 1989-2003, superimposed on a rainfall pattern that includes very low precipitation during the first three years of the period. Test 7 of the Experimental Program of Water Deliveries, which became fully operational in 1993, and the Interim Operating Plan (IOP), which began in 2000, are also notable in the record. ENP recorders at P33, NP203, and G620 show that spring water levels were high throughout all portions of Shark Slough west of the L-67 extension canal during the Test 7 period. Subsequently, IOP was designed to lower spring water levels in western Shark Slough and adjacent marl prairies, in order to improve prospects of successful breeding by the endangered Cape Sable seaside sparrow. Under these regulations, water levels in spring were by far the lowest at G620, the westernmost of the three stations we examined.

Patterns of seasonal variation in water level among ecosystems within individual islands are more difficult to interpret. For instance, relative water levels in SL communities (which are generally within several centimeters of one another throughout the year) varied seasonally. During most of the year, relative elevations of the local water tables were HH<B<BS<M, but these positions reversed during the short December-February dry-down period. The reason for this reversal is unknown, but could result from differential retention of water in the soil during drainage; hence, a higher water table may be retained at higher soil elevations during the spring dry-down period, before eventually reaching equilibrium.

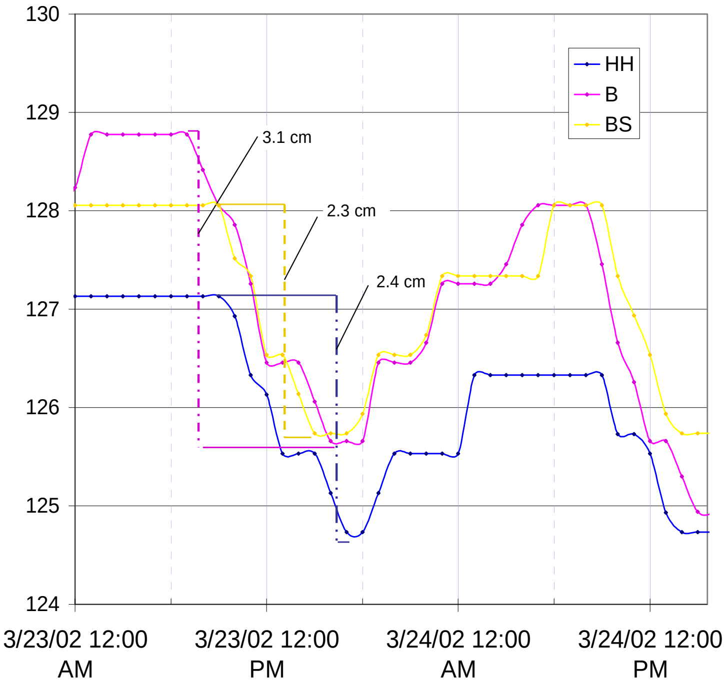
Differences in water level among GL sites were greater than in the other two tree islands. This may simply have been a consequence of the spatial scale of the tree island; that is, GL is a much larger tree island, and distances between plots chosen to represent different communities were further apart than in BL or SL. Furthermore, deeper peat at GL, as well as lower bedrock and soil elevations, also may have played a role, by affecting the rate of water drainage from the soils.

During the rapid decline of water levels in December through February, as water depths subsided below the surface in the B sites in the three islands, a clear order in local depths among islands was established, with BL greater than GL and GL greater than SL (Figure 1-8). It should be noted that calculated local water depths rarely mimicked the patterns of soil elevations across all tree islands. That is, in a month with uniform water elevation across this portion of the slough, one would expect relative differences in water depth to track variations in soil elevation. Only in December 2002 was this condition approached. Instead, in accordance with an apparent dip in water elevations in the central slough (Figure 1-5), all GL communities remained drier than expected from a uniform water elevation.

These observations lead us to our current view of local variation in water level within and among Shark Slough tree islands; namely, seasonal shifts in water elevation driven by regulatory releases from the S-12 structures may be modified substantially by soil permeability and drainage characteristics, as well as by local differences in evapotranspiration. The effect of soil variables may be expressed regionally as well as locally, through the effects of the deepening of soils toward the south and east in the study area. The mechanisms involve the interactions of ground and surface water flow patterns with the mosaic of soils present in the slough.

Diurnal Recovery

The first stage of diurnal recovery is driven by ET. Evaporation rates depend on temperature, humidity, wind speed, cloud cover, site drainage, and water depth (Dolan et al. 1984, Gunderson and Stenberg 1989, German 1996). Dolan et al. (1984) used a graphical estimation of ET, where daily maxima were compared over successive days to produce daily loss, and the nighttime water outflow was subtracted. In our case, we assume that tree islands are drawing water from sites of higher potential energy 24 hours a day, though this rate may vary. During the daytime, inflow is exceeded by loss due to ET. Thus the diurnal recovery pattern represents the balance between net inflows (via groundwater or soil water) and outflows (via ET) throughout the day. The component processes occur throughout the year. The classic pattern, however, is not easily observed in stage records when water elevations are high, as the daily oscillation is overwhelmed by surface flow and direct precipitation inflow. The chart that follows illustrates the diurnal pattern during the 2002 dry season in SL:



During March 23, the daytime declines in HH, B, and BS were 2.4 cm, 3.1 cm, and 2.3 cm, respectively. Because the drop in water level represents loss of water occupying only the soil pores, not the entire soil volume, one needs to know about the water holding capacity of the soil as well as the inflows in order to calculate ET directly from this daytime decline. A simple equation for ET rates derived from stage data that incorporates groundwater influx is taken from White (1932):

$$ET = S_y * (24h \pm s)$$

where S_y is the contemporaneous specific yield of soil, h is the hourly rate (12 AM-4AM) of recharge from groundwater sources, and s is the total change in water table in the 24 hour period. Tromble (1977) used White's (1932) equation to estimate ET in a southeastern Arizona stream channel from stage data that closely resembled the pattern illustrated above. Gunderson and Stenberg (1989) used a similar equation incorporating slope in two locations in ENP, one near P33. The term S_y is not known for our tree islands, making a direct estimate of ET impossible at this time.

ET is primarily dependent on five key factors: local water elevation, site soil elevation, sunlight, temperature, and humidity (Dolan et al. 1984, Gunderson & Stenberg 1989). The latter three factors change dramatically during daylight hours. Maximum daily temperatures occur between noon and 2 PM. This is coincident with the midday plateau in water level described earlier. Both evaporation and transpiration are greatly reduced or cease after sunset, and transpiration decreases to nearly zero once vapor pressure deficit (VPD) decreases, slightly lagging behind photosynthetically active radiation (PAR) decreases, depending upon species (Oren et al. 2001). Guttation and subsequent water loss across the root cortex has been implicated as a cause of nighttime water level recovery in some desert ecosystems. However, in Everglades tree islands, recharge of soils is more likely a function of groundwater recharge.

As described above, the 2-3 hour static period that occurs during the ET drawdown may be explained by temperature fluctuation. Daily high temperatures occurring between noon and 3 PM may cause stomata to close, effectively stopping both passive water uptake and immediate water loss through transpiration. Any water regained by the soil might balance evaporative loss. During this period, water levels remain stable or, in many cases, slightly increase. This increase is indicative of a water influx that may be attributable to groundwater recharge. As temperature drops later in the afternoon, stomata reopen and transpiration resumes for a few hours, reinitiating water table decline.

Future Directions

The effects of the vegetation structure (e.g., leaf area) or type on ET in Shark Slough ecosystems is currently unknown, though the among-site variation we have seen in diurnal water level patterns suggest that the role of vegetation is important. Diurnal fluctuation estimates have implications for use in slough drainage and groundwater flux modeling. Future studies of diurnal recovery should include at least three recorders per site: one extending into the bedrock and open at the base; a second extended to the soil-bedrock interface and capped to reduce groundwater pressure effects (current design); and a third terminating closer to the surface, e.g.,

~50 cm deep (in the case of the M sites, below the rhizosphere). Such a multi-depth layout is necessary to account for soil constituent and moisture gradients in the profile, moisture potentials in the root zone, and groundwater influx. Important physical factors should be measured where feasible. These include PAR, relative humidity (RH), air temperature (currently measured), and sap flow (Oren et al. 2001). PAR, RH, and temperature can each be accurately estimated at relatively low cost and effort. Sap flux measurements using Granier type sensors require minimal cost, though implementation and monitoring are more costly. Effective integration of such data may allow for modeling of seasonal site drainage and even groundwater flux, both of which are necessary to understand meso- and micro-scale hydrology in Shark Slough.

2

Vegetation Mapping and Landscape Pattern in Shark Slough

Pablo L. Ruiz and Michael S. Ross

Introduction

The vegetation and physiography of Shark Slough and adjacent marshes in Everglades National Park is well documented (e.g., Willoughby 1898, Small 1923, 1927, Harper 1927, Davis 1943, Craighead 1971, Gunderson 1994, Davis et al. 1994, Ross et al. 2001b). In general, the slough consists of a mosaic of linearly arranged, mixed-species patches interwoven by monotypic stands of sawgrass (*Cladium jamaicense* Crantz) that may exceed two meters in height. Adding complexity to this "ridge and slough" matrix are forested communities (tree islands) of varying sizes that dot, and in places, dominate the landscape. The boundaries between these communities are generally abrupt and are typically controlled by topography, hydrology, soil depth, and fire (Davis 1943, Craighead 1971, Herndon et al. 1991). These boundaries are known to change through time but controls on the rates of change and directionality are not well understood nor effectively documented, even though a number of vegetation maps have been produced in the last several years (Rutchey and Vilchek 1994, Welch et al. 1995, Olmsted and Armentano 1997, Ross et al. 2001b). Furthermore, a paucity of information exists about the regional variation in landscape structure within the slough and adjacent areas.

With one exception (i.e., Ross et al. 2001b), mapping efforts in the Everglades have not been used to determine and interpret temporal changes in community boundaries resulting from either natural processes (i.e., fires, droughts) or management decisions. Moreover, these maps were not analyzed with the aim of describing and comparing the regional variation in landscape structure within the slough and adjacent marshes. For the most part, large-scale Everglades mapping efforts to date have not incorporated sufficient vegetation sampling and groundtruthing along with the remote sensing work to accomplish these functions.

With this in mind, we established a network of mapping points within Shark Slough and adjacent areas for the purpose of describing and documenting local and regional variations in landscape structure. The data presented in this section, in the form of maps, tables, and landscape indices, serve as a benchmark for the conditions of Shark Slough and adjacent areas in the fall of 2000, after several years of above average mean water levels (Ross et al. 2001b).

Methods

Twelve regionally distributed sites were chosen throughout Shark Slough (Figure 2-1). All of the sites except one (Chekika) were centered on an existing hydrological monitoring station and were accessible by airboat. The area mapped at each site ranged from approximately 50 ha to 314 ha (Table 2-1). Sites where grouped into five regional groups to assist data analysis (see Table 2-1).

Table 2-1. Location of the mapping area center (WGS84, UMT 17), mapping radius, and total area mapped for the twelve vegetation mapping sites in Everglades National Park. NESS =Northeast Shark Slough; CSS = Central Shark Slough; SSS = Southern Shark Slough; WSS = Western Shark Slough; SESS = Southeast Shark Slough. See Figure 2-1 for site locations with respect to Shark Slough.

Regional Group	Site	Latitude (UMT 17)	Longitude (UMT 17)	Circle Radius	Area Mapped (ha)
NESS	Chekika	2836955	542652	0.4 km	50
	NE-1	2841587	536632	1.0 km	314
	NE-2	2844716	544364	1.0 km	314
CSS	NP-202	2838399	529205	0.7 km	154
	NP-203	2834057	526199	0.6 km	113
	P33	2833061	529867	0.7 km	154
SSS	P36	2823476	520545	1.0 km	314
	SH1	2817264	515258	1.0 km	314
WSS	NP-205	2841308	515231	0.7 km	154
	OT	2829111	503546	1.0 km	314
	P34	2832347	505922	1.0 km	314
SESS	P38	2806004	516734	1.0 km	314

Vegetation Mapping

Thirteen distinct vegetation classes (communities) and two hydrologic features were defined (Table 2-2). One of these classes, the mixed-marsh community was created to handle the difficulty associated with mapping fine-scale differences within the marsh graminoid communities (i.e., the boundary between spikerush marsh and sparse sawgrass). As a result, this class is treated throughout the slough as a homogeneous matrix of *Cladium jamaicense* and *Eleocharis cellulosa* Torr.

At all sites, except Chekika, vegetation units were first identified and catalogued in the field using the Trimble AgGPS 122 connected to a Panasonic Toughbook laptop computer running DynaMo GIS 1.2. This software package allows real time positioning and visualization of the mapping area by incorporating geo-rectified aerial photos (the 1994-96 NAPP CIR series for this effort) with the output display. At Chekika, the only site not accessible by airboat, field observations were conducted on foot and the location of each vegetation unit was recorded using a handheld Garmin GPS unit with the aid of the 1994 NAPP CIR aerial photograph for this area. The data collected from both methods was pooled and imported into ArcView GIS 3.2 for final processing, map making, and analysis.

Table 2-2. The 13 vegetation classes and their descriptions.

Class	Class Description
Hardwood Hammock	Closed canopy (>80%) wooded forest on topographical highs (rock-outcrop) with canopy heights averaging 10 meters. The dominant species include *B. simaruba*, *S. foetidissimun*, *C. laevigata*, and *Ficus* spp.
Bayhead	Closed canopy (>50%) wooded forest with extended hydroperiods. Maximum canopy height about 8 meters. The dominant species include *Ilex cassine*, *Magnolia virginiana*, *Annona glabra*, *Persea borbonia*, *Chrysobalanus icaco*, and *Salix caroliniana*.
Riverine Forest	Tall closed canopy (>50%) seasonally flooded wooded forest found along the edges of coastal rivers and creeks very similar to bayheads. The dominant species are the same as "Bayhead."
Bayhead Swamp	Open canopy (< 50%) wooded forest with longer hydroperiods than bayheads. Canopy height generally below 4 meters. The dominant species include *Magnolia virginiana*, *Annona glabra*, *Chrysobalanus icaco*, and *Salix caroliniana*.
Cypress	Open or closed tall canopy forest of *Taxodium distichum*. This class also represents scattered individuals or groups of individuals ranging from 2 to 8 meters in height found peppering the marsh.
Mangrove	Individuals or groups of individual *Rhizophara mangle* generally less than 3 meters in height.
Casuarina	Individuals or groups of individual *Casuarina* spp. sometimes forming monotypic stands.
Melaleuca	Individuals or groups of individual *Melaleuca quinquenervia* sometimes forming monotypic stands.
Tall Sawgrass	Dominant species *C. jamaicense* with canopy heights > 2 meters.
Tall-Dead Sawgrass	Total *C. jamaicense* live cover between 25% and 75%.
Dead Sawgrass	Total *C. jamaicense* live cover < 25%.
Cattail	Dominant species is *Typha domingensis* with live vegetation cover > 25 % and canopy heights > 2 meters.
Mixed-Marsh	Homogeneous mixed-species matrix dominated or co-dominated by either *C. jamaicense* or *E. cellulosa*.
Water	Open deep-water areas within the marsh lacking vegetative cover.
Creek	A small shallow natural stream of water acting as an intermittent tributary to a river or other larger body of water.

Landscape Anisotropy

The directionality of all landscape features, if any, was investigated by first determining the longest axis for each polygon or longest vector length (LVL). When two or more polygons shared a common border, these polygons were grouped into one and treated as a complex unit. For example, if a tree island had a tall sawgrass or sawgrass tail associated with it, the forested part and the tail were combined to form a tree island complex. The longest axis of each polygon or complex unit was determined using Longest Straight Line v. 1.2, an ArcView extension that calculates the distance between all vertices in a polygon and then identifies the two most distant from one another. These data were then imported into MS Excel, where the distance and angle (vector) between the paired vertices was calculated. Vector calculations were performed using traditional trigonometric functions. All vectors correspond to the angle of depression from the northernmost vertex to the southernmost vertex (Figure 2-2). Polygons whose total area was less than 200 m^2 were removed from the data set to eliminate a directionality bias associated with small, nearly circular features which tend not to have a single significant longest axis.

Landscape Patch Shape

A fundamental problem in geospatial analysis is the ability to compare and describe the shape of features within a landscape beyond verbal descriptors like circular, ellipsoid, linear, or sinuous (see Clark and Gaile 1973, Maceachren 1985). Over the years, however, many quantitative indices have been suggested (e.g., perimeter-area, related circumscribing circle, linearity index). The elongation ratio (R_e) is relevant to the Everglades landscape, and is used here to address the issue of landscape patch (polygon) shape. This index, developed by Schumm (1956) to describe drainage basin shape, is stated as

$$R_e = \frac{2 \bullet \sqrt{\frac{A}{\pi}}}{LVL}$$

where Re is the ratio between the diameter of a circle having the same area of the patch (A) and the maximum length of that patch (LVL). The index increases from zero to one with increasing compactness (e.g., index values of 1.0 are characteristic of circular features while values between 0.3 and 0.6 are characteristic of ellipses or oblong shapes) (Figure 2-3).

Statistical Analysis

Univariate comparisons among sites of the mean LVL and R_e of a composite group of non-matrix (i.e., other than Mixed Marsh) patches (vegetation classes) were made with the nonparametric Kruskal-Wallis test using Statistica 6.1 (StatSoft, Inc.). Analyses of landform directionality and landscape angle concentration (r) among regions and sites were performed using Oriana v. 2.01b, a software package specializing in circular statistics. In general, r is a circular statistic analogous to the standard deviation of linear data; it has no units and ranges from 0, where a mean angle cannot be described, to 1 where all the data are concentrated in the same direction (Zar 1974). Watson–Williams *F*-tests (Zar 1974, Batschelet 1981) were used for multi-sample comparisons of landform directionality. The Watson-Williams test determines if the mean angles of two or more samples differ significantly. It can be performed in a pairwise fashion, a pair at a time, or as an overall test for all samples. Regional differences in *r* among sites were also analyzed. Sites were divided into three groups: Group 1 included sites in the lower portions of the main (central) slough (P33, NP202, NP203, P36, SH1), Group 2 included sites in semi-impounded, water-deprived (Van Lent et al. 1999) NESS (NE1, NE2), and Group 3 included sites in regions peripheral to the main slough (NP205, OT, P34, P38, Chekika). Differences among these three groups were tested using one-way analysis of variance, followed by a multiple comparison test (Fisher's LSD test).

Results

Vegetation Maps

The twelve vegetation maps of Shark Slough are presented in Figures 2-4 to 2-15. The slough's landscape is generally characterized by a mosaic of patches interwoven within a mixed-marsh community matrix. These patches, with their associated vegetation class, varied throughout the slough in both density (Figure 2-16A) and size (Figure 2-16B), with most patches (97%) being less than 1 ha in size (Figure 2-17).

Mixed-marsh had the highest percentage of all the classes, and except for two sites (NP-202 and SH1), was generally well above 70% (Table 2-3). The percentage of tall sawgrass, on the other hand, varied from a low of < 1% at P38 to a high of 15% at NP-205. However, at most sites tall sawgrass accounted for less than 5% of the total area mapped (Table 2-3). Dead sawgrass was primarily restricted to CSS and SSS (Figure 5-18) where vegetation class values ranged from a low of < 1% at P33 to a high of 23% at SH1 (Table 2-3). Within theses two regions, the mean percentage of dead sawgrass was higher in SSS (13%) than in CSS (8%). Across regions, the mean percentage of tall and dead sawgrass decreased in the order of SSS (17%) > CSS (13%) > NESS (7%) > WSS (7%) > SESS (<1%).

Despite their ecological importance, as wildlife refugia for example, the five native forested vegetation classes (Hardwood Hammock, Cypress, Riverine Forest, Bayhead, and Bayhead Swamp) accounted for only about 5% of the total area mapped. The percentage of the hardwood hammock class throughout the slough was surprisingly low, generally less than 1% at all sites except NP-205 on the western fringe of Shark Slough (Table 2-3, Figure 2-18). The cypress and riverine forest classes were restricted to one site each, P38 in SESS and OT in WSS, respectively (Table 2-3). In contrast to the hardwood hammock, riverine forest, and cypress classes, the bayhead and bayhead swamp classes were well represented throughout the slough (Fig. 2-18): site coverage values ranged from < 1 % (SH1, OT, P34) to 9 % (NP203) (Table 2-3). Mean cover percentages for bayhead and bayhead swamp classes were highest in CSS, at 3 % and 5 %, respectively, and lowest in SESS (both < 2%). At most sites, the bayhead swamp class had higher coverage percentages than the bayhead class (Table 2-3). However, in WSS and SESS, this pattern was reversed (Table 2-3).

Mangroves were restricted to two sites, OT and P38. Cover percentages at both sites were well below 1% (Table 2-3) and consisted of scattered clumps of individuals associated with either tidal creeks or other forested communities (see Figures 2-13 and 2-15).

The two exotic classes, Casuarina and Melaleuca, were restricted to the northeastern fringe of

Table 2-3. Percent of total area of each site covered by each of the 13 vegetation classes.

Region	Site	Hardwood Hammock	Bayhead	Riverine Forest	Bayhead Swamp	Cypress	Mangrove	Casuarina	Melaleuca	Tall Sawgrass	Dead Sawgrass	Cattail	Marsh	Water
NESS	Chekika		1.0		2.1			1.5		2.3			92.9	
	NE-1	< 1.0	2.7		2.3					7.8		< 1.0	87.1	
	NE-2				2.3				< 1.0	9.8			87.8	
CSS	NP-202		2.9		6.0					3.4	20.2	< 1.0	67.0	
	NP-203		5.5		8.8					9.5	2.3		73.9	
	P33		< 1.0		< 1.0					4.4	< 1	< 1.0	94.5	
SSS	P36	< 1.0	1.2		5.3					4.2	2.0	< 1.0	87.3	< 1.0
	SH1		< 1.0		2.9					4.8	23.4	< 1.0	68.6	< 1.0
WSS	NP-205	9.6	< 1.0		1.5					14.7			73.9	< 1.0
	OT	< 1.0	3.2	2.7	< 1.0		< 1.0			3.8		< 1.0	89.8	< 1.0
	P34	< 1.0	1.0		< 1.0					1.5			96.3	< 1.0
SESS	P38	< 1.0	1.6			4.2	< 1.0			< 1.0		< 1.0	92.6	< 1.0

Shark Slough (Table 2-3 and Figure 2-18), where anthropogenic disturbances and modifications have significantly altered the species composition, hydrology, and overall physiography of the landscape.

Longest Vector Length and Landform Directionality

The mean LVL of complex and simple units was about 109 meters and ranged from 3 meters to nearly 2.8 km (Table 2-4). Most units (77%) were less than 100 meters long, with longer units, those exceeding 300 meters in length, accounting for about 6% of all landscape features (Figure 2-19). Analysis of variance indicated a significant difference in LVL between complex and simple units at $p < 0.05$ (Kruskal-Wallis test, $H_{1,626} = 140.690$, $p < 0.001$). LVL was about 243 meters for complex units and 64 meters for simple units. Analysis of variance also indicated a significant difference in LVL between some complex and simple units (Kruskal-Wallis test; $H_{13,626} = 233.924$, $p < 0.001$) (Table 2-5).

At the regional level, LVL decreased in the order CSS ($\bar{x}$ = 143 m) > SSS ($\bar{x}$ = 135 m) > WSS ($\bar{x}$ = 122 m) > NESS ($\bar{x}$ = 77 m) > SESS ($\bar{x}$ = 67 m) (Table 2-4). This difference in LVL between regions was significant at $p < 0.05$ (Kruskal-Wallis test; $H_{4,626} = 56.360$, $p < 0.001$). The LVLs of the two easternmost regions, NESS and SESS, were significantly different from CSS, SSS and WSS at $p < 0.05$ (Table 2-4). Except for Chekika, in NESS, sites within regions did not differ in LVL at $p > 0.05$ (Table 2-6). Furthermore, the LVL of units in Chekika were significantly different than those of all the other sites, except P38 (Table 2-6).

Table 2-4. Mean, standard error, and minimum and maximum longest vector length for complex and non-complex units in Shark Slough. Regions with same subscript do not differ at *p* > 0.05.

Region	N	Mean Longest Vector Length (m)	± 1 S.E.	Minimum Longest Vector Length (m)	Maximum Longest Vector Length (m)
$NESS_a$	199	77	16.2	4	1919
CSS_b	107	143	30.5	8	2766
SSS_b	166	135	20.4	8	1936
WSS_b	86	122	21.4	9	1326
$SESS_a$	68	67	13.7	3	627
Totals	628	109	9.7	3	2,766

The landscape features of Shark Slough were naturally oriented between 90° and 270°, with the majority of features (92%) having an orientation between 180° and 270° (Figure 2-20). Mean directionality in the mapped landforms was approximately 216° but varied from region to region and decreased along a latitudinal and topographical gradient from SSS ($\bar{x}$ = 225°) to CSS ($\bar{x}$ = 211°) to NESS ($\bar{x}$ = 206°) (Figures 2-21 and 2-22). Analysis of variance indicated a significant

Table 2-5. Mean, standard error, and minimum and maximum longest vector length for patch types (complex and non-complex units) in Shark Slough.

Patch Type (Vegetation Class)	N	Mean Longest Vector Length (m)	± 1 S.E.	Minimum Longest Vector Length (m)	Maximum Longest Vector Length (m)
Cypress	29	18	3.4	3	101
Exotics	38	21	4.3	4	133
Bayhead	64	44	5.5	5	255
Bayhead Swamp	79	65	6.9	8	373
Tall Sawgrass	234	73	9.1	8	1,327
Hammock	16	98	34.1	13	545
Bayhead Complex	61	133	15.7	19	662
Cypress Complex	2	137	11.2	126	148
Bayhead Swamp Complex	66	178	33.0	21	1,937
Dead Sawgrass	8	194	76.4	17	550
Sawgrass Complex	4	239	90.6	69	418
Tall Dead Sawgrass	2	254	128.6	125	383
Tall Sawgrass Complex	3	362	299.2	52	960
Hammock Complex	20	793	190.6	65	2,766

Table 2-6. Kruskal-Wallis *p*-scores ($H_{11,475} = 4.829$, $p < 0.001$) for longest vector length (LVL) for the 12 mapping sites. Marked differences are significant at $p < 0.05$.

Region	Site (Mean ± 1 S.E.)	NESS		CSS			SSS		WSS			SESS
		NE1	NE2	NP202	NP203	P33	P36	SH1	NP205	OT	P34	P38
NESS	Chekika (33.3 ± 5.5)	**0.001**	**0.016**	**<0.001**	**<0.001**	**0.008**	**<0.001**	**<0.001**	**0.001**	**0.001**	**<0.001**	1.000
	NE1 (97 ± 27.7)		1.000	0.091	0.059	1.000	1.000	**0.022**	1.000	1.000	1.000	0.308
	NE2 (86 ± 37.1)			0.174	0.115	1.000	1.000	0.071	1.000	1.000	1.000	1.000
CSS	NP202 (179.9 ± 54.9)				1.000	0.273	0.656	1.000	1.000	1.000	1.000	**<0.001**
	NP203 (234 ± 97.5)					0.181	0.431	1.000	0.863	1.000	1.000	**<0.001**
	P33 (67 ± 8.5)						1.000	0.125	1.000	1.000	1.000	0.909
SSS	P36 (115 ± 21.5)							0.263	1.000	1.000	1.000	**0.007**
	SH1 (182 ± 45.9)								0.832	1.000	1.000	**<0.001**
WSS	NP205 (139 ± 38.8)									1.000	1.000	0.205
	OT (90 ± 15.2)										1.000	**0.044**
	P34 (115 ± 23.6)											**0.004**
SESS	P38 (67 ± 13.7)											

difference in landform directionality between regions at $p < 0.05$ (Watson-Williams F-test, $F_{4,482} = 11.700$, $p < 0.001$). Landform directionality in NESS, SSS, and WSS were significantly different from each other at $p < 0.05$ (Figure 2-21). In contrast, the landform directionality in the two fringing areas, WSS and SESS, were not significantly different from each other at $p > 0.05$ (Figure 2-21); this was also true for the neighboring regions NESS and CSS. Sites within regions showed little variation in landform directionality (Figure 2-23) and, except for NP203 and P33 (CSS), did not differ from each other at $p > 0.05$ (Table 2-7).

Landscape angle concentration (r) differed significantly (one way-ANOVA; $F_{2,9} = 5.171$, $p = 0.032$) among the central (Group1), semi-impounded (Group 2) and peripheral (Group 3) slough sites. The r of semi-impounded and peripheral sites differed from the central sites at $p < 0.05$ (Figure 2-24); however, the former two did not differ from each other a $p > 0.05$. Overall, the r statistics increased from the semi-impounded sites to the peripheral sites to the central slough sites ($\bar{x}$ = 0.843, 0.889, and 0.963, respectively) (Figure 2-24).

Landscape Patch Shape

The R_e for landscape features in Shark Slough was approximately 0.63 ± 0.001 SE, with 46.5% of all features having a R_e between 0.5 and 0.7 (Figure 2-25). This range in values indicates that most features in the Everglades are elliptical or oblong in shape.

At the regional level, the R_e of features decreased in the order SESS ($\bar{x} = 0.70$) > NESS ($\bar{x} = 0.69$) > WSS ($\bar{x} = 0.68$ m) > CSS ($\bar{x} = 0.57$ m) > SSS ($\bar{x} = 0.55$ m) (Figure 2-26). This regional difference in R_e was significant at $p < 0.05$ (Kruskal-Wallis test; $H_{4,626} = 132.562$, $p < 0.001$). R_e for CSS and SSS were significantly different than those of NESS, WSS, and SESS at $p < 0.05$ (Kruskal-Wallis test; $H_{4,626} = 132.562$, $p < 0.001$) (Figure 2-26). Except for P34 and OT, in WSS, sites within regions did not differ in R_e at $p > 0.05$ (Table 2-8). Figure 2-27 illustrates the covariance of r and R_e, with the former being higher and the latter lower in the main slough sites than in the semi-impounded NESS and peripheral sites.

The R_e of complex and simple units (i.e., 0.55 and 0.65, respectively) differed significantly (Kruskal-Wallis test; $H_{1,626} = 63.671$, $p < 0.001$). In most cases, the R_e of complex units was less than those of simple units, suggesting a less compact and more elliptical or oblong shape (Figure 2-28). However, the R_e of tall-dead sawgrass and dead sawgrass was lower than that of several complex units but did not differ significantly at $p > 0.05$ (Table 2-9).

Discussion

The data presented in this section depict Shark Slough as a highly complex landscape whose physiognomy is controlled by local (within region) and regional variation in hydrology, topography, and disturbance history. However, the processes that shape this landscape, and especially the spatial and temporal scales at which they operate, remain open questions. Ecosystems and vegetation communities, in general, lag in their response to temporal variations in natural phenomena or management practices. As a result, it is sometimes impossible to determine with certainty which factor or combinations of factors are responsible for controlling or regulating the direction and rate of change within an ecosystem or vegetation community.

Table 2-7. Watson-Williams *F*-test ($F_{11,475} = 4.829$, $p < 0.001$) on landform directionality for the 12 mapping sites. Marked differences are significant at $p < 0.05$.

Region		NESS		CSS			SSS		WSS			SESS
	Site	NE1	NE2	NP202	NP203	P33	P36	SH1	NP205	OT	P34	P38
NESS	Chekika	0.577	0.384	0.629	0.720	0.464	**0.024**	**0.012**	0.370	0.578	0.364	0.164
	NE1		0.486	0.915	0.805	0.066	**< 0.001**	**< 0.001**	**0.041**	0.165	0.062	**0.006**
	NE2			0.489	0.437	**0.046**	**< 0.001**	**< 0.001**	**0.039**	0.116	0.058	**0.007**
CSS	NP202				0.719	**0.045**	**< 0.001**	**< 0.001**	0.066	0.029	**0.024**	**0.001**
	NP203					0.075	**< 0.001**	**< 0.001**	0.099	0.042	**0.037**	**0.002**
	P33						0.078	**0.012**	0.692	0.899	0.618	0.321
SSS	P36							0.091	0.408	0.076	0.519	0.746
	SH1								0.126	**0.012**	0.157	0.155
WSS	NP205									0.667	0.931	0.701
	OT										0.560	0.283
	P34											0.782

Table 2-8. Kruskal-Wallis *p*-scores ($H_{11,475} = 4.829$, $p < 0.001$) for the elongation ratio (R_e) for the 12 mapping sites. Marked differences are significant at $p < 0.05$.

Region	Site (Mean ± 1 S.E.)	NESS		CSS			SSS		WSS			SESS
		NE1	NE2	NP202	NP203	P33	P36	SH1	NP205	OT	P34	P38
NESS (0.69 ± 0.001)	Chekika (0.67 ± 0.012)	0.218	1.000	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	1.000	**0.005**	1.000	1.000
	NE1 (0.67 ± 0.017)		1.000	**0.019**	**< 0.001**	1.000	**< 0.001**	**< 0.001**	1.000	1.000	1.000	1.000
	NE2 (0.73 ± 0.015)			**0.022**	**< 0.001**	1.000	**< 0.001**	**< 0.001**	1.000	1.000	1.000	1.000
CSS (0.57 ± 0.012)	NP202 (0.56 ± 0.022)				1.000	1.000	1.000	1.000	**0.011**	1.000	**< 0.001**	**< 0.001**
	NP203 (0.51 ± 0.024)					0.512	1.000	1.000	**< 0.001**	1.000	**< 0.001**	**< 0.001**
	P33 (0.61 ± 0.017)						0.838	1.000	0.839	1.000	**0.029**	**0.041**
SSS (0.55 ± 0.010)	P36 (0.55 ± 0.013)							1.000	**< 0.001**	1.000	**< 0.001**	**< 0.001**
	SH1 (0.53 ± 0.019)								**< 0.001**	1.000	**< 0.001**	**< 0.001**
WSS (0.68 ± 0.014)	NP205 (0.68 ± 0.019)									0.900	1.000	1.000
	OT (0.60 ± 0.016)										**0.043**	0.126
	P34 (0.75 ± 0.030)											1.000
SESS	P38 (0.70 ± 0.015)											

Table 2-9. Kruskal-Wallis *p*-scores ($H_{13,626} = 155.367$, $p < 0.001$) for complex and non-complex elongation ratio (R_e) for the 12 mapping sites. Marked differences are significant at $p < 0.05$.

Patch Type	Tall Dead Sawgrass	Tall Sawgrass Complex	Dead Sawgrass	Bayhead Swamp Complex	Cypress Complex	Bayhead Complex	Hammock Complex	Tall Sawgrass	Bayhead Swamp	Bayhead	Hammock	Cypress	Exotics
Sawgrass Complex	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	**0.013**	**0.021**	**0.004**	**0.001**
Tall Dead Sawgrass		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.631	0.605	0.287	0.127
Tall Sawgrass Complex			1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.754
Dead Sawgrass				1.000	1.000	1.000	1.000	1.000	1.000	**0.033**	0.084	**0.009**	**0.001**
Bayhead Swamp Complex					1.000	1.000	1.000	**0.003**	0.105	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Cypress Complex						1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Bayhead Complex							1.000	0.427	1.000	**< 0.001**	**0.002**	**< 0.001**	**< 0.001**
Hammock Complex								1.000	1.000	**0.004**	0.058	0.001	**< 0.001**
Tall Sawgrass									1.000	**< 0.001**	0.217	**< 0.001**	**< 0.001**
Bayhead Swamp										0.001	0.234	**0.001**	**< 0.001**
Bayhead											1.00	1.00	1.000
Hammock												1.00	1.000
Cypress													1.000

Furthermore, because of this inertia, the relationship between cause and effect can become convoluted and lead to erroneous assumptions and/or conclusions.

In the Everglades, it has been suggested that hydrologic flow velocities and direction are responsible for the "ridge and slough" characteristic of the Everglades landscape, as well as landscape feature orientation (Aumen 2003, Ross et al. 2003; but see also Stone et al. 2002). This conclusion is hard to escape upon examining, at a broad scale, the calculated predominant flow directions at our 12 study sites superimposed on the topographic map of the lower Everglades (Figure 2-22). However, the large-scale relationship between flow and landscape may lose focus when viewed more closely, as we attempt to do in the following paragraph.

Flow rate and direction data from two sites, NP203 in CSS and SH1 in SSS, indicate that flow rates and directionality do indeed differ throughout the slough (Riscassi and Schaffranek 2002). During 1999-2001, the ranges of flow rates during the wet season were 0.0-0.75 cm/s at NP203 and 1.5- 4.5 cm/s at SH1 (Riscassi and Schaffranek 2002). In another study conducted by Childers et al. (2003) in 2002-2003, flow rates in the slough near NP203 were found to range between 0.14 and 0.24 cm/s. Several authors have demonstrated that flow velocities at specific sites within the Everglades are influenced by vegetation density and type (Childers et al. 2003, Bazante et al. 2004). Another factor that could affect flow rates is the topographical gradient of the landscape. In the case of NP203 and SH1, the gradient is markedly steeper at SH1, near the mangrove ecotone, than upstream at NP203 (Figure 2-22). Furthermore, Riscassi & Schaffranek (2002) reported flow directions with a stronger westerly component at NP203 than SH1 (235^o and 210^o, respectively). This contrasts with our landscape analysis which shows a more westerly landscape orientation at SH1 (228^o) than NP203 (208^o) (Figure 2-23).

Clearly, because of biological inertia, short term variations in flow direction should not be expected to instantaneously manifest themselves within the landscape. As a result, it is unlikely that in the short term, small temporal modifications to flow velocities and directions by either natural phenomena or management practices will have much of an impact on the present anisotropy of Shark Slough. However, our data suggest that relatively long-term changes in flow patterns, such as those imposed on NESS marshes, can reduce the ridge-and-slough character of the landscape, as reflected by the landscape metrics we have developed in this section.

With this is mind, we suggest that restoration efforts attempt to determine and quantify the rate and direction of change, if any, in the "ridge and slough" landscape of the Everglades since the 1940s (the year of the oldest comprehensive set of aerial photos available for the Everglades). This can be accomplished by comparing how the elongation ratio (R_e) and the angle concentration index (r) for landscape features in the Everglades have changed since the 1940s. These two indices are strong indicators of "ridge and slough" morphology because they address the shape as well as the angular concentration of features within a landscape, region, or area. They can also be useful in determining how quickly the "ridge and slough" landscape of the Everglades responds to hydrologic manipulations designed to restore its essential character.

3

Characterization, Biogeochemistry, Pore Water Nutrient Chemistry, and Other Aspects of Soils in Tree Islands of Shark Slough

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Part A

Soil Characterization and Biogeochemistry

Introduction

Our interests in Everglades National Park tree island soils are multifold. It is commonly known that soils serve as a media for plant growth, exchange and storage of nutrients. Also, their structural profiles provide a record of soil formation and site history. Nutrient cycles play a large role in tree island structure, function, and interactions with the surrounding marshes. These nutrient cycles also show a strong interaction with hydrologic conditions. To date, only a few studies have analyzed soil nutrients (N and P) and their cycling in tree islands. Nitrogen and phosphorus concentrations are also known to change along hydrologic gradients in tree island soils and leaves, with N becoming more limiting to plant growth in the raised hammocks. In this project, we were interested in understanding the interactions of three key components of tree islands ecosystems - hydrology, vegetation, and soils. How are the recent changes in hydrology affecting the vegetation mosaic and soils? Are these soils functioning similarly to the adjacent marsh soils? Are these soils nutrient sinks or sources? Do they differ in their elemental composition? How does this elemental composition affect vegetation? With these questions, we established baseline physical and chemical properties of soils from three tree islands in Shark Slough: Black, Gumbo Limbo, and Satinleaf Hammocks. We have also attempted to understand the biogeochemistry of nutrient cycling, particularly phosphorus.

Methods

Composite surface soil samples at 0 to 10 cm depth were collected from three tree islands in November 2001. Each tree island consisted of tropical hardwood hammock, bayhead, and bayhead swamp communities. To evaluate spatial variation in soils within each island, soil samples were collected at 5 to 25 meter intervals along a transect traversing the long axis (signified as “North-South” in figures) of the island, and covering (commencing at the north end) marsh, hardwood hammock, bayhead, bayhead swamp, and again marsh communities. Soil samples were also collected at 25 meter intervals along three transects traversing the island perpendicular to its long axis (termed “East-West”), and also included hammock, bayhead, and bayhead swamp communities. During the wet season (November), approximately more than 300 surface soil samples were collected. By using a 10 cm diameter soil auger, several 0-10 cm deep cores were taken at each sampling location, composited in a 4 mill thickness sampling bag, and transported to the laboratory for physical description and physicochemical analysis. Soils were homogenized in the bag and refrigerated until further analysis. Sub-samples from each bag were transferred to a plastic sample cup, weighed wet (g), and measured for sample volume (cm^3).

Later, these samples were analyzed for dry weight (80º C), bulk density (g dry cm^{-3}), fractional water content, total C, carbonate content, inorganic and organic C, organic matter content, total N, and total P. Another set of sub-samples was diluted with distilled, deionized water to a nominal 1:1 dilution and homogenized in a blender for 90 s. The pH and electric conductivity (EC) of the soil slurries was recorded. Eight representative soil samples were prepared for scanning electron microscopy (SEM) and energy dispersive X-ray micro analysis using JEOL 5900-LV SEM with EDAX EDS-UTW Detector (made available at Earth Sciences Department, FIU). Each sample was polished by fine alumina (0.1 – 0.3 μ) using micro-cutting technology. The polished samples were coated with thin carbon layer and observed under SEM. These samples were also used to fractionate different forms of phosphorus using standard phosphorus fractionation method.

Results

Black Hammock. The pH of the soils ranged from 5.2 to 8.2 (Figure 3-1). Near the center of the hardwood hammock area, the measured soil pH was above neutral (8.0 to 8.2), while pH was below neutral in the rest of the communities. The bayhead swamp soils in particular indicated acidic conditions. There was no apparent difference in soil EC measurements along the transects. Bulk density measurements indicated differences in soil composition among marsh, hardwood hammock, bayhead, and bayhead swamp forests. An average bulk density of 0.40 g cm^{-3} was recorded in hardwood hammock, followed by bayhead (0.15 g cm^{-3}), and bayhead swamp and marsh (~0.1 g cm^{-3}). Although the bulk density recorded in hardwood hammock was not close to that associated with typical upland soils (1.4 g cm^{-3}), soil minerals including carbonates contribute to a higher bulk density in comparison with adjacent communities. The relatively high mineral content also becomes apparent when rubbing the soils between thumb and forefinger. The bayhead and bayhead swamp communities have soil bulk density similar to the adjacent marsh communities. The lower bulk density is primarily a function of the partially decomposed root-rhizome mat and high organic matter content.

The organic matter content of Black Hammock soils ranged from 25% to 90% (Figure 3-1). Most of the bayhead and bayhead swamp soils had >70% organic matter, whereas organic matter in hardwood hammock soils was generally <50%. An opposite trend in total carbonate content suggested that a significant portion of hardwood hammock soils derived from weathering of limestone bedrock materials. However, a considerable amount of carbonates were also recorded in bayhead and bayhead swamp soils. Total nitrogen ranged from 1.0 to 3.75%, with an average measurement of 3% in all communities except the middle of hardwood hammock, where the lowest total nitrogen content was observed. Total nitrogen content was positively correlated with total carbon (r^2=0.882) and with organic matter (r^2=0.727), and negatively correlated with carbonate content (r^2=0.301) (Figure 3-2). This is because most nitrogen in these tree islands is present in the organic form. A similar observation was made in our assessment of marsh vegetation responses to hydrological restoration in Shark Slough (Ross et al. 2001b). A lag in C and N accumulation in the hardwood hammock may be related to the dynamic decomposition of leaf litter and the development of a deep root system, which would contrast with expected slower decomposition rates in bayhead and bayhead swamp communities, and development of a root-rhizome mat, a major source of C and N to wetland soils. Total phosphorus content in the majority of the hardwood hammock soil samples exceeded 3% by weight, whereas bayhead soil samples averaged ~0.1% and bayhead swamp soil samples averaged ~0.07% (Figure 3-7). Based on the current results, soils in various plant communities of Black Hammock differ considerably from one another. In particular, soils in the hardwood hammock differ from those of the other three communities in their physicochemical properties. We postulate that hardwood hammock soils have distinct mineral composition, which warrants further investigation.

Gumbo Limbo Hammock. The pH and EC of Gumbo Limbo Hammock soils are similar to those of Black Hammock, with an alkaline pH in the hardwood hammock area, particularly in the center, and acidic pH in the rest of the communities (Figure 3-3). The bayhead swamp and even the adjacent marsh communities indicated acidic conditions. The marsh pH values are particularly interesting, since pH values <6.5 were not observed in the Shark Slough marsh soil profiles described in Ross et al. (2001b). Bulk density measurements again were different in hardwood hammock and adjacent wetlands. An average bulk density of 0.60 g cm^{-3} was recorded in Gumbo Limbo hardwood hammock, slightly higher than in the hardwood hammock portion of Black Hammock. The bayhead and bayhead swamps have similar bulk density (0.15 g cm^{-3}), and the marsh communities at Gumbo Limbo have a bulk density of 0.1 g cm^{-3}.

Soil organic matter ranged between 10 and 90% (Figure 3-3). Most of the bayhead and bayhead swamp soils averaged ~80% organic matter, while hardwood hammock soils averaged about 20%. Organic matter content increased to 90% in the marsh on either side of the East-West transects. Carbonate content in Gumbo Limbo Hammock was different from Black Hammock, with lower levels of carbonates measured in the hardwood hammock area compared to bayhead and bayhead swamp. Since there was less organic matter in hardwood hammock area, other minerals must be contributing to these soils. Weathering of limestone bedrock materials is a secondary process in this tree island.

Total nitrogen ranged from 0.75 to 4.75%, with an average measurement of 3% in all communities except in the middle of hardwood hammock, where the lowest total nitrogen content was observed. This observation is similar to the nitrogen content measured in Black Hammock. Total nitrogen content was positively correlated with total carbon (r^2=0.916), and with organic matter (r^2=0.669) (Figure 3-4). Nitrogen was negatively correlated with total carbonate, however the correlation was weak (r^2=0.015). Total phosphorus content was similar to Black Hammock (Figure 3-7).

Satinleaf Hammock. Soils in Satinleaf Hammock were different from those in Gumbo Limbo hammock, but resembled those of Black Hammock in several soil parameters. The pH of the soils ranged from 6.2 to 8.0 (Figure 3-5). The hardwood hammock area was slightly alkaline and the pH of the bayhead and bayhead swamp areas was below neutral. However, the North-South transect indicated some locations with above-neutral pH in both bayhead and bayhead swamp communities. The marsh communities adjacent to Satin Leaf Hammock also had slightly higher pH compared to the marshes adjacent to Black and Gumbo Limbo Hammocks. As in the other two tree islands, there was no notable difference in EC of the soils along the Satinleaf Hammock transects. Soil bulk density was similar to that in the Black Hammock, showing differences among soils of marsh, hardwood hammock, bayhead, and bayhead swamps in each island.

In Satinleaf Hammock, organic matter content ranged from 10 to 90% (Figure 3-5). The bayhead, bayhead swamp, and adjacent marsh soils had an average 70% organic matter content, whereas hardwood hammock soils had an average 25%. Carbonate content in the soils of Satinleaf Hammock was similar to Black Hammock, with an average 15% carbonates in hardwood hammock, and 10% carbonates in bayhead and bayhead swamp communities. There was no difference in carbonate content between bayhead and bayhead swamp communities. Total nitrogen ranged from 0.6 to 3.4% with an average of 2.5% in all communities except in the middle of hardwood hammock, where the lowest total nitrogen content (<1.0%) was observed. Total nitrogen content was positively correlated with total carbon (r^2=0.956), whereas a poor correlation was observed with organic matter (r^2=0.332) (Figure 3-6). This is because most nitrogen in these tree islands is present in the organic form, as indicated by the close correlation of C and N. A negative but weak correlation (r^2=0.054) was observed between total nitrogen and carbonate content in the soils. Total phosphorus content in the Satinleaf Hammock hardwood hammock was similar to that of Black and Gumbo Limbo Hammocks. However, there was no difference in total P between bayhead and bayhead swamp communities, averaging ~0.06% (Figure 3-7).

Phosphorus Biogeochemistry – All Tree Islands. Total phosphorus content in the majority of the hardwood hammock soil samples in all three tree islands soils exceeded 3% by dry weight. In contrast, bayhead samples averaged ~0.1%, and the bayhead swamp soils averaged ~0.07%. However, there was no difference in total P between bayhead and bayhead swamp communities, which averaged ~0.06% P. The elevated level of P in hardwood hammock soils is a result of external P influx from biological and chemical processes. Preliminary electron microanalysis and P fractionation studies suggest that P is adsorbed to calcium rather than to iron and aluminum in soils rich in carbonate content with alkaline pH (Figure 3-8). Sorption/desorption, mineralization/immobilization, and solubilization/dissolution experiments are important to describe the role of carbonate rich hardwood hammocks soils in P biogeochemical cycling in the Everglades tree islands.

Discussion and Conclusions

We have established baseline physicochemical properties of soils on three tree islands. Gumbo Limbo Hammock seems to be different from Black and Satinleaf Hammocks in several soil properties. In general, soils in the hardwood hammock communities, particularly the raised part of the community, have alkaline pH, low organic matter, abundant carbonate minerals, and low nitrogen. The measured phosphorus content is very high (>3%) in all three tree islands, especially in the hammock portions. Several factors may be contributing to the accumulating high P levels in hammocks region of tree islands. One factor is the contribution of animal (bird) inputs to elevated P levels. Second, we believe that dissolved phosphorus/particulate phosphorus may be carried with the ground water stream toward the tree islands, especially during the dry season. In this process, groundwater is expected to move toward tree islands because tree-dominated systems typically have high transpiration rates relative to the marsh communities. The differences between tree island and marsh transpiration rates are expected to be highest during the dry season when the deep-rooted trees have greater access to declining water tables. In support of this hypothesis, our initial observations showing night time increases in groundwater levels in tree island sampling wells indicates a net diurnal movement of groundwater from the surrounding marshes. Over longer time periods, P transported to tree islands in this manner builds up due to adsorption onto soil particles as calcium phosphate under alkaline conditions. A third contributing factor may involve the dynamics of organic matter in the hardwood hammock. As the leaf litter undergoes decomposition, carbon and nitrogen is cycled into the gaseous phase (low total carbon and nitrogen in hardwood hammock). The phosphorus cycle does not include a gaseous phase, thus it is a relatively immobile element. We therefore cannot rule out the possibility of phosphorus accumulation as a by-product of organic matter decomposition. The mineral composition and the high phosphorous content in hardwood hammock soils are surprising results, and may play an important role in the ecology of Everglades tree islands. We have attempted to asses the capacity of the very different soils found in the tropical hardwood hammock and bayhead zones of the tree islands in sequestering P and overall nutrient cycles, but a detailed study on nutrient cycling and the interactions and influence of hydrology and vegetation is important for the health of tree islands in the Everglades.

Part B
Pore Water Nutrient Chemistry

Introduction

Pore water or soil interstitial water physicochemical properties provide important information regarding labile form of nutrients in soil and availability to plants and soil microorganisms. Pore water chemistry has been described from the Water Conservation Areas, northern Everglades, and southern Everglades in Shark Slough (Ross et al. 2001b), but research linking soil physicochemical characteristics, pore water properties, and plant nutrient uptake by the plant communities in the tree islands of the Everglades is lacking. In this section, we describe the pore water nutrient chemistry from selected locations of all three tree islands, and try to link labile form of nutrients, N and P, to plant uptake.

Methods

During the wet season in 2002, soil interstitial (pore) water was collected by inserting a temporary sampling device (sipper) into intact soils at selected locations at 25 to 50 m intervals along North-South and East-West transects of three tree islands. Sippers consisted of a filter (pore size 60 µm, Porex 6810, Interstate Specialty Products, Leicester, MA, USA) 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 30 mL of soil solution was withdrawn. Suction lysimeters were permanently installed to a depth of 20-30 cm in the hammocks part of the tree islands. Hand held vaccum was applied to collect soil interstitial water from these lysimeters. Approximately, 30 mL of soil solution was collected from each lysimeter. The sample was filtered through a syringe filter (Whatman GF/F, pore size 0.45 µm) into a 30 mL polyethylene sample bottle. Samples were stored in cooler box until returned to the laboratory. Soil pore water samples were analyzed for

NO_2-N (EPA 353.2), NO_3-N (EPA 353.2), NH_4-N (EPA 350.1), and soluble reactive phosphorus (SRP, EPA 365.1).

Results

Black Hammock. Pore water nutrient data for all four sampling transects are presented in Table 3-1. The NO_2-N of the soil solution ranged from 3.19 to 35.89 µg L^{-1}. There was no apparent difference in NO_2-N levels among marsh, hardwood hammock, bayhead, and bayhead swamp forest systems. NO_3-N level seemed to be higher than NO_2-N levels in all locations. NO_3-N measurements ranged from 14.57 to 95.74 µg L^{-1} across the landscape. Similar to NO_2-N, there was no apparent difference among different communities. NH_4-N levels ranged from 7.04 to 5806.46 µg L^{-1}. Hardwood hammock soil solutions contained the lowest levels of NH_4-N. SRP levels ranged from 0.70 to 142.62 µg L^{-1}. Most of the bayhead and bayhead swamp soils had <10 µg L^{-1} SRP, whereas SRP in hardwood hammock soils was generally >50 µg L^{-1}. Pore water from marsh soils was generally <5 µg L^{-1} SRP.

Gumbo Limbo Hammock. Pore water nutrient data for all four sampling transects are presented in Table 3-2. The NO_2-N of the soil solution ranged from 8.05 to 79.14 µg L^{-1}. There was no apparent difference in NO_2-N levels among marsh, hardwood hammock, bayhead, and bayhead swamp forest systems. NO_3-N level seemed to be slightly higher than NO_2-N levels in all locations. NO_3-N measurements ranged from 4.99 to 82.72 µg L^{-1} across the landscape. Similar to NO_2-N, there was no apparent difference among different communities. NH_4-N levels ranged from 85.97 to 10504.95 µg L^{-1}. Hardwood hammock soil solutions contained the lowest levels of NH_4-N. SRP levels ranged from 1.84 to 250.24 µg L^{-1}. Most of the bayhead and bayhead swamp soils had <20 µg L^{-1} SRP, whereas SRP in hardwood hammock soils was generally >50 µg L^{-1}. Pore water from marsh soils was generally <5 µg L^{-1} SRP.

Satinleaf Hammock. Pore water nutrient data for all four sampling transects are presented in Table 3-3. The NO_2-N of the soil solution ranged from 8.28 to 37.13 µg L^{-1}. There was no apparent difference in NO_2-N levels among marsh, hardwood hammock, bayhead, and bayhead swamp forest systems. However, lower levels of NO_2-N were measured in hardwood hammock soils. NO_3-N level seemed to be higher than NO_2-N levels in all locations. NO_3-N measurements ranged from 1.12 to 83.03 µg L^{-1} across the landscape. Similar to NO_2-N, there was no apparent difference among different communities. NH_4-N levels varied across the transects, with no clear trend. In general, NH_4-N levels were lower than Black and Gumbo Limbo Hammocks. SRP levels ranged from 0.31 to 376.10.62 µg L^{-1}. Most of the bayhead and bayhead swamp soils had <10 µg L^{-1} SRP, whereas SRP in hardwood hammock soils was generally >50 µg L^{-1}. Pore water from marsh soils was generally <5 µg L^{-1} SRP.

Total phosphorus content in the majority of the hardwood hammock soil samples exceeded 3% by weight. In contrast, bayhead samples averaged ~0.1%, and the bayhead swamp soils averaged ~0.07%. Based on the current results, soils in various plant communities of Black Hammock differ considerably from one another. In particular, soils in the hardwood hammock differ from those of the other three communities in their physicochemical properties. We postulate that hardwood hammock soils have distinct mineral composition, which warrants further investigation.

Table 3-1. Pore water nutrients along four transects in Black Hammock.

Distance (m)	NO_2-N (µg L^{-1})	NO_3-N (µg L^{-1})	NH_4-N (µg L^{-1})	SRP (µg L^{-1})
		North-South Transect		
0	11.04	44.03	1704.37	3.28
30	21.16	26.60	38.08	2.48
65	9.11	30.51	7.04	142.62
105	7.18	95.74	137.48	64.63
120	9.66	48.93	97.07	9.23
150	11.96	35.35	171.51	6.13
200	29.68	48.68	106.75	18.49
250	35.89	58.85	87.43	6.81
300	16.56	35.04	60.13	4.65
350	11.04	39.69	276.40	5.26
400	6.40	38.32	228.34	9.82
450	3.19	56.13	83.53	0.70
500	11.50	42.48.	-	17.41
550	12.65	33.11	2575.46	3.84
600	9.57	37.14	165.81	3.72
		East-West Transect 1		
0	7.87	28.71	3332.86	3.75
40	15.14	50.41	5806.46	65.58
80	10.58	37.14	113.85	133.00
100	9.29	14.57	84.04	1.77
End	23.70	59.96	2948.96	5.45
		East-West Transect 2		
0	10.44	55.37	2411.49	31.87
50	5.18	18.39	43.82	3.34
100	21.07	47.19	-	12.17
135	14.63	42.29	1459.22	14.22
		East-West Transect 3		
0	7.78	45.14	1895.56	3.10
50	7.22	44.52	60.80	2.57
100	9.29	48.86	46.73	2.88
150	3.96	33.55	8.77	3.00
205	9.62	39.50	51.91	5.98

Table 3-2. Pore water nutrients along four transects in Gumbo Limbo Hammock.

Distance (m)	NO_2-N (µg L^{-1})	NO_3-N (µg L^{-1})	NH_4-N (µg L^{-1})	SRP (µg L^{-1})
		North-South Transect		
0	12.17	4.99	7026.28	1.84
50	25.86	35.59	7276.70	2.79
100	23.01	22.94	980.71	13.47
135	16.56	39.69	564.10	28.18
250	17.02	42.79	3061.60	8.64
300	79.14	46.32	4149.06	11.92
350	52.68	21.33	7308.36	250.24
400	37.54	19.47	2069.38	20.29
450	19.32	22.63	284.38	13.94
500	11.50	42.45	-	9.29
550	33.59	7.19	1506.00	5.11
600	20.52	32.43	-	7.71
650	9.66	26.04	130.53	8.92
700	29.63	29.45	4792.32	14.87
750	23.47	15.38	676.21	8.76
800	9.66	24.06	220.29	14.06
850	17.02	19.22	947.85	13.32
900	15.64	25.36	4970.21	3.72
950	15.64	44.65	6578.24	3.34
1000	17.94	35.04	85.97	8.02
1100	25.88	31.72	6651.18	8.98
		East-West Transect 1		
0	21.62	35.66	3090.83	13.16
50	34.92	27.72	478.26	16.32
80	22.77	48.68	441.90	79.28
160	21.16	82.72	146.86	11.30
200	29.45	44.65	5768.39	7.22
230	24.66	39.31	2137.67	6.19
		East-West Transect 2		
0	17.94	24.18	4806.14	5.88
50	25.77	31.44	10504.95	15.18
100	13.80	36.34	204.06	8.92
150	13.25	26.70	149.53	23.54
200	11.04	44.65	566.70	6.88
250	12.42	41.40	1711.60	9.91
280	23.28	36.96	4283.71	5.82
		East-West Transect 3		
0	21.90	60.15	3258.35	4.52
50	21.62	45.39	3454.32	2.85
100	11.64	20.62	1733.66	5.48
150	11.50	20.46	2063.73	2.79
200	8.05	64.18	541.98	9.91
250	10.08	32.31	522.64	3.10
300	23.42	43.47	4266.30	45.22
350	20.06	38.07	341.35	4.86
400	22.54	52.71	3050.18	6.81
430	24.62	44.96	7601.02	1.86
465	21.12	31.44	4232.30	2.48

Table 3-3. Pore water nutrients along four transects in Satinleaf Hammock.

Distance (m)	NO_2-N (µg L^{-1})	NO_3-N (µg L^{-1})	NH_4-N (µg L^{-1})	SRP (µg L^{-1})
		North-South Transect		
0	19.78	8.06	1579.22	3.41
25	16.10	20.15	1523.47	0.93
50	17.48	32.56	378.34	3.72
75	8.28	83.03	51.60	98.17
100	9.66	24.25	9.35	42.74
125	11.50	26.48	36.49	5.26
150	12.42	35.41	976.61	23.23
175	37.13	34.42	17.84	4.83
200	26.96	-	27.17	11.46
250	27.88	1.12	39.69	1.24
275	17.76	16.56	85.52	3.62
300	20.01	111.18	40.32	2.11
325	19.97	17.49	55.66	6.38
350	12.88	34.48	65.04	1.83
		East-West Transect 1		
0	14.72	21.70	40.96	0.56
25	13.80	32.25	26.79	13.44
80	6.86	11.22	7.34	376.10
90	8.28	25.67	9.15	258.41
125	25.31	60.77	45.29	6.91
150	21.65	13.21	57.71	2.20
175	13.90	16.62	-	4.34
200	14.22	15.56	-	3.04
		East-West Transect 2		
0	15.60	29.21	-	3.10
25	27.01	35.41	-	4.89
50	16.15	18.54	95.44	0.31
75	18.40	6.01	36.83	2.79
100	13.34	29.14	-	0.93
110	13.30	18.04	2492.50	1.24
		East-West Transect 3		
0	18.57	8.00	1981.16	2.45
25	26.23	17.98	7040.89	7.22
50	14.26	25.73	154.08	4.21
75	25.77	35.22	4879.28	8.36
100	21.03	21.02	4761.83	5.17
125	15.37	37.27	2221.51	4.34

Discussion and Conclusions

Different forms of nitrogen analysis in pore water samples revealed that NH_4-N is the dominant form of nitrogen, followed by NO_3-N and NO_2-N. A similar observation was made by Ross et al. (2001b) in their study of Shark Slough marshes. Concentrations of NH_4-N exceeded >50% of labile inorganic forms of N. The accumulation of NH_4-N does not in itself present a problem, since this form of nitrogen is preferentially utilized by most plants and microorganisms. In this study, it is interesting to observe that higher levels of NH_4-N were documented in marshes, bayhead, and bayhead swamps, while significant lower levels of NH_4-N were measured in the hardwood hammocks of the tree islands. Extremely higher concentrations of NH_4-N indicate that ammonification is the dominant process in the nitrogen cycle. The higher pH in soils, as well as in pore water, favors the ammonification process. It is clear from this study and others (e.g., Craft et al. 1995, Vaithiyanathan and Richardson 1997, Sutula et al. 2003) that the Everglades ecosystem is not nitrogen-limited. However, the hardwood hammocks seem to function in the opposite direction. While we don't have a possible explanation for lower levels of NH_4-N in hardwood hammocks, it is clear that nitrogen cycling is a complex process involving physical, chemical, and biological factors, and it is extremely difficult to interpret from the limited dataset.

Unlike nitrogen, soluble reactive phosphorus (SRP), an inorganic labile form of P, represents a very small proportion of the limited pool of phosphorus in tree islands. SRP in bayhead and bayhead swamps measured <10 $\mu g\ L^{-1}$ and the surrounding marshes <5 $\mu g\ L^{-1}$ SRP. In comparison, SRP in hardwood hammocks measured >50 $\mu g\ L^{-}1$. Total phosphorus content in the majority of the hardwood hammock soil samples exceeded 3% by weight. In contrast, bayhead samples averaged ~0.1%, and the bayhead swamp and marsh soils averaged ~0.07%. These data support the contention that readily available inorganic phosphorus is incorporated into organic form as fast as it can be mineralized in organic matter-dominated bayhead, bayhead swamps, and marshes. Higher levels of SRP in hardwood hammock soil solution may be attributed to solubilization/mineralization/dissolution phenomena. Further studies are warranted to understand the phosphorus biogeochemistry and nutrient cycling in the Everglades tree islands.

Part C
Other Aspects of Tree Island Soils

Two master's theses relating to tree island soils were produced by FIU students working under the supervision of one of us (KJ). Abstracts of both theses are presented below.

The Relationship between Soil Moisture and Nutrient Availability in Tree Islands of Shark Slough

by Elizabeth M. Struhar

Tree islands are an important component of the Everglades ecosystem and should be considered when formulating water management policy. Limited information exists on the influence of hydrology upon tree islands and in particular tree island soil dynamics. The purpose of this study was to investigate the relationship between soil moisture and nutrient availability in tree island soils of Shark Slough, Everglades National Park. To meet this objective, soil samples were collected from three tree islands, incubated under different soil moisture regimes (-50kPa, -1500kPa, Flooded, Air-Dried, and an alternating Wetting and Drying schedule), and analyzed for available phosphorus and nitrogen after 10, 30, 60, and 120 days. Moisture treatments significantly affected only available nitrogen while incubation time had a significant influence upon both nutrients. The greatest amount of nitrate was found in the field capacity samples while ammonium was more prevalent in the flooded samples. The greatest change in nitrogen availability occurred within the first 60 days for all moisture treatments; changes between 60 and 120 days were minimal compared to the first 60 days. Although ammonium initially increased when flooded, a decrease was seen after 60 days of flooding. Ammonium decreased over time in the air-dried treatment though nitrate did not appear to change much over time with this particular treatment. Phosphorus availability steadily decreased over the 120 day period for all moisture treatments. These results indicate that soil moisture plays an important role in determining nitrogen availability in tree islands and that the effects of wetting and/or drying are more pronounced in the first 60 days following the event. These results also indicate that there may be another mechanism besides soil moisture that is influencing the availability of phosphorus. More research is needed to determine the relationship between soil-available nutrients and overall plant growth and success in Everglades tree islands.

Influence of Biogeochemical Factors on Microbial Community Structure on Tree Island Ecosystems of Florida Everglades

by Ramakrishna Ruttala

A detailed study was conducted to understand the ecosystem-scale controls on soil microbial composition of the three Everglades tree islands - Black Hammock, Gumbo Limbo Hammock, and Satinleaf Hammock. Amplicon Length Heterogeneity – Polymerase Chain Reaction. (ALH-PCR) was used for semi-quantitative determination of eubacterial community structure. In the tree islands, ecosystems were significantly different for total carbon (TC), moisture content, microbial counts ($p \leq 0.001$) and pH ($p \leq 0.05$) at surface and subsurface. Pearson (two-tailed) correlation between parameters at both surfaces, TC is negatively correlated with pH, total phosphorous (%TP), and microbial counts ($p \leq 0.05$) but positively correlated with moisture ($p \leq 0.001$). ALH-PCR analysis showed high relative ratio of 340-361 amplicons in hammocks compared to bayheads and swamps. Diversity indices showed hammocks were rich and more diverse in eubacteria than bayheads and swamps. Thus, eubacterial diversity in tree island ecosystems may be driven by TC and TP under the influence of moisture. Future studies on establishing phylogenetic relationships and exploiting functional diversity would greatly enhance the understanding of microbial community interactions at ecosystem levels.

4

Winter Air Temperature Patterns in Tree Islands and Adjacent Marshes of Shark Slough

Pablo L. Ruiz

Introduction

Located between 25.25° and 25.75° N Latitude, Shark Slough is just a few degrees north of the Tropic of Cancer (23.5° N Latitude) and as such lies in a transitional zone between temperate and tropical areas (Gunderson 1994). Consequently, both the climate, which is more similar to that of tropical regions than to any other area in the continental United States (Duever et al. 1994), and its flora, which is characterized by species from both tropical and temperate regions (Gunderson 1994), interact to form unique species assemblages found nowhere else in the world. The relationship between climate and the distribution of plants is generally well understood (Woodward 1990). In the case of southern Florida and the Everglades, many species (e.g. *Sideroxylon celastrinum* (Kunth) T.D. Penn., *Coccoloba uvifera* (L.) L., and *Conocarpus erectus* L.) show a U-shaped regional distribution (Figure 4-1), extending further north along the Atlantic and Gulf coasts than in the center of the peninsula (Little 1978). This distribution is very similar to the pattern observed for mean minimum January temperatures in southern Florida (Figure 4-2). However, very little is known about how contrasting vegetation cover (tree islands *vs.* marshes, for example) within a climatic envelope - the climatic region which a plant or vegetation community is considered to exist naturally (Box et al. 1993) - influences ambient air temperature.

Methods

Temperature monitoring stations were placed at seven locations in Shark Slough (Figure 4-3). At each site, a temperature station was placed in the interior of a hardwood hammock and in the adjacent marsh. Stations where constructed from four plastic terracotta water dishes painted white and held together by three 7" stainless-steel lag bolts with 1½" spacers between each plate (Figure 4-4). Stations were placed 1.5 meters above the soil surface by securing the station to ½" electrical metal tubing (EMT) using a ½" EMT connector. Each temperature station contained two iButton® high resolution thermochrons (Dallas Semiconductor Corp., Dallas, TX, USA) secured to the first plate from the bottom with ½" bolts. Two thermochrons were needed, a DS1921H-F5 and a DS1921Z-F5, for temperatures above 15° C and below 26° C, respectively, because at the time of purchase, no iButton® thermochron was available which covered the range in temperature expected in Shark Slough during the 2002-03 winter. Each thermochron had an accuracy ± 1° C with a resolution of 0.125° C.

Stations were deployed on December 17, 2002, and retrieved on March 11, 2003. During this period, temperature data was collected hourly starting on Dec 18, 2002, at 0:00 hours and ending Feb 28, 2003, at 23:00 hours.

Results

Regionally, all seven sites were within a few tenths of a degree from each other in mean and mean minimum ambient temperature (Table 4-1). This was also the case for the two habitat types studied (Table 4-1). Daily mean temperatures were generally higher in the marsh than in the hardwood hammock (Figure 4-5), with mean ambient temperature in the marsh generally 0.1° C higher than in the hardwood hammocks (Table 4-1). Mean daily minimum and periodic minimum ambient temperatures were higher in the hammock than in the marsh by 0.4° C and 0.2° C, respectively (Table 4-1), while mean daily maximum and periodic maximum ambient temperatures were higher in the marsh than in the hammocks by approximately 1° C each (Table 4-1).

Table 4-1. Periodic mean and mean daily minimum and maximum temperature for two contrasting environments in Shark Slough between December 18, 2002, and February 28, 2003.

Site	Hammock					Marsh				
	Mean Temp (°C)	Mean Minimum Temp (°C)	Mean Maximum Temp (°C)	Periodic Minimum Temp (°C)	Periodic Maximum Temp (°C)	Mean Temp (°C)	Mean Minimum Temp (°C)	Mean Maximum Temp (°C)	Periodic Minimum Temp (°C)	Periodic Maximum Temp (°C)
Black Hammock	17.9	13.5	23.7	3.3	30.5	18.0	13.0	25.0	3.1	32.0
Gumbo Limbo Hammock	18.6	13.7	23.8	2.9	30.4	18.2	13.7	23.8	3.0	29.8
Vulture Hammock	18.0	13.6	23.7	3.3	30.4	18.2	13.3	24.6	3.3	32.1
CR3	17.9	12.3	24.5	2.6	31.1	18.0	12.2	25.1	2.8	32.0
NP205	17.7	12.9	23.4	2.1	30.3	18.0	12.2	25.0	2.1	31.6
P38	18.4	13.8	23.7	3.3	30.0	18.4	13.1	24.8	2.6	31.0
T6	17.7	12.5	24.3	2.1	30.6	17.9	11.9	25.7	1.9	31.9
TOTALS	18.0	13.2	23.9	2.1	31.1	18.1	12.8	24.9	1.9	32.1

The morning of January 24, 2003, found ambient hammock and marsh temperatures at their lowest for the period throughout the study area (Figure 4-6). The diurnal track of hourly ambient temperatures for this cold spell (Figure 4-7) clearly shows how ambient temperature varies throughout the day in both environments. As a general rule, hammock ambient temperature closely followed changes in marsh ambient temperature but rarely exceeded the temperature in the marsh during the hottest part of the day (see 1/23/03 14:00 in Figure 4-7), nor did it fall below the coldest marsh temperature during the coldest part of the day. Except for rare periods of an hour or so, this pattern held true for all days of record during the winter of 2002-03. As a result, winter ambient temperature in the hammocks tended to be warmer than the marsh during the coldest part of the day and cooler than the marsh during the warmest part of the day (Figure 4-7).

Analysis of variance indicated a significant difference in periodic minimum temperature among sites (factorial-ANOVA; $F_{6,1008} = 3.516$, $p = 0.002$) but not in periodic maximum or mean temperature at $p < 0.05$ (Table 4.2). In contrast, there was a significant difference in periodic minimum (factorial-ANOVA; $F_{1,6} = 13.894$, $p = 0.010$), periodic maximum (factorial-ANOVA; $F_{1,6} = 23.700$, $p = 0.003$), and mean temperature (factorial-ANOVA; $F_{1,6} = 12.550$, $p = 0.012$) between the marsh and hammock environments (Table 4-2). However, there was no significant site x environment interaction at $p > 0.05$ for these three climatic parameters (Table 4-2).

Table 4-2. Analysis of variance results (factorial-ANOVA) of minimum, maximum, and mean ambient temperature among sites, between environments, and the interaction of site x environment.

	df	df (Error)	Minimum Temperature			Maximum Temperature			Mean Temperature		
			MS	F	*p*	MS	F	*p*	MS	F	*p*
Site	6	1008	58.0	3.516	**0.002**	26.0	1.733	0.110	6.1	0.424	0.863
Environment	1	6	40.7	13.894	**0.010**	256.7	23.700	**0.003**	5.5	12.550	**0.012**
Site * Environment	6	1008	2.9	0.178	0.983	10.8	0.720	0.630	0.4	0.030	1.000
Error	1008		16.5			15			14.4		

Discussion

Clearly there is a difference in ambient temperature between the hammock and marsh environment of Shark Slough during the winter months. This difference appears to be related to shading and insulation as a result of canopy cover which is significantly higher in the hammock environment than in the marsh. The amelioration of low temperatures by tree cover may make it possible for tropical hardwoods to persist in the center of a wetland in which freezing temperatures are reached every few years (Duever et al. 1994). It also suggests that temperate species may have an easier time invading the open marsh than tropical species, and once established, might facilitate invasion by species of the latter group. However, canopy cover alone does not fully explain the difference in temperature between hammock and marsh environments.

For example, at Gumbo Limbo Hammock, the mean marsh ambient temperature was actually lower than mean hammock ambient temperature (Table 4-1). This anomaly appears related to the location of the marsh temperature recorder in a section of marsh devoid of all vegetation. As a result, it is likely that a cooler microclimate existed around the marsh temperature recorder as a consequence of increased evaporation rate resulting from a more uniform heated water column and better air movement. Possibly, changes in marsh community structure resulting from restoration of natural (longer) hydroperiods might make the Gumbo Limbo Hammock anomaly a normal occurrence as a result of sawgrass being replaced by more open water communities.

The uniformity of winter temperatures within the slough is surprising, given the coastal distribution of many tropical tree species within Florida. However, our sample network did not include sites near the Atlantic or Gulf Coasts, and therefore were not well suited to address these biogeographic relationships directly. Our data did indicate that minimum temperatures did not drop as low in the slough proper as in peripheral sites (i.e., CR3, P38, NP205, and T6) (Table 4-1), perhaps because of the moderating effects of water on the temperature range. Though these flanking sites differed in mean daily minimum temperature from the group of sites representing the interior of the slough (i.e., Black Hammock, Gumbo Limbo Hammock, Vulture Hammock), the between-group difference was less than 1^{o} C (i.e., less than the precision of our measurements). Such patterns are suggestive only, and should be repeated over a longer period at more sites.

5

Sediments, Stratigraphy, and Aspects of Succession, Chronology, and Major Prehistoric Disturbance in the Principal Type of Large Tree Island in Shark Slough

Pete A. Stone and Gail L. Chmura

Introduction

Tree islands are distinct patches of trees or large shrubs in an otherwise non-woody vegetational landscape. They occur worldwide, but the "hammocks" in the Everglades are the most widely recognized. Many marshes have tree islands, as do many prairies, savannas, and tundra. Typically, some environmental stress prevents woody plant establishment or growth (or at least substantial presence) that is ameliorated at the site of the tree island. In wetlands, presumably the degree of flooding is the limiting stress (perhaps additionally with fire). In marshes, a tree island site is often slightly higher, reducing or largely eliminating the flooding stress. The locally higher ground may be relict, a remnant of undulations on a geologic surface predating the wetland itself, or a recent sedimentary feature associated with the wetland. The latter are common in peatlands such as the Everglades. Here we discuss mainly tree islands that have two distinct vegetational and topographic portions (Loveless 1959). These in turn are associated with a dichotomy of relict-focused and more recently and purely wetland-accretionary portions of the two-tiered topographic feature that supports the tree island. The term "tree island" often is extended to include this local geomorphic feature that supports the patches of trees.

Tree islands that have accreted appreciable thickness or area of sediment are in large part a product of their own making, that is, biogeomorphological features, usually slight mounds or ridges. These have different environmental histories from those that originated on a pre-existing topographical high spot. Organic-rich sediments (peat or muck, described later) are the principal accreted sediments. The sediment stratigraphy (stacking) records important aspects of previous conditions and processes in the history of the development of the tree island. Furthermore, the organic sediments typically contain well-preserved microfossils (including pollen and spores) that can yield detailed information about past flora of the tree island site and its surroundings. Finally, both organic and recent calcareous sediments, such as marsh marl, are datable by radiocarbon (^{14}C), giving a reasonable approximation of the timing of the accretion and of any stages or events.

Types of Tree Islands Investigated

Our investigation included typical examples of large elongated tree islands. All but one had the two-component or two-tiered arrangement with a distinctly raised, rounded, upstream "head" supporting tropical hardwood (hammock) forest, that lies above a local mound in the shallowly buried limestone bedrock capped with organic-rich sediment. Extending downstream from the heads are long and slightly raised ridges of peat unrelated to the bedrock topography beneath (though obviously related in some way to that of the nearby upstream head) that support forest communities ranging from bayhead to swamp forest (Figures 5-1 and 5-8). The interesting exception is Ficus Hammock, a locally less common type. It is a large elongated bayhead forest, without an associated hammock "head", and thus appears to exist unrelated to a buried limestone mound. In the immediate area, most bayheads are smaller and more rounded in outline. Olmsted and Armentano (1997) and Armentano et al. (2002) discuss tree island types and their varied distribution in Shark Slough. Ficus Hammock resembles a type of large tree island found more commonly on deep peats of the northeastern Everglades. It is of special interest by appearing to be (at the present degree of examination) solely a peatland feature, formed completely by the peatland and not focused on an older feature.

Data on soil thickness, obtained by others by probing (Figure 5-2), coupled with cores from the hammock "heads", showed clearly that ancient relict topography of the bedrock was involved in the origin and location of these portions of the tree islands, even though elevation had been increased by tree island deposition in the Everglades wetland era. But the origin of the downstream ridge of organic sediment and the bayhead forest tail of the tree islands remains enigmatic. More importantly, the bayhead forest seemed far more susceptible to modern changes in hydrologic environment—the driving interest in the study—by being regularly flooded. Its boundaries presumably are determined in major part by flooding tolerances, and also likely by tolerance to marsh fire, probably indirectly related to periods of low water.

Principal Questions

A main initial question concerns the possible ecological influence on these tree islands of historical era regional drainage and subsequent water management. Evidence of any detectable effect on the vegetation was sought, initially simply by noting any unusual character or change in uppermost sediments, then by the record of fossil pollen and spores plus other microscopic biotic remains (termed microfossils) in the peaty sediment. Other questions relate to the overall developmental and environmental history of the tree islands, including sedimentation, pre-tree island environment, origin, shaping (elongation), vegetational succession, and disturbance. Sediments, sedimentation, and overall aspects are discussed first followed by the more detailed studies using pollen and other microfossils.

The pre-tree island wetland environment at present tree islands also is very important. Several characteristics of the tree island arrangement and of the surrounding marshes suggest plausible theories to describe how the bayhead tail portions of typical tree islands might have arisen and were shaped, or at least what forms they might have previously taken even if actual developmental or shaping mechanisms are not understood. One is that their shaping as elongated and slightly raised features took place as sawgrass strands. The immediately surrounding marsh typically is a "halo" of relatively dense sawgrass (with a wider zone aside and especially down flow of the tails). Beyond that fringe, out in the surrounding marshes, sparser wet prairie is widely important, but denser elongated flow-aligned "strands" of sawgrass occur in places interspersing the wet prairie. Were early sawgrass strands lying downflow of hammock "heads" the precursors to the bayhead covered present tails, now the main bodies of the existing tree islands? This was one conjecture at the start.

Investigation and Rationale

Our intent was to determine for several representative tree islands if evidence existed for modern shifts in the environment that might be associated with regional Everglades drainage or later water management that has occurred in the past 100 or 120 years (times of initial Everglades drainage and initial Lake Okeechobee drainage, respectively). This evidence would be mainly from sedimentary or related vegetational response sources; modern era examples of vegetational changes suspected to be hydrology related were known to have occurred elsewhere in Everglades National Park (ENP) (e.g., Atwater 1954, Higer and Kolipinski 1988). Detection of historical era changes would of course require "looking back" farther for comparison, at least another 50 to 100 years. The Shark Slough marsh environment just north of Tamiami Trail began at least 4500 radiocarbon years ago (Gleason and Stone 1994), thus any evidence for shifts should exist very near the top of peat profiles. There is little information on sediment stratigraphy of typical large tree islands in Shark Slough within ENP, and the information available was very generalized, such as soil-series identification (Davis 1946, USDA-SCS/UF 1946, Jones 1948, Gallatin et al. 1958). The several tree islands for which stratigraphies were reported had thick peat based in a bedrock solution depression (Smith 1968, Spackman et al. 1976, Gleason et al. 1984) or lacked the rock-mound hammock head (Kremer and Spackman 1981), different from the islands in this study. Since the start of this study, additional information from the northern extension of the slough in WCA 3A has become available (Willard et al. 2001, 2002). Initial plans to examine peats in the same manner as was suitable for large tree islands in the northeastern Everglades turned out to be unrealistic as the sediments differed substantially. There, the peats are purer and more fibrous and the formation processes apparently more biological. In Shark Slough, additional questions arose involving sediment composition and strata, necessitating a more geological, initial investigation.

The plan was to examine sediment (mainly peat) profiles from typical tree islands by means of extracted cores. The two main zones of the tree islands were examined: the raised hammock "heads" and the elongated and lower bayhead tails (the tails constitute the main body and most area of each tree island). Enough tree islands were cored to allow selection of the most appropriate profiles. This was useful because some abbreviated, or pre-drainage disturbed or otherwise mineral-dominated profiles, were discovered. Disturbed and mineral-rich sediments predominated on the hammock heads, and a decision was made to concentrate on the bayhead tail portions as they showed the greatest promise for a continuous sedimentary record and are more sensitive to hydrologic shifts.

The core profiles were examined for changes at their uppermost zones. Potentially for a bayhead profile, there might have occurred an uppermost thin zone of blacker and probably more granular or degraded peat overlying a typical fibrous peat, with the top zone degraded by drier conditions during region-wide Everglades drainage. Alternatively, a thin zone of more fibrous peat could occur at the very top, above the degraded peat, corresponding to the ENP and water management era of less drained hydrological conditions. Presence of a burn layer might even represent the drainage era, again perhaps with peat now forming above it. Possibly even the bayhead itself, especially for farther downflow reaches of the bayhead tail, may have succeeded marsh only in the drainage era, with thin bayhead peat over typical sawgrass peat of an earlier sawgrass strand. These were the sorts of shifts that were conjectured as possibly occurring, indicators of modern environmental changes. While some visually noted sedimentary shifts do in fact occur close to tops of several core profiles, several are not in the overall direction anticipated for the drainage era (i.e., more fibrous at top, and in a zone seemingly too thick to be completely from after the era of less controlled drainage, still less than 50 years now). In any case, the nature of the contrasting previous environments are not nearly as obvious as might have been the case had more fibrous peats and less mucky sediment sequences occurred (as was naively anticipated). The tree island peats here have much more content of very fine granular material than the northeastern Everglades tree islands, and more even than in marsh profiles observed in Shark Slough. Some first analyses then went into determining the origins of these materials and this included (as a final field effort) collecting and examining profiles from the marshes near several examined tree islands for clues. The fine material is of special interest in that it might represent matter physically transported by flow, whereas most Everglades fibrous peat materials are formed by plants in place. Finally as it turned out, much interesting and unanticipated stratigraphy occurs in deeper zones of the profiles, from well before the drainage era, but which speaks to the long-term development and rare but natural severe disturbance of tree islands.

Initial examination of the sediment profiles showed that no distinct gross sediment evidence for shifts in hydrologic environment was apparent at the very tops of profiles, or at least none involving upper strata so thin as to suggest a relation to regional drainage (in one case this is confirmed by ^{14}C dating showing an age of at least several hundred years at the base). The immediately underlying, more mucky sediments confounded straightforward analysis by stratigraphic peat type analysis (using standard petrography). Pollen analysis alone then offered the best potential for detecting and characterizing any final stage shifts in environment, that is by its effects on local vegetation, mainly that of the tree island itself. Mucky sediments fortunately are of no inherent disadvantage to pollen analysis. While planned for inclusion from the onset, pollen analysis then became the main paleoecological effort. To detect modern shifts, one extends the analysis much deeper than the zone (era) of interest for comparison and this depth was not known. For ascertaining whether such shifts might have occurred naturally in earlier times, and to understand the overall development of the tree island feature, the pollen analyses included the entire peat profiles.

The modern conditions and the sediment profiles of the several hammock heads examined, and the archeological and historical records of similar features not far away, suggest that local disturbance was both focused and long common there (Figures 5-6 and 5-7). The single profiles are interesting and useful, but several pollen profiles per head would be necessary to determine with reasonable confidence (by correlation) that the environment change detected is a response to external (exogenic) environmental change and not just extremely local shifts such as sediment redistribution from the all-too-common tree throw root “tip up” or even ancient camp fire or posthole. Another unknown is whether the peat at the top of these emergent sites has been lost through modern fires. We expected a thicker layer of fibrous forest peat with low content of mineral sediment to be present at the surface. Without this or additional cores for correlation, we cannot confirm the presence of a recent sedimentary record. Additionally, with more mesic trees on an elevated emergent site, the head is probably much more immune to vegetational shifts directly associated with slight lowering (or perhaps even slight raising) of water levels. Impacts would more likely have been from fire with possible loss of uppermost sediment. If these hammock heads were examined in sufficient detail, they might even show evidence of considerably higher seasonal water levels in pre-drainage times, thus making an important contribution to our knowledge of the regional hydrology. For the reasons outlined, the bayheads were instead emphasized.

Some Intentional Bias

Selection of coring sites was intentionally biased, but in a manner that should not affect their being typical representations of the record for most recent times. We cored in typical areas of the surface environment, but by initial probing (which was also necessary to avoid thick woody roots), selected an immediate coring site where sediments were thicker. This was done mainly to avoid coring atop a bedrock pinnacle (which could have protruded up into or above the surrounding peat of a developing tree island and blocked the record of that time), but also to obtain a longer sedimentary record of the wetland itself in the immediate vicinity. Offsets were on the order of only a few meters and no attempt was made to find the very deepest spot. This minute initial effort has allowed the intrinsically important additional interpretation of the evolution of the Everglades wetland at the tree island locales and prior to their development; much of this record is as sub-peat marl. To put the history of the tree islands into context, a brief reconstruction of the evolution of the local Shark Slough wetland is included.

Methods

Coring and Profile Examination

Main cores were obtained using a hand driven piston corer (Figures 5-3 and 5-4) of a type widely used successfully in this region (Ginsburg and Lloyd 1956). Most cores were collected in 3 inch diameter aluminum irrigation tubing with standard pitcher-pump leathers as the piston seals. The piston (via a partial vacuum formed above it) assists first in drawing in the cored sediment to minimize its vertical compression in the tube, and second in holding the core contents in the tube as it is pulled upward (using a hand winch and portable tower for support). Short cores of 2 inch aluminum irrigation tubing were taken ca. 30 cm away from main cores to provide additional sampling material of the uppermost zone of youngest sediment (not piston cored). Steel core tubes of 2 and 3 inch diameter (standard geotechnical Shelby tubes) were used for coring harder sediments (sometimes partially cemented or with limestone pebbles) on the hammocks heads (Figure 5-5). The latter coring did not use pistons. Intense driving with a 15 pound sledge hammer or fencepost slide hammer (Figure 5-6) was necessary to penetrate these firmer sediments, and occasionally to drive the piston corer.

Thick (deep) sediment was cored as successive sections down the same corehole. The bottom of the corehole after each extraction was marked with a small amount of red aquarium gravel dropped down it so that material sloughed off the wall in inserting the next empty core tube would be clearly marked as contamination. The separate core sections are combined in the figures (compare Figures 5-11 and 5-12).

All cores were capped in the field for transport. Using a fabricated core holder and saw guide, cores were later cut lengthwise by sawing just through the tube walls on opposite sides. A standard handheld electrical circular saw and standard carbide-tipped saw blade was used for aluminum tubing, and an abrasive blade for the steel tubes. The core contents were then sliced lengthwise with a long knife through these cuts in the tube. The two halves of the core were laid open for examination, description, and finally sampling after carefully scraping the sediment faces clean. Core halves were stored sealed and cool in thick polyethylene tubing. Core holes in the sediment were used for installing monitoring wells for the hydrological study carried out by others.

Cores typically become slightly compressed compared to the original thickness in the undisturbed sediment. Unsaturated conditions and lack of a piston produce the most compression (i.e., as in the hammock cores). Compression is minimized but often not insignificant even with piston coring of saturated sediment. The compression also occurs during core transport. To minimize any uneven displacement in settling (most troublesome for fine scale sampling of uppermost youngest strata), cores transported for long distances and exposed to vibration were raised at their tops, which then promoted some vertical settling (less troublesome and correctable in final descriptions by calculation). Cored depths measured in the field were compared to actual lengths of sediment in the cores, and the original depths of various positions in the cores (i.e., strata boundaries, samples) were calculated assuming a linear distribution of the compression.

Mineral Content Analysis

Organic matter and mineral contents of peaty sediments (including mucks) were determined by loss on ignition methods conducted by and at FIU/SERC using standard soils methods (i.e., same as used in other sections of this report). These are analogous to normal sedimentological methods, but required slightly different calculations for the purposes here.

After drying at 80ºC, weighed sediment was heated in air to 550ºC, reweighed, reheated similarly to 1000ºC, and reweighed a final time. The loss of weight in the first heating is considered to represent volatilization and oxidation of organic matter (lost partly as organic "volatiles" and partly as combustion product CO_2, H_2O, and nitrogen and sulfur compounds). The loss of weight in the second heating is considered to represent the CO_2 lost in the thermal decomposition of mineral carbonates, mainly being $CaCO_3$, which leaves solid CaO in the final "ash." Carbonate mineral was calculated as the second lost weight times 2.27 (the mass ratio of $CaCO_3/CO_2$). The equivalent proportion of $CaCO_3$ is the value reported here, as all carbonate mineral is considered to be $CaCO_3$. The final weight (often called "ash") represents minerals. It is primarily siliceous (noncarbonate) minerals in clay, silt, and sand, if these are present in appreciable abundance, but also contains any remnants of the mineral carbonate (as CaO). The "ash" weight is corrected by subtracting the appropriate weight of CaO (here calculated from the weight loss of the second heating times 1.27, the mass ratio of CaO/CO_2) to calculate a proportion of siliceous minerals. Computed values for "organic matter," "carbonate mineral," and "siliceous minerals" are given as percentages of the original dry sediment weight. The small amount of mineral cation coming originally from the organic matter is ignored (e.g., from cell wall Ca or K).

There are several other minor interferences and unknowns. Of importance and uncertainty is the fact that internally layered clay minerals apparently can retain some tightly bound water at 550º

C but lose it at 1000º C, slightly overestimating mineral carbonate in the analysis. This effect should not be great in any event. Other common hydrated minerals (especially gypsum) are not expected in these sediments. Opaline (hydrated noncrystalline) silica in sponge spicules and diatom remains will similarly give up water in the second heating but are not abundant here.

Radiocarbon Dating

Radiocarbon dating was carried out by Beta Analytic (Miami, FL, USA) using standard (benzene synthesis) analysis of bulk samples of sediment, including humic acid fraction in the organic matter dated. Carbonates were removed by acidification from the organic samples prior to dating. Marl samples were sieved through no. 100 mesh screen (150 µm) to remove shell fragments, and the fine fraction was dated. Organic carbon did not contribute to marl dates as the dated carbon was extracted from marl by acidification.

Dates are given as ^{14}C years (which are not equal to calendar years) and are corrected only for isotopic fractionation, which is a minor correction for the organic matter dates (they are already near the standard -25 o/oo δ^{13}C value for ^{14}C dating) but adds approximately 400 years to the uncorrected age for the marl carbonates (with ~ 0 o/oo δ^{13}C). Both "raw" and corrected dates are given for the marl dates.

Pollen Analysis

Samples were processed with conventional palynological treatments, as described by Moore et al. (1991). Treatments included HCl, KOH, glacial acetic acid, acetolysis, and hot HF. All samples were washed through a 125 µm sieve and retained on a 6 µm sieve, stained with safranin, and pollen aliquots mounted in glycerin jelly. Pollen was identified with the use of published keys (McAndrews et al. 1973, Faegri et al. 1989, Moore et al. 1991) and a reference collection held at the McGill Paleoenvironmental Research Lab, McGill University, Montreal, Quebec, Canada.

Microfossils and charcoal were counted with objectives of 400x and 630x magnification. All charcoal fragments over 6 µm were counted. Greater than 300 pollen and plant spores were counted in the Gumbo Limbo Hammock core, with the exception of sample 1 (depth 0.7) in which only 247 were counted. Greater than 200 pollen and plant spores in the Black Hammock core, with the exception of 0.7 cm (count =184) and 181.7 cm (count = 194). In other samples, pollen counts ranged from 214 to 1139. Pollen concentrations were low in samples from the Ficus Hammock bayhead core, particularly towards the surface. Total pollen and spore counts in the samples from 4.2, 8.3, 19.5, and 25 cm depth and above were 33, 79, 118, and 113, respectively. Counts in samples from lower depths ranged from 234 to 481 pollen and plant spores.

Pollen percentages were calculated on the sum of all pollen and plant spores. Counts of non-pollen microfossils and charcoal were normalized to the total pollen and plant spore sum, thus they may be represented by values >100%. Microfossils were plotted in diagrams if they occurred at an abundance of >1% in more than one sample.

Interpretations of palynological data (pollen and plant spores as well as other microfossils) must consider differences in pollen production and the processes responsible for the transport, deposition and differential decomposition of microfossils. Pollen from plants growing closest to the sample site and with high pollen production and wind dispersal typically are found in greatest abundance (Birks and Birks 1980). Pollen of some local species may be rare or absent if these plants are insect-pollinated (thus produce little pollen) or have pollen grains that are easily decomposed. Thus, pollen of pine is abundant in sediments of the southern Everglades, as pine has prolific pollen production and its pollen is noted for its ability to travel long distances. However, pollen representation is more precise for many important plant taxa (e.g., *Nymphaea* is likely to have been an important component of the vegetation where its pollen is represented by a few percent). The variability in abundance of pollen of most of the broadleaf woody plants suggests that this pollen is a good indicator of local importance of shrubs and trees. Finally, these pollen data are relative to the total, so that if pollen supply from one type increases, others must decrease even if no change in the supply of pollen from the source vegetation.

These uncertainties in pollen representation can be addressed by studying pollen assemblages from a known vegetation community. These assemblages (called modern analogues) are determined using surface sediments from known vegetation. Willard et al. (2001) examined pollen from surface samples in different vegetation types of the Everglades and identified characteristics of the pollen and plant spore assemblages to differentiate tree islands, sawgrass marshes, and sloughs. (That study did not include non-pollen microfossils.) Paleoenvironmental interpretations of the cores from Black, Gumbo Limbo, and Ficus Hammocks' bayhead forests applied the following pollen criteria reported by Willard et al. (2001): (1) tree islands have >20% fern spores, plus presence of *Salix*, *Cephalanthus* and *Myrica* pollen, (2) sawgrass marshes have a sum of *Cladium* and *Sagittaria* pollen >4%, and <2% *Nymphaea*, and (3) sloughs have > 3% *Nymphaea* pollen. It is important to note that these paleoenvironmental interpretations are based upon pollen and spore assemblages from modern plant communities and which may differ substantially from communities of the pre-drainage era. We may also be missing analogues for the vegetation that exists as the incipient stage of tree island development, but assume that, palynologically, it would most resemble a "tree island edge."

Taxonomic Affinity of Pollen Types

Few species have unique pollen types; the finest taxonomic resolution possible is usually to the level of genus. In many cases taxonomic, resolution is much coarser.

Poaceae. Genera of the family Poaceae cannot be distinguished without dimensional analysis of individual pollen grains and reference material of probable species.

Cyperaceae. Faegri et al. (1989) separate the Cyperaceae into seven types. One is *Cladium mariscus* (*C. jamaicense* Crantz), recognized by an elongate narrow tip of the cone-shaped grain. In palynological preparations, many pollen grains are folded and the shape of the tip cannot be distinguished; such grains are designated as "undifferentiated Cyperaceae", a category that may include *Cladium* pollen. In this study, five categories or types of Cyperaceae are recognized: (1) "*Cladium*", (2) "Cyperaceae 1" corresponding to *Schoenus* and *Schoenoplectus* types, (3) "Cyperaceae 3" corresponding to *Dulichium* and *Eriophorum* types, (4) "Cyperaceae 4" corresponding to *Rhynchospora alba* type, and (5) "undifferentiated Cyperaceae."

Polypodiaceae spores. Ferns of the Asplenaceae, Blechnaceae, and Polypodiaceae families produce morphologically simple spores that cannot be differentiated and are collectively termed Polypodiaceae spores by most palynologists (e.g., McAndrews et al. 1973, Moore et al. 1991). Thus, spores from the fern genera *Thelypteris* and *Blechnum* found on tree islands cannot be differentiated.

Osmunda spores. Spores produced by ferns of the Osmundaceae are distinctive from other fern families, but species cannot be differentiated, thus all are reported as *Osmunda*.

Other/undifferentiated fern spores. Spores from ferns other than *Osmunda* or Polypodiaceae types were not abundant and grouped together as other or undifferentiated fern spores. This group likely includes the species *Acrostichum danaeifolium, Nephrolepis biserrata, Nephrolepis exaltata* and *Pteridium caudatum* that occur on tree islands in the study area.

Polygonum lapathifolium Type. Species of *Polygonum* may have four different type morphologies. McAndrews et al. (1973) note that *Polygonum lapathifolium* type includes *P. hydropiperoides*, a species recognized in the Everglades flora.

Chenopodiaceae-Amaranthaceae Type. Pollen from these two families are difficult, if not impossible to separate, thus grouped together. The Chenopodiaceae-Amaranthaceae type pollen reported in this study likely comes from *Amaranthus australis,* which Brandt et al. (2002) report occurring in the vicinity of tree islands.

Asteraceae-Tubuliflorae Type. This type includes all genera of the Subfamily Tubuliflorae, with the exclusion of *Artemisia* and *Ambrosia* type (McAndrews et al. 1973).

Ambrosia Type. This type includes some species of *Iva* and *Xanthium*, as well as the common ragweeds (Moore et al. 1991).

Chrysobalanus. The status of pollen identified as *Chrysobalanus* is unclear. This is a triporate, psilate grain with an external appearance similar to *Myrica* pollen. However, the interior of the pollen pores distinguish it from *Myrica*. *Chrysobalanus* pollen reportedly resembles *Myrica* and is suspected to be the origin of the enigmatic grains. No key or reference material was available to provide a definitive answer.

TCT. This pollen type has source vegetation from the tree families Taxaceae, Cupressaceae, and Taxodiaceae. In this region, the likely source is cypress, *Taxodium*.

Results and Discussion

Coring details, locations, and depths are listed in Tables 5-1 and 5-2. An example of stratigraphy in a hammock head is shown in Figure 5-7; stratigraphy of main investigation bayhead profiles in Figures 5-12, 5-20, and 5-26; radiocarbon results in Table 5-3 and Figures 5-15, 5-21, 5-27, and 5-28; sediment organic and mineral analyses in Table 5-4 and Figures 5-16 to 5-19, 5-22 to 5-25, and 5-29 to 5-32; and stratigraphic pollen, other microfossil, and charcoal results in Figures 5-35 to 5-40. Brief descriptions of the sediment profiles at all coring sites are give in Appendix 5-1.

Sediments

Sediments in tree islands include those main general types found elsewhere in the Everglades system (i.e., peats and freshwater marl), plus some additional kinds. The latter includes mixed types found on the raised hammock head (which were not surprising judged from archeological reports on tree islands elsewhere) and unanticipated types from the bayheads in places. Though unsampled except as detached pebbles, the nature of the marine limestone bedrock surface also plays an important role in tree island location and formation in Shark Slough.

We define peat as organic sediment derived from plants that is sufficiently undecomposed as to retain a large amount of visible fiber content, though within this matrix of fibers may occur substantial amounts of finer organic matter. Where the fines predominate, the material is called muck. In some mucks, the fines are mainly organic but in others they are mainly mineral (e.g., marly or perhaps clayey). Mixtures of both types of fines occur, as do mixtures of fibrous peat materials and fines. A compositional series (peat: mucky peat : peaty muck : muck) corresponds to decreasing fiber content and increased proportion of fines, whether the latter are organic or not. Peats are formed both in marshes (e.g., sawgrass, waterlily) and forests (here mainly bayhead) where prolonged flooding helps to preserve the organic matter. Some forests in raised, rarely flooded sites (e.g., hammocks) can form peat also, but often a more decomposed or granular organic sediment or “soil” is formed instead. Muck is little studied in the Everglades and its possible origins and significance are only initially and briefly approached here. In hammocks, the organic matter (peaty or mucky) characteristic of uppermost sediments are typically intermixed with less-fine mineral material at shallow depth and some mixtures do not have any established sedimentary terms. Additionally, the origins of some sediments found in the hammocks is uncertain (in cases probably archeological, but in others not) and have not been classified (Figure 5-7).

Marl, or carbonate mud (silt), is another common freshwater sediment in the southern Everglades. It presently forms in sparser and generally shallower seasonal marshes (e.g., certain types of wet prairie) that experience a long season of annual exposure and drying. The sparse marsh allows the water column to be well lighted for the prolific growth of mats of photosynthesizing blue-green algae that precipitate the marl carbonate as calcite crystals from dissolved calcium and bicarbonate. The long dry seasons allow the accompanying (diluting) organic matter to be decomposed and the algae-encrusting crystals to be liberated to the surface; this probably helps select for the more open marsh in the first place. Marsh snail shells are often a minor component of marl sediment. Mixtures with peaty materials are also quite common. Where a mucky sediment is known to be formed by marl, the more specific name is used (e.g., marly peat, peaty marl, or mucky marl where the intermixed organics are fine).

Unusual Sediments

Several sediments encountered are unfamiliar or previously undescribed as wetland sediment in the Everglades. Some detrital or debris-like sediment (often with much bone? fragment) is found in the hammocks and may be largely archeological in origin (Figure 5-7). Everglades hammock heads have long histories of human occupation and thus disturbances (e.g., Laxson 1970, Carr et al. 1979, Masson et al. 1988), well into historical times and locally (e.g., Sturtevant 1953). The mixed hammock sediments are not yet understood well enough to discuss. Incipient cementation of midlevel sediments was detected in some hammock profiles. This has been described in a much more developed state in tree islands north of ENP (Mowers 1972), but is not yet adequately explained.

More important here, other unusual sediments were found in the bayheads of the investigated tree islands. These are (1) mucky sediments (muck, peaty muck, and mucky peat) that appear to include considerable fine mineral matter along with fine organics, and (2) purer strata of a superficially marl-like mineral sediment, but apparently ash and not marl. These are most notable because they lie well above the local base of the organic sediment profile (peat and muck) and arose not simply as upward extensions of the underlying mineral sediment (i.e., bedrock limestone, detritus from its decomposition, or from the marl that commonly directly overlies the rock). These mucky and mineral layers indicate that some starkly different conditions existed in the bayhead areas in the past but not the distant past of the developing Everglades. Instead they date from well within the era of the present freshwater wetland and peatland. The mucky sediments are extensive at depth. The mineral dominated sediment is more discretely distributed but widespread. In Black Hammock's bayhead tail, the apparently same mineral layer was found at both coring sites, over 300 meters apart, showing perhaps a large disturbance in the past (Figures 5-12 to 5-14). In Gumbo Limbo Hammock's bayhead tail, a similar layer exceeded 20 cm thick, a very substantial deposit (Figure 5-10). The ages are difficult to estimate even roughly, but the relatively shallow burial by overlying peaty sediment suggests the mineral layers formed as recently as a few hundred years ago, though perhaps several times that.

The muck and mucky peat sediments found mainly in the bayheads were not expected, at least in the case of apparently more mineral rich mucky material. Peats degraded to a mucky consistency were not as surprising, but still not expected in this area of the Everglades that was less impacted by drainage than elsewhere. The origin of the fine material is perplexing. The mineral matter must have been transported, and the organic fines may have been. Any downflow (lateral) physical transport then of course may also relate to shaping of the elongated bayheads, as well as to other questions of water column or bedload (flocculent) transport in the Everglades. Degradation of peat into mucky peat (as well as some sapropelic peat derived apparently from "soupy" organic sediment in deep water marshes) is known from the Everglades elsewhere, but in these cases the fine mucky material is organic matter. Mucks with fine mineral matter require a lateral input, except for basal organic sediments that are intermixed with underlying mineral sediment. Elsewhere in places in the southern and mid-latitude Everglades, mucky peat can occur well above the bottom boundary and these have been presumed to have marl carbonate intermixed, as that can precipitate in place and constituents are easily delivered downflow in dissolved form. But these marly peats or mucks are not thought to be quite as slick (slippery) or

Table 5-1. Core details from ten tree island hammock, bayhead, and marsh sites. All core tubing was aluminum unless noted as "ST" (for steel Shelby tube).

Core Type	Core Name	Community Type
Satinleaf Hammock		
3"	SL1	Hammock
2"	SL1a	Hammock
3"ST	SL2	Hammock
3"	SL-BHS	Bayhead Swamp
2"	SL-BS 3a	Bayhead Swamp
3"	SL4	Bayhead Swamp
2"	SL-BH 4a	Bayhead Swamp
Black Hammock		
3"ST	BH1	Hammock
2"	BH-Ham1a	Hammock
3"	BH-BH1 145m	Bayhead Swamp
2"	BH-BH1a 145m	Bayhead Swamp
3"	BH-BHS 450m	Bayhead Swamp, 3 core sections
2"	BH-BHS 450m	Bayhead Swamp
Gumbo Limbo Hammock		
3"	GL1-Ham	Hammock
2"	GL	Hammock
3"ST	GL2	Hammock Edge, two core sections
3"	GL-BH1 260m	Bayhead Swamp
2"	GL-BH1 260m	Bayhead Swamp
3"	GL-BH 820m	Bayhead Swamp
2"	GL-BH 820m	Bayhead Swamp
3"	GL BHS/M	Bayhead Swamp/Marsh interface (Outside hammock head)
Manatee Hammock		
2" ST	Man C1 S1	Hammock, two core sections
2" ST	Man C2	Hammock
Vulture Hammock		
2" ST	VH H	Hammock, two core sections
2" ST	VH H2	Hammock
Ficus Hammock		
3"	Ficus BS	Bayhead Swamp
Marsh Core: Transect 2		
3"	T2 800 m	Marsh, two core sections
Marsh Core: Shark Slough marsh (between Satinleaf and Seagrape Hammocks)		
3"	SS marsh	Marsh
Marsh Core: North of Gumbo Limbo Hammock		
3”	GL marsh	Marsh
North of Black Hammock		
3”	BH marsh	Marsh

Table 5-2. Core total depths from ten tree island hammock, bayhead, and marsh sites.

Core name	Community Type	Total Depth (cm)
	Satinleaf Hammock	
SL1	Hammock	107
SL2	Hammock	50
SL-BHS	Bayhead	74
SL4	Bayhead	57
	Black Hammock	
BH1	Hammock	43
BH-BH1 145m	Bayhead	104
BH-BHS 450m	Bayhead	261
	Gumbo Limbo Hammock	
GL1	Hammock	90
GL2	Hammock. Edge	140
GL-BH1 260m	Bayhead	113
GL-BH 820m	Bayhead	125
GL BHS/M	Bayhead/Marsh interface	157
	Manatee Hammock	
Man C1	Hammock	69
Man C2	Hammock	56
	Vulture Hammock	
VH H1	Hammock	89
VH H2	Hammock	64
	Ficus Hammock	
Ficus BS	Bayhead	115
	Marsh Core: Transect 2	
T2 800 m	Marsh	186
	Marsh Core: *Shark Slough marsh (between Satinleaf and Seagrape Hammocks)*	
SRS marsh	Marsh	77
	Marsh Core: North of Gumbo Limbo Hammock	
GL marsh	Marsh	93
	Marsh Core: North of Black Hammock	
BH marsh	Marsh	53

shiny when slicked on a cut surface as the several midlevel muck or mucky layers found here. Still unresolved is the origin of the fine organic matter and whether transport and deposition of fine matter account for bayhead tail origin and shaping. And did the shaping take place in or just prior to a sawgrass stage? In connection with this last question, many visible tail extensions occurring both laterally and downflow are of sawgrass, and bayhead has succeeded sawgrass marsh at tree islands elsewhere in the Everglades. These questions regarding succession are examined with the pollen evidence.

The mucky sediments (and even much of the peat beneath bayheads) are further notable by the very dark color. The fines are often black where abundant. In contrast, peats in the northeastern Everglades are typically dark reddish brown to even medium brown. Fine charcoal darkens peats but usually not so intensely or uniformly as the darkening here. This characteristic is not yet understood.

The enigmatic marl-like mineral sediment layers found in three of the bayhead profiles had a conspicuous light color, strongly contrasting with the dark peats and mucks (and organic mixtures) that encompass them (Figure 5-13). They resemble marls, except for slight added color, and a sample tested did react with nitric acid to reveal some carbonate present, though most of the bulk was nonreactive, noncarbonate insoluble mineral. The light orangish color of these mineral sediments in places reminds one distinctly of peat ash (seen previously in the laboratory, and in the field after severe fires with peat burns). Ash can produce a sediment with some carbonate; calcium in plant cell walls results in calcium oxide (CaO) in ash, that then reacts with water to form $Ca(OH)_2$ that in turn combines with carbon dioxide (CO_2) in the atmosphere or evolved from the organic soil to produce the calcium carbonate ($CaCO_3$). Any carbonate already in the burning peat would likely proceed through the same series. But ash of typical peat could not create the thickest layer here; it would require burning of an impossibly thick original layer. Ash from mucky sediment with a high enough organic content to burn but enough mineral content to leave copious ash appears to be the origin. No other mode of origin is obvious; stable carbon isotope ratio in the carbonate might reveal an ash nature by isotopically light carbon from atmosphere or soil, in contrast to isotopically heavy marl carbonate. If the black granular material that lies aside the mineral sediment in places turns out to be charcoal by closer analysis, this would add strong support to an ash origin (the fragments examined were suspiciously too shiny to be a typical wood charcoal fragment, but their interiors might yet reveal wood origins).

Radiocarbon dating

Sample depths for radiocarbon dates were initially selected on the basis of sediment type and the results are discussed here with relationship to sediment stratigraphy. Results are given in ^{14}C years (BP actually denotes a date "before present," which is established as AD 1950) (Table 5-3). Uppermost samples showing modern enrichment of ^{14}C by contamination from nuclear weapons testing would calculate to negative ages; thus results are given as radiocarbon concentrations >100 PMC (Percent Modern Carbon). This refers to percentage of the radioactivity of the modern carbon dating standard (100 PMC is equivalent to 0 BP). All $\delta^{13}C$ values are as deviations from the standard value in per mil with 0 o/oo representing a typical marine carbonate sediment as the standard (PDB standard). Freshwater marl carbonate from the Everglades similarly has values near 0 o/oo.

The Slough Marshland. The marsh sites were examined with respect to specific aspects of tree island development in the overall study. However, the ^{14}C dates are discussed first to put tree island development into the context of the history of the wetland (and finally a peatland) environment surrounding and encompassing it.

Dating the base of the thickest marsh peat thus far encountered (i.e., Transect 2 of Ross and colleagues, near the 800 meter mark) gave an estimate of the initial onset of peat marshes and peatland deposition in Shark Slough (Figure 5-28). The date of 4760 ±60 BP is in keeping with the few other basal dates from slightly north of Tamiami Trail (e.g., ca. 4500 BP at Gage 3-28 in southern WCA 3A, Gleason and Stone 1994) and shows that the entire area surrounding the tree island sites has a long history of long hydroperiod wetland and peatland that is considerably older than the tree island bayhead forests. This older condition of the peatland was not established prior to the study. The tree islands (except for Ficus Hammock) are associated with rock mounds that are much older than the wetland and peatland. More importantly, tails on tree islands in marl areas of the park show that such features can develop prior to or without the development of surrounding peatland.

A marsh core was obtained near Satinleaf Hammock to determine when the surrounding peatland developed locally, that is, when did the underlying marl or limestone that were potential sources of transported carbonate become buried and thus isolated by peat? The core also gave evidence of severe pre-drainage natural disturbance, reinforcing this same evidence (if perhaps not the exact same disturbance) from several bayhead cores in two tree-islands. The base of the curiously thin (ca. 30 cm) marsh peat dated only 880 ±70 BP, while the top of relatively thick marl just beneath it dated much older, 4400 ±50 BP (corrected for δ^{13}C = 1.5, or 4010 ±50 BP without the correction). The disjunction between dates from basal peat and immediately underlying marl in the few places studied elsewhere in southern Florida are less than about 1500 ^{14}C years. This large discrepancy in lengths of dating gaps between basal peat and immediately underlying marl suggests a difference in process. The much larger gap here seems to be a real hiatus and may involve a severe disturbance some 900-1000 years ago (i.e., slightly older than the date of the overlying basal peat). The marl marshes are interpreted to have been drier than the succeeding peat marshes. Elsewhere in southern Florida (e.g., at Corkscrew Swamp, at Kreamer Island by the south shore of Lake Okeechobee, and implied for the eastern shore of the lake at the Everglades edge) there are large but lesser gaps (<1500 ^{14}C years). Peat deposition may have started fitfully, with years or a century of accumulation later lost in especially dry years, until finally it became wet continuously enough for peat to remain and be buried. Or possibly the earliest peat marshes corroded or dissolved the top layer of marl. Or perhaps with thick marl—a soft pasty sediment in an animal-filled marsh—there simply was some vertical mixing, bringing older underlying marl to contaminate the surface layer. Thinner marls have mostly given better agreement, but at least one thick marl has shown far less discrepancy at top (none of this dating bias has received sufficient directed attention, and apparently no attention since the development of well-suited AMS dating). Finally, we know that root intrusion will bias the basal peat young by some yet unknown amount. One or more of these factors likely explains a commonly large date gap between basal peat and the uppermost part of thick marl. But no other site examined or reported approaches the gap seen in the marsh core here.

Table 5-3. Radiocarbon dates of cores. OM = organic matter, CO_3= carbonate.

Site/ Location/ Depth (cm)	Date ^{14}C yr*	$\delta^{13}C$ (o/oo, PDB)	Beta Lab No.	Fraction Dated
	Black Hammock, bayhead swamp			
BH/ BHS/ 450m/ 0-7.6	113.16 ±0.74 PMC**	-29.4	183026	OM
BH/ BHS/ 450m/20.3-25.4	105.20 ±0.70 PMC**	-27.7	183207	OM
BH/ BHS/ 450m/ 38.1-43.2	1560 ±60 BP	-27.6	183028	OM
BH/ BHS/ 450m/ 111.8-116.8	3800 ±60 BP	-27.3	183029	OM
BH/ BHS/ 450m/ 152.4-160	4280 ±60 BP	-26.6	183030	OM
BH/ BHS/ 450m/ 213.4-218.4	5850 ±60 BP	+1.0	183031	CO_3
Corrected***	6280 ±60 BP			
BH/ BHS/ 450m/ /250.2-256.5	6310 ±60 BP	-1.6	183032	CO_3
Corrected***	6690 ±70 BP			
	Gumbo Limbo hammock, bayhead			
GL/ BH / 29.3-34.3	390 ±50 BP	-27.6	183033	OM
GL/ BH/ 820m/ 35.6-40.6	920 ±60 BP	-27.8	183034	OM
GL/ BH/ 820m/ 80.1-90.2	3560 ±70 BP	-27.5	183035	OM
GL/ BH/ 820m/ 90.2-95.3	3580 ±50 BP	-27.0	830361	OM
GL/ BH/ 820m/ 105.4-110.5	4000 ±50 BP	-26.7	183037	OM
	Shark River Slough, marsh (between Satinleaf and Seagrape Hammocks)			
SRS / 21.6-54.8	880 ±70 BP	-27.2	183038	OM
SRS / uppermost marl	4010 ±50 BP	-1.5	183039	CO_3
Corrected***	4400 ±50 BP			
	Shark River Slough marsh transect, thickest peat			
T2/ 800m (67-186cm) 77.5-82.6	4760 ±60 BP	-24.9	183040	OM

*Date corrected only for isotopic fractionation
**"modern" in ^{14}C, post-ca. AD 1954, >100 PMC
***See text for description of corrections to dates from carbonate dates

A plausible cause for the much larger age difference in this Shark Slough marsh core is the removal of a substantial layer of peat by severe peat fire very roughly 1000 BP. It is unlikely that in this vicinity peat only became originally established ca. 1000 BP, as the top of the marl then would have been much younger. A predicted date for the base of the peat would have been on the order of 2500 BP or older estimated solely on the ca. 4000 BP (uncorrected) uppermost marl date (using the maximum offset seen elsewhere [likely with uncorrected dates] and described above). No remnant anomaly in the marsh was apparent at the coring site (we intentionally cored in what seemed to be typical marsh, and would have avoided a patch of distinctly deeper marsh). The timing implied by the date from the base of the peat is roughly compatible with severe disturbances evidence for two tree islands examined (see below). Can there possibly have been one extreme drought and enormous conflagration about 1000 years ago that is now so widely evidenced in this part of Shark Slough? Or maybe it was an era of severe droughts and various peat fires. The sedimentary history of the Shark Slough peatland is considerably more complicated than is commonly recognized.

This curious situation with a marl surface being exposed in the not distant past and well within the present peatland area of Shark Slough is reinforced by the existing marl surface exposed at a marsh-core site near Black Hammock, a more interior site in the slough (Figure 5-34). The uppermost marl there is not dated but is possibly not modern as it is not a marl-forming marsh area at present. Olmsted and Armentano (1997) note such anomalous marl-surfaced areas as well in marsh that otherwise hydrologically resembled the surrounding peatland. This would imply that peat fire had removed a surface layer and not long ago, as peat deposition has not resumed (though it could easily be many decades). Winkler et al. (2001) report a marl-surfaced coring site in northeastern Shark Slough (East Everglades) with a ca. 1400 BP date coming from very near the top (AMS date on organic matter, not carbonate, as the marl was organically enriched in upper parts). This similarly suggests that a peat layer was removed and not long ago. Marsh cores are also discussed below with respect to mineral contents of the organic sediments in bayheads.

Black Hammock Bayhead. Discussion proceeds from the uppermost sample downward, youngest to oldest. The surface layer peat sample and the next deeper peat sample from the Black Hammock bayhead (Figure 5-15) clearly show the dominant presence of modern carbon from nuclear era atmospheric contamination (113 PMC and 105 PMC, respectively). These “dates” (especially from the surface layer) have more than chronologic importance. They suggest that the irregular hummocky or tussocky surface topography found in the bayhead (here and in the other tree islands examined) does not result from the occurrence of a modern severe peat fire. This irregular surface, found also in large bayhead tree islands in the northern Everglades, mimics that of severely burned peat forest where the tussocks are mainly focused on resprouted or recolonized stumps and the hollows resultant of peat burning (e.g., Okefenokee Swamp, Georgia, Hell Hole Swamp, SC). Recently burned sites will have older peat exposed at or near the surface. This site has not had a severe peat burn recently enough to show this; instead a substantial thickness of modern or else well-intruded peat from the nuclear era lies at the surface. (Similarly, no distinct layer of coarse wood-origin charcoal was noted.) Thus the irregular surface topography is apparently of accretionary origin rather than formed by pocketing in a severe peat fire (a condition it might otherwise have suggested, say with peat fire having mostly destroyed a hypothesized former, more pronounced peat ridge).

The deeper sample exhibiting “bomb” radiocarbon (105 PMC) demonstrates the inherent added uncertainty of dating peat sediment versus, say, a shell or piece of wood of short formation time. Roots of peat-forming plants penetrate the underlying peat and reduce the apparent age of the peat in the zone that is heavily rooted. Perhaps woody plants have the greatest effects, either volumetrically or in depth. This is yet little understood quantitatively. This root intrusion is assumed to be the cause here. It seems implausible that ca. 25 cm of peat (not merely forest litter) could have accreted in the past half century or so. Recent accretion rates are very poorly known, however, and one study (Donders et al. 2004) has differences that are hard to reconcile with the longer records. Other dating methods better suited than ^{14}C for the past hundred years or so are far less affected by root intrusion and could help resolve this lingering question.

Unfortunately, this problem of intrusion negated the chance for readily dating the apparent ash layer lying just below. The underlying bounding peat is not suitable for dating a peat fire. When a severe peat fire burns off an upper layer of peat, a date from the oldest (uppermost) surviving peat then lying immediately beneath the ash is not a good estimate of the date of the fire itself (though it gives a maximum possible age, and can give evidence of the severity of the fire because as more peat thickness burns away, the older is the top of the underlying surviving peat). It is reasonably assumed that peat deposition quickly resumes after the season of the fire, upon the resumption of prolonged flooding. Thus the bottom of the overlying peat (above a charred or, less commonly, an ash layer) best dates the fire itself. Root intrusion tends to minimize that apparent age, in this case to a “modern” and unusable value. The thin layers of peculiar mixed sediment of fine-grained muck with intermixed coarse-grained apparent charcoal is of unsure sedimentation and thus inappropriate for dating. The apparent charcoal fragments are datable (by AMS), but are they from above-ground wood at the time of the fire (good dating material), or charred but formerly buried wood of age well older than the fire? The fine organics in the muck are of even more uncertain origin and thus here too no single date or few dates would be strong evidence of the age of the fire. If this ash layer were to be dated, one might start by using several dates from the coarsely granular materials (assuming this is charcoal) and interpreting the youngest date to lie closest to the age of the fire (similar rationale is used in dating sandy [not directly datable] beach ridges by their included datable shells, which may vary in age).

Ash is not considered datable. While this ash possesses some carbonate (with small sample dating possible by AMS), a date from this might be useful but would not be diagnostic. If CO_2 had been absorbed directly from the atmosphere above by the new ash when dampened, a reliable date would be obtained, but as likely there was a substantial upward flux of CO_2 from the older peat soil below. The origin should be discernable by $\delta^{13}C$ value.

Questions of origin and ultimately the age of this apparent major fire (and that on Gumbo Limbo Hammock bayhead in one core at 260 meters) almost certainly can be resolved with additional analyses and multiple dating of the several sediment fractions. ^{14}C, like ^{13}C, has sedimentary diagnostic value beyond just dating. First, the ^{14}C and ^{13}C contents could be used to indicate sediment origins and then the results from the most suitable sample taken to date the fire itself. This and the methods discussed above were beyond the scope of this study but should eventually be done (along with a better assessment of the ash) as this represents severe late stage disturbance to these now well studied modern tree island forests.

The top of the mucky peat directly underlying the ash and muck zone dates to 1560 ±60 BP and gives a maximum (bounding) age for the severe fire. This assumes that no significant root intrusion took place through the ash layer itself (the layer itself was not notably intruded). But the date must be significantly older than the fire because the former organic sediment that resulted in the substantial thickness of ash (ca. 4 cm), or the ash and bounding muck (ca. 10 cm), required an extended time to accrete, that is after the dated peat layer had formed but before the fire partially consumed this later sediment. Unfortunately the original thickness of these burned materials and the time to accrete them cannot readily be estimated.

Deeper in the peat profile, a midlevel gave a date of 3800 ±60 BP, and near the base of the mucky peat zone 4280 ±60 BP. The absolute base of the organic rich sediment here is not dated (it is a mixture of peat or muck organics and marl carbonates), but the 4280 BP date from the deep though not basal sample shows that peat (i.e., organic) sedimentation began at this tree island site as early as at older parts of the surrounding peatland marsh in this part of the Everglades. The mixed peat and marl sediment represents the onset of peat co-dominated sediment in this core. This uppermost and intermixed marl carbonate was either physically intermixed from marl sediments below or else was still forming locally to a degree, resulting in the marly peat (or muck) deposition. This too would be resolvable by multiple dating of fractions.

A distinctly three zoned marl layer lay below the organic sediments (this may be the first reported indication of environmental change in the pre-peatland marl wetland of the Everglades). A typical looking marl layer lay beneath an upper organically enriched layer and above a grayer layer that somehow was different (possibly had some detrital material from the bedrock). The top of the typical marl dated 6280 ±60 BP (using the theoretical correction based on the $\delta^{13}C$ values of +1.0 o/oo, or 5850 ±60 BP without it). The base of this layer yielded 6690 ±70 BP (based on -1.6 o/oo, or 6310 ±60 BP without the correction). The corrected date is assumed to be closer to the real age. For some reason (not yet understood, but possibly related to root intrusion bias in peats), under Everglades conditions, the uncorrected date is often more directly comparable with associated peat material, thus the uncorrected date is given here as well, merely to allow ready comparison with the more numerous peat dates. Many marl dates reported in the literature from this region are not corrected, and the latter (younger) date is the one to compare with them.

Everglades wetland had established at this present Black Hammock bayhead site, and thus the wider locale, by roughly 6700 BP. This is in general agreement with the few basal marl dates from other parts of the Everglades where subpeat marl is typically found (ca. 6300 BP and 6500 BP [probably uncorrected], eastern and southern Lake Okeechobee/Everglades boundary: Brooks 1984, Gleason et al. 1984). The thin layer of gray marl farther below, nearest the bedrock, obviously extends this age somewhat. Solution pits in the limestone would have accumulated carbonate-rich erosional debris with possibly severe dating problems (due to a partial origin from ancient limestone, and possibly long before wetland flooding).

Gumbo Limbo Hammock Bayhead. The base of an upper fibrous peat zone (above more mucky material) dated 390 ±50 BP and must be at least that old, as root intrusion could bias this date to appear only younger (Figure 5-21). This layer is thus not a feature of post-drainage origin, but a natural shift to a more fibrous peat compared to the mucky sediments below. The top of the peaty muck zone below dated 920 ±60 BP. The ca. 500 ^{14}C year separation of these dates from near-bounding samples might suggest a hiatus. Peat fire is always suspect and especially here, given that the top of a thick apparent ash layer lay at roughly similar depth at a core site 560 meters farther toward the head. Unfortunately, the inherent uncertainties in dating bayhead sediment prevents its proof of a loss of peat record. If there is no loss of record (and no ash was seen), the end of the era of mucky sedimentation occurred ca. 900 BP, well before the drainage era. The base of the peaty muck zone dated 3560 ±70 BP. An underlying thinner zone of purer peat dated 3580 ±70 at the top and 4000 ±50 BP at its base. This in turn overlay very thin marl.

The basal peat was thus followed by deposition of more mucky sediment. This mucky layer is again of considerable interest to the origin of the tree island bayhead tail and perhaps to its shaping. Its deposition dates very roughly 3500 to 1000 BP (which is a more realistic view of the available precision). The question was raised as to how can this immediate site in the Everglades wetland go from forming a fibrous (likely marsh) peat of the developing peatland, to depositing a more mucky sediment for several thousand years, and then back to a fibrous peat (though now of bayhead origin)? More detailed investigation would be necessary (using closely spaced cores), but there are several possibilities. A typical "wet" earliest peatland may have become absolutely or seasonally less wet with a more degraded (finely granular) and perhaps more marl enriched sediment then forming. Or a vegetation type that is now not common and not yet well known in the peat record may have routinely produced a more mucky sediment (the now unknown but formerly reported "lake" [actually very sparse marsh] stands is a possibility). Or finally, perhaps dramatically increased flow occurred, allowing some fine detrital materials to be moved and concentrated in deposition. The last might have occurred under external climatic forces, or more mundanely merely when the slowly rising peat and water levels came to well above most of the rock of the solution pitted limestone surface. But it can hardly be unrelated to the distinct change that took place in deposition at marsh sites near Tamiami Trail, lying not far upstream from the tree islands investigated, in the era ca. 3000-2000 BP (Gleason and Stone 1994) and probably for at least 500 ^{14}C years before and after (unpublished dates; see also Atlschuler et al. 1983 [Fig. 1], Winkler et al. 2001). Unusual hydrological conditions occurred in that long era, starting well after the beginning of the peatland and ending long before the drainage era. The peat-marl-peat stratigraphy there suggests via the nature of marl deposition that it was seasonally drier than before and after. But marl deposition is compatible with fairly high water stages and flows; it just seems to require the dry conditions also, so greater seasonality is at least possible. There is much yet to learn.

Mineral Content and Fine Organic Matter in Sediments

A preponderance of the sediment found in the bayheads had at least a partially mucky consistency, that is abundant fine-grained particles (in mucky peats), to dominantly so (peaty mucks), up to, in some thinner zones, almost exclusively these fines. The apparent density in small hand sample of these sediments (e.g., the pollen samples) and especially the slipperiness and ability of core faces to "slick" when rubbed gently on the surface (to test for a slippery nature) suggested that not only were fine grained organics present but very fine minerals were in appreciable abundance. Marl carbonates (typically silt size) are not usually this slick, so siliceous clays were suspected as well. The noncarbonate nature and the apparent origin of the interpreted ash layers also strongly suggested an abundance of noncarbonate, that is siliceous, very fine mineral matter. The mucky sediments in the main investigation cores (those giving the pollen and ^{14}C samples) were then examined for proportion (% by weight) of organic matter, carbonate mineral, and siliceous mineral. The more peaty layers (i.e., more fibrous-dominated and less mucky layers) in the same cores were examined for comparison. A core from the marsh was also examined to see if these areas might have served as source areas (or at least throughflow transit areas) for the minerals (and also plausibly the organic fines). Results for the bayhead cores are given in Figures 5-16 to 5-19 and 5-22 to 5-24, and for the main marsh core in Figures 5-29 to 5-32. These give (1) clear information on mineral types and sedimentation through time, including changes, (2) important strong suggestions, down to constraints, on the nature of origin and introduction of the minerals, and (3) implications to plausible ultimate origins and actual mechanism or transport.

Mineral matter was found to be important and is distinctly more abundant than in the peats of the tree island area of the northeastern Everglades, but is less important than suggested by the observations mentioned above. And while there is indication of a greater proportion of mineral matter in the muckier sediments, the enrichment in fine mineral matter is also apparent for the peats (both beneath the bayheads and the marshes) relative to the northeastern Everglades.

Organic fines must predominate, although this is inferred. The analyses were from bulk sediment, including the fibrous component. Despite this added uncertainty, the codominance to dominance by fines, the overwhelming preponderance of organic matter (shown in the analyses), and the much greater (2+ times) densities of mineral matter over the organic matter itself (the particles, not including the pore space) imply that the organic matter greatly predominates in volume in the fines. Further work should include separation of fine particulate from fibrous components and analyzing them separately. This was attempted by wet sieving, but the water spray force required to disaggregate the sediment appeared to disintegrate many fibers. Some chemical assistance with disaggregation (say by a nonreactive and completely soluble surfactant) and gentle particle size separation by differential settling in a large settling tube, with subsequent rinsing of subsamples with centrifuging to prevent any loss of solids, would overcome the problem.

Black Hammock. The bayhead profile from Black Hammock showed an increase in organic matter from bottom to top (Figures 5-16 to 5-19). The highest content of mineral matter thus is at the base of the organic zone (base of mucky peat) where its high carbonate content shows residual marl production in the local change over from marlland to peatland (most likely), or some shallow or near-surface mixing by marsh animals in the early peatland era (it seems too great for this process), or lateral transport from nearby higher areas upflow that were then still producing marl (this merely speculated). The carbonate mineral content sharply declines not far up into the organic sediment profile, but some carbonate remains to the surface. Upward mixing becomes implausible then, but local production and inflow remain. However, at the shallowest levels that represent bayhead, how could carbonate generate locally at the site? Bayhead swamp forest (*sensu* Olmsted and Armentano 1997) can be open enough in the canopy and flooded long enough to allow bladderworts and marsh aquatics (e.g., arrowhead) to grow, but can periphyton grow too, and in an abundance to produce appreciable carbonate in the sediment? It seems unlikely.

More evidence is provided by the abundant siliceous mineral content. This almost certainly must come from some other place and in solid form, and this in turn lends some support for the same transport mechanism and route for the carbonate. It was noted incidentally (in the area where the airboat was parked several times) that extremely shallow peat overlay more tabular, not notably pinnacled, limestone just outside the forest. It seems likely that for much of the peatland era of the wider marshland, and for much of the organic sedimentation era of the bayhead site itself, there occurred nearby some exposed limestone (exposed in the sense of not buried; it may well have been immersed). Slow dissolution of limestone is a possible source of noncarbonate residual minerals. (This situation led to the coring in the nearer marshes to see when the limestone and marl became buried and then isolated as possible mineral sources.) The steady and pronounced decrease in siliceous mineral content to the top of the organic sediments indicates a declining input (assuming here no large increase in rate of organic sediment accretion, which is not suggested) and this implies that either the source became increasingly unavailable (e.g., more and more of the residual-rich mineral surface finally became covered with peat) or a decline in the transport mechanism (e.g., reduced flow, better baffling by vegetation, or with shallower water in the present bayhead area itself). What is clear, though, is something has moved appreciable fine siliceous mineral matter from somewhere else and into the bayhead area and over a long period of time. It is hard to envision any other mechanism than water flow.

The results from the marsh sites (discussed below) suggest that no large amount of siliceous mineral matter was flowing through the entire vast slough region and thus a more nearby source is implied (though whether from tens or hundreds of meters, or kilometers [say from the mixed marls and silicates lying to the west], is not known). The decline in ratio abundance of siliceous to carbonate mineral implies that the sources differ. Carbonate can of course still be produced in a peat marsh where the siliceous minerals have long been buried.

Gumbo Limbo Hammock. The bayhead profile at Gumbo Limbo Hammock showed some similarities and some important differences (Figures 5-22 to 5-25). Considering the upper three-quarters of the organic sediment profile first, again there is a decline in mineral content (of both types) toward the surface. But this decline is slight and not steady, and both carbonate and siliceous mineral codominate within the mineral fraction. More intriguing is the apparent zoned nature of the mineral abundance, occurring in parallel with the gross stratigraphy: the mucky peat below with abundant and slightly more mineral matter of each type and thus in total, and the peat above with less though still abundant mineral. The abundance of carbonate throughout and especially toward the top is even harder here to explain, unless it is transported in from the marshes outside by whatever mechanism that had to have brought in the abundant siliceous matter.

The basal peat zone of the Gumbo Limbo site, below the peaty muck, adds still more evidence of early shifts or changes. In contrast to the Black Hammock bayhead, the *lowest* content of mineral matter is found in the earliest organic sediments just above the marl. It is as if the transport mechanism had not yet fully “turned on.” There is appreciable mineral content of both types, which also requires explanation, but more came later, and this during an extended period of mucky sediment formation. Did the peat sedimentation start in a small shallow solution depression, and only later did general water levels in the marsh rise above most of the higher bedrock surfaces to allow regular and prolonged above-ground flow? We would predict such peatland initiation in general in the southern Everglades, but only if the marlland had not typically filled such depressions already. (It would take multiple-point closely spaced probing and augering or coring at several sites in the marshes to adequately assess this.)

There is circumstantial support for an alternative explanation. Perhaps the mucky zone represents that enigmatic long middle part of the peatland era that has so much scattered but yet uncorrelated and unresolved evidence. Some notable examples are (1) resumed formation of marl along the Tamiami Trail and to some distance north and south, (2) Lake Okeechobee apparently overflowed much more vigorously into the northern Everglades, and (3) vegetation shifted slightly at Corkscrew Swamp and at The Savannahs (near Ft. Pierce) and around certain central Florida lakes (Altschuler et al. 1983, Gleason and Stone 1994). Winkler et al. (2001) noted other signs of such shifts within Shark Slough itself. If the middle zone rather than the basal zone here is the anomaly, then the peatland initiated by rising average water level, but was later influenced by a long period of altered hydrology, which eventually shifted fully or partly back to the earlier hydrologic conditions (but long before drainage). The approximate age of the intervening peaty muck zone (say roughly 3500 to 1000 BP, due to limited accuracy and precision of bulk sediment dates) is in general agreement with the shifts noted elsewhere.

Deep Peat Marsh. The vertical series from the thick marsh peat core (Transect 2, 800 meter mark) shows the strong presence of siliceous mineral just above the mineral muck at the base (Figures 5-29 to 5-32). Apparently the pre-peat marlland did not fully (or long) establish at this exact location and clayey residua from the prolonged previous dissolution of limestone, either nearby or far away, is found mainly instead. Farther up the core, it is a different matter: carbonate mineral matter is significantly present and becomes more abundant still in a thick zone nearer the top. In terms of tree island bayhead stratigraphy, it is clear that some marshes have had an abundance of carbonate mineral, with this possibly available for delivery by flow to the locations of present tree islands. That these latter locations mostly occur in the downflow lee of a pre-existing flow obstruction, the low rock mound now beneath the head, may be further circumstantial evidence for a role of flow. (Ficus Hammock and similar large elongated bayheads lacking the head of course suggest that such obstruction in not absolutely necessary, even if it does facilitate. A next step should be to examine stratigraphically a few distinctly shaped sawgrass strands.) The presence of the carbonate mineral matter does not prove that it was mobile though, as intermediate density marsh may be dense enough to form peat but sparse enough and well enough lighted in the water column to allow abundant periphyton growth and production of carbonate silt locally, as still happens today in places in Shark Slough (Olmsted and Armentano 1997).

The siliceous mineral matter almost certainly was introduced by flow from some upstream source. Organic precipitation from dissolved cations (in vascular plant cells or diatoms or sponges) and dust-fall both seem implausible as explanations under Everglades conditions (such presumably should have then occurred elsewhere as well in the Everglades). Unfortunately, removal of carbonates and organics in muck in a manner suitable to allow x-ray identification of unaltered minerals has not been done. Material is still available for these identifications. The presence of the siliceous matter is tentatively considered proof that flow somehow can introduce mineral matter to a location, though the ultimate origin is unclear (Mullet Slough? more siliceous-mineral-rich marly sediments on the west side of Shark Slough?), as is the exact mode of transport (suspended clay flowing with water? mineral-rich organic flocculent oozing along the bottom?). The alternatives deserve more rigorous testing (e.g., organic and perhaps especially decomposed cryptocrystalline or biogenic silica grains [plant phytoliths, diatoms, sponge spicules] or dust).

The other indication from the thickest peat marsh core is that carbonate mineral matter apparently became notably more abundant in a prolonged period within the latter part of the peatland era. The "apparently" delimiter is for one plausible but seemingly unlikely explanation. Mineral matter can concentrate relative to organic matter by partial degradation of the latter by bio-oxidation, say during the drainage decades. Northeast of ENP (beyond the East Everglades), it is known that drainage effects were pronounced enough to allow peat fires, and a loss of an uppermost peat zone is suspected for east of Krome Avenue (Gallatin et al. 1958). Still, there is yet no known strong indication for substantial peat subsidence, much less any appreciable drainage-era peat loss, for the peatland in the park itself (subsidence first compacts upper peat before any actual material loss occurs, and this compaction would not notably alter organic vs. mineral matter weight ratios). It is difficult to tell (without a ^{14}C date) whether the shift back to lower abundance at the very top represents possibly the drainage and water management era or merely an earlier end of a natural environmental stage (hydrological and vegetational). In any event, no matter when it ended or how, a long period of significantly increased local carbonate mineral production or receipt by flow is strongly suggested. Was this the ultimate carbonate mineral source in the present bayhead profiles, by means of flow? Or were somehow the areas of the present bayheads open enough to have periphyton growth and carbonate deposition in the immediate locality?

The shift to marl production just north of ENP for more than a thousand years indicates that some environmental shift was large enough to cross a threshold of marsh type or of annual surface oxidation. This almost certainly requires a reduction in low water levels and duration, the seeming opposite of what one would expect for enhanced flow (i.e., higher high water levels). However marl production is compatible with relatively deep water at high water, it just probably tends to produce a mucky marl or marly muck without strong seasonal drying, or a mineral-rich flocculent with no seasonal drying (for the last, using the vicinity of Gage 2-17 in WCA 2A as the analog). That these layers do not result from a plausible alternative, that is peat fire in marly peat or peaty marl, is pretty much proved by the common presence of snail shells and fragments, which would not survive such burning, and by the $\delta^{13}C$ values (ca. 0o/oo, which are much heavier than if the carbon were scavenged from atmospheric or soil CO_2 by alkaline ash from thermally decomposed marl).

Other Marsh Sites. Several additional marsh sites were cored near the tree islands investigated. This was to determine how closely to the surface the mineral sediments lay and thus determine if marlland or rockland marshes were likely potential source areas for minerals during organic sedimentation at the bayhead sites. One site, discussed in the radiocarbon section (Figure 5-27), may have been isolated for much of the period of interest but re-exposed briefly very roughly 1000 BP. Another site, north of Gumbo Limbo Hammock, showed relatively thick peat (93 cm) and has not been available as a potential marl sediment source for a considerable but unknown period of time (Figure 5-33). More intriguing even than the first core is one from north of Black

Hammock (Figure 5-34). This is marl all the way to the surface: a marl area patch (of unknown size) in an overall very large peatland. The immediate locality did not seem unusual (which would have been avoided) other than it was chosen for convenience in the wet prairie rather than the sawgrass just meters away.

Others have noted such local marl surfaces in Shark Slough (e.g., Olmsted and Armentano 1997, and a surveyor ca. 1920 in the present Tamiami Trail vicinity of the East Everglades of ENP, though that possibly may have been from generalizing the peat-marl-peat stratigraphy found widely there). Can these have remained marl marshes the entire time, never having been encroached by peat marsh? As Olmsted and Armentano (1997) note, their hydrology would suggest they be peatland. Were they uncovered by peat fire in relatively recent times? There is certainly no overt suggestion of this (say, compared to if these patches were notably deeper than the immediate surroundings, and perhaps had sharp if irregular edges as modern severe peat-burn areas in the conservation areas to the north often do). One might not notice edge characteristics as readily if the area were large, say many hectares to hundreds of hectares, but if a substantial thickness of peat were removed, it should be apparent in the vegetation and in water depth. If the removal of only thin peat uncovered the marl, though, the implication to tree island sedimentation is about the same as if it stayed marlland all along; it was a nearby and upflow of mineral terrain until relatively recently. How common are these patches of marl soil? One would assume they are not large and not highly abundant, or they should have been mapped or noted more strongly and specifically in the soil surveys (USDA-SCS/UF 1946, Gallatin et al. 1958). Still, ecologically and in sedimentary history, they may be important.

One final comment on the Black Hammock marsh core with marl extending all the way to the surface relates to relatively recent ecological change (i.e., is this somehow a relict marlland patch?). There is a zone of distinctly organic-stained marl lying beneath a top layer of typical light-colored marl (extending to the present surface) and lying above a similar typical light-colored marl (Figure 5-34). The organically enriched layer presumably represents somewhat wetter conditions relative to the top (and underlying) more typical marls. There has not been time to deposit the upper whitish marl layer in the drainage era. Plausibly, drainage conditions could have led to bleaching of a more organic stained marl, but the sharp upper boundary of the buried organic-stained layer argues against this. Maybe the marsh environment had changed late in the pre-drainage era. Olmsted and Armentano (1997) found elsewhere in Shark Slough fairly extensive places where surface sediments were distinctly more marly than the peat ("muck" in that reference) prevailing below. Did this whole wide area become drier in recent times, perhaps even before regional drainage? The possibility of relatively recent environmental change prior to the drainage era deserves more attention.

Other Sources? The hammock head as a possible source area for fine-grained sediment is appealing in that it lies just upstream and is raised, but this seems implausible. How could it account for so much volumetrically, as the heads are small and no ongoing mechanism for significant erosion is apparent? Tree tip-overs in storms bring some granular mineral material to the surface in the root mass (Figure 5-6), and certainly there is fine-grained organic matter generated by the aerobic decomposition of litter at the ground surface, but there is no ready way to get this entrained into the marsh waters except perhaps once or a few times per decade at highest water. Even then, the fibrous interwoven roots and peaty material just below the recent litter would be very resistant to erosion by slowly moving water (peat is even fairly resistant to direct wave attack in lakes and gulf shore). And while mineral-enriched sediment lies at shallow depth currently, it is not highly abundant at the surface on the heads (notably even now after extreme Hurricane Andrew passed right through this area and tipped many trees). If the archeological evidence for tree island hammocks suggested an intensive occupation for thousands of years, we might suspect that human forest clearing, campfires (especially), and attendant erosion played an important role, but the evidence is far more in keeping with occasional or season use, not permanence or high intensity. The hammock as a source of some particulate material downstream still deserves investigatory attention, but at present seems insufficient to explain the mineral or fine organic components in the tails. But if pre-drainage waters were higher (as might be suggested by the circumstantial evidence for waterlily abundance in the marshes in the past), and if the present hammocks have not lost much height in the drainage era (there is no clear evidence or suggestion they have), then it is at least possible that flooding of the hammock was considerably more common or flow there more vigorous than in the past century. But even so, the best guess would be for dissolved (or particulate) phosphorous or some other nutrient to be significant downstream in the present tail area, not a substantial mass of eroded and redeposited sediment. Still, the heads by their very location are obviously important somehow in the development of the tails, perhaps by nutrients and perhaps as a physical barrier to cross-marsh flow (others have suspected eddy effects on cross-marsh flow, presumably mostly at high water). We are left with the marshes upstream as the likely sources for any transported fine matter, organic or mineral.

Exposed limestone undergoing mostly solution erosion, and the surface residua of a long past pre-peatland era of such erosion, offered possible sources of noncarbonate minerals concentrated from traces in the limestone. Small amounts of particulate carbonate might be liberated as well. But younger, uncemented marl offered a most obvious source of the fine carbonates and possible of fine noncarbonate mineral matter (collected previously from the erosion of limestone). The limestone mapped for the immediate area (Miami Limestone) would be fairly low in noncarbonate minerals) but the Tamiami Formation in Big Cypress Swamp to the west and upstream in the distant sense of Mullet Slough has much more noncarbonate mineral. Even within Shark Slough, the westward part of the study area (near the tram road to the overlook tower) has sandy and less-cemented limestone near the surface (Olmstead and Armentano 1997) whose effect was noted in the cores from nearby Satinleaf Hammock (Figure 5-9).

Nature of Transported Particles? It seems implausible that particulates even as fine as clay could travel very long or far in suspension in these sluggish-water shallow marshes. For one, organic material or micro-organisms themselves would probably flocculate them. Movement in a flocculent seems more likely. Here, the coarser flocculent particles would be more easily baffled, but they also would, by their low density and larger sizes, resuspend more easily with renewed flow. The lower density of organic-rich flocculent particles may especially enhance movement of the less-fine mineral particles (if the carbonate crystals are silt size as in marl). The movement of flocculent at the bottom of a slough seems intermediate to the more dichotomous transport in suspension or by saltation (bouncing along the bottom) that is normally understood for movement of mineral particles in stream and rivers.

Flocculent formed in sloughs may be naturally enriched in carbonate at the onset (the noncarbonate mineral content is yet unknown). Most marsh peat seems to have formed mainly from intruded tissues (roots, rootlets, rhizomes, etc.) while detritus from the abundant above-ground tissues may be largely destroyed in the low water seasons of exposure. Deeper marshes have less frequent episodes of exposure and thus better preservation potential for the partially decomposed detritus. Waterlily sloughs have abundant above-ground tissues of a more succulent nature that tend to degrade to small more roundish particles rather than long firm fibers (e.g., waterlily leaves and bladderworts) judged by slough-bottom detritus. Where calcareous periphyton is abundant, there is additional contribution of organic matter without lignin-cellulose fibers and of abundant carbonate grains. While periphyton does not attach to waterlily itself for some ecological reason, waterlily sloughs can have abundant periphyton, often on floating bladderwort masses, and abundant mineral-rich flocculent detritus at their bottoms. This carbonate is probably more readily entrained into currents and moved than even individual mineral grains from an exposed marl surface, which by seasonal drying tends to aggregate particles and also tends to be capped by dried and fairly cohesive algal mats.

Extreme wind events can move a relatively large amount of floating organic material and attached periphyton from the surface of a slough into a windrow at the sawgrass edge. It is hard to envision this as a principal process as it cannot penetrate far into dense vegetation, and tails and strands are more or less symmetrical on their long axis, implying a downflow process.

In-Place Origin of Fine Organics and Carbonates? Note also that we cannot yet reject the possibility that the fine organics were simply generated in place by degradation. But they do not look right for that origin, and most are with a fairly homogeneous (for any few centimeters depth interval; it does vary more over larger separations) matrix of fibers, more so than one would assume for a later colonization and root-intrusion of an existing thick degraded mass. In at least one core, the least fibrous zone is near the top. (Separate AMS ^{14}C dating of fiber and fines would offer evidence here.)

If the organic fines were formed in place by microbial degradation of fibrous or more coarsely granular organic matter, this would imply one of three very different conditions, and perhaps a fourth acting alongside (the last being greater above-ground detritus production, as opposed to root intrusion): 1) long seasonal aerobic conditions by emergence, degrading but not eliminating detrital organics (cypress swamps, where deciduous debris is abundant, can sometimes form fine-grained mucky peats: Corkscrew Swamp is an example), or 2) a prolonged era of emergence (frequent drought or decades or centuries of reduced rainfall) whereby pre-existing peats are degraded microbially but the organic matter not lost completely, or 3) semipermanent flooding where water column detritus is degraded to fine material but most of this is preserved by avoiding subaerial exposure. Examples thought to represent each of these can be found in southern Florida. Or, finally, perhaps the fine-grained material was formed elsewhere and transported in. If the hammock heads are discounted as likely sources, then the flocculent material in the sloughs is the most obvious possible source.

Even the carbonate component has some remote possibility of origin in place. It seems unlikely, though not impossible, that sparse marshes occupied the locations of the present tails well into the peatland era and deposited peat sediment enriched in marl from local production in periphyton. But the hammocks existed already (or at least their basal rock mounds) and most areas downflow of mounds now seem to be denser marsh rather than sparser. Still, some bayhead tree island peat mounds have nothing out of the ordinary for the surrounding marshes downstream (are they too young?). And the unexplained recent opening up of the vegetation in the farther parts of the mixed shrub and marsh tail downflow of one hammock shows that we do not understand the range of dynamics here. A peat burn in an original slightly raised, thus more-susceptible, sawgrass ridge might readily deepen the location and allow more open marsh along with periphyton growth and carbonate sedimentation. But could it remain open for centuries? And could this be a general explanation for a number of tree islands? It doesn't seem likely. We are left with seeming transport of carbonate from an outside source unless sparse marsh could have long occupied these sites now of forest and whose closest geographic affinities among marshes is dense sawgrass, not open marsh with periphyton abundant.

Non-Pollen Microfossils

Many of the organisms or their parts preserved in pollen processing have not been comprehensively studied in an ecological framework. Few studies have addressed their occurrence in surface soil samples for which biotic and abiotic parameters can be established. Thus, our knowledge of the environmental context of many of the non-pollen microfossils described below is derived from their co-occurrence with other fossils. In this study, paleoenvironments were determined on the basis of pollen and plant spores in samples (see later), avoiding circular reasoning in assessment of the non-pollen microfossils.

Algae

Botryococchus. *Botryococchus*, part of the Family Botryococcaceae within the Order Chlorococcales, are colonial green algae found in temperate to tropical regions. Most reports of this form are from paleoecological studies in which shallow and temporary waters are interpreted (van Geel 2001). However, there are modern reports of its occurrence (primarily *B. braunii*) in large (presumably deep) lakes, sometimes as a bloom. On his website, Dr. Jiunn-Tzong Wu reports allelopathic effects of *B. braunii*, citing a bloom that was associated with massive fish death in a lake of eastern Taiwan (http://botany.sinica.edu.tw/english/personnel/427-n.html).

Pediastrum. Species of *Pediastrum* can be differentiated in paleoecological studies, but the small number and condition of *Pediastrum* colonies found here did not merit differentiation. These green algae are thought to generally occur in shallow waters (Komarek and Jankovska 2001). Some species have value as indicators of paleotemperature and others of pH; a high pH indicator species, *P. anugulosum*, was identified in some samples from this study. Selective sieving (i.e., separating large-size fractions) may be useful in concentrating *Pediastrum* colonies in future research.

Type 209 and 128. These are microfossils of unknown taxonomic affinity described by van Geel (2001). They are probably algal spores. Van Geel (2001) reports that in paleoecological studies, type 128 is associated with shallow eutrophic fresh water, probably slowly moving water. These types occur in the cores from Black Hammock and Gumbo Limbo, but not Ficus Hammock. Their occurrence is primarily in slough and sawgrass marshes, although there is a minor occurrence (1%) of Type 209 in the buried tree island deposit of the Gumbo Limbo core.

Zynemataceae. The Zynemataceae are filamentous green algae, found in shallow stagnant water or even wet soil (van Geel 2001). Spores, found as microfossils in this study, are resistant to desiccation (van Geel 2001) and thus may reflect the presence of seasonal droughts. Spores of the genera *Mougeotia* and *Spirogyra* were identified in this study. Taxonomic affinity of spores named "Zygnema-type" and "Zygnemataceae zygospore" within the Zygnemataceae family is fairly certain. Algal form 1 (joint) is likely produced by a Zygnemataceae taxon. *Spirogyra* and *Zygnema*-type zygospores were the only Zygnemataceae zygospores found in the Ficus Hammock core. They also were found in Black Hammock and Gumbo Limbo and in all types of deposits. *Mougeotia* occurs at low abundances throughout the Gumbo Limbo core, but only at the base of the Black Hammock core. Algal form 1 occurs in low percentages in sawgrass and slough deposits of Gumbo Limbo. It occurs in the lowermost sample of the surface tree island deposit of Gumbo Limbo and is absent from the tree island deposit of Black Hammock. Its highest percentages occur in slough deposits. Zynemataceae zygospore 1 only occurred rarely in Gumbo Limbo.

Fungi

Sorariales Ascospores. Of spores produced by the Sorariales, some could be identified as produced by the genus *Tripterospora.* Van Geel et al. (2003) note that this fungal group is mostly coprophilous, thus may indicate high density of fauna. Sorariales ascospores were found in all three cores, but only in tree island deposits. They were not found in the buried tree island deposit of the Gumbo Limbo core. They tend to increase towards the surface and are probably and indication of elevation of the island, as their source is likely wildlife whose use intensifies when the islands are sought as refuge during high water (Meshaka et al. 2002).

Glomus. These microfossils are chlamydospores of the fungus genus *Glomus*. Species of *Glomus* are known to be mycorrhizal, for example, *G. fasciculatum* occurs with the roots of *Betula* (van Geel 2001). *Glomus* was found in all three cores. With the exception of the two lowermost samples from Black Hammock (identified as sawgrass marsh), the occurrence of *Glomus* was exclusive to tree island deposits. *Glomus* was never present at the base of a tree island deposit and absent from the buried tree island deposit in the Gumbo Limbo core. Declines in percent *Glomus* in the surface are expected as it is associated with plant roots. It is assumed that *Glomus* is in mycorrhizal association with one or more of the tree island arboreal taxa. Connor et al. (2002) note that N-fixing mycorrhizae associate with roots of *Myrica cerifera*, which could be the host for *Glomus*.

Other Spores and Fruiting Bodies. A number of microfossils were clearly of fungal origin, but taxonomic affinity was not established. Some are probably associated with taxa that require dry conditions (i.e., not saturated soils). Non-coprophilous fungi are most abundant in tree island deposits, but are not restricted to them. The percent of these fungal forms generally increases towards the surface of tree island deposits, presumably in response to a drier environment.

Cyanobacteria. Hyaline sheaths of *Gloeotrichia* were observed. This is a nitrogen-fixing cyanobacteria (van Geel 2001). *Gleotrichia* occurs in most samples of the tree island deposits of Black Hammock and Gumbo Limbo, but is absent from any sample analyzed from Ficus Hammock. When *Gleotrichia* was found in a deposit not interpreted as tree island origin, pollen from Poaceae or *Typha domingensis* was also found. These were often discrete occurrences in deposits that probably pre-date post-European settlement influences. This suggests an increase in the phosphorous-nitrogen ratio in the ecosystem.

Testate Amoebae. Testate amoebae are protozoans that form tests, or shells (Beyens and Meisterfeld 2001). The nature and morphology of the test is the principal means to differentiate taxa. Tests may be calcareous, proteinaceous, and agglutinate. Agglutinate forms cement foreign material such as mineral particles or diatoms to form their test. Calcium carbonate, silicate minerals, and diatoms are dissolved during conventional palynological processing, thus only test linings are usually visible, and taxonomic designation is severely limited. In this study, testate amoebae were observed with tests composed of charcoal fragments. The category "testate amoebae" in microfossil diagrams includes both test linings and the charcoal-agglutinated forms. Testate amoebae were found in all three cores, but only in deposits identified as tree island origin, including two samples from a buried tree island deposit in the Gumbo Limbo core. Highest percentages of testate amoebae were consistently found at the surface of the modern tree island deposits.

Paleoenvironmental Interpretations

Gumbo Limbo Hammock. Abundance of *Nymphaea* (Figure 5-37) and other submerged aquatics (not shown on the diagram) suggest that the two lowermost samples from Gumbo Limbo Hammock were deposited in a slough environment, but abundance of algal forms is very low (Figure 5-38). The cyanobacteria *Gleotrichia* is present (4-11%) in this slough section, the only occurrence of *Gleotrichia* in any core slough section. Another oddity is the appearance of *Typha domingensis* pollen (>4%) in this section.

By 103 cm, slough is replaced by sawgrass marsh, indicated by the aggregate sum of pollen of *Sagittaria, Cladium* and undifferentiated Cyperaceae (>4%, Figure 5-37). In this section, charcoal increases to one of three maxima in the core (Figure 5-38). The relative abundance of algae increases towards the top of this section, until sawgrass marsh is eventually replaced by slough at ~58 cm, as indicated by 6% *Nymphaea* pollen. At this point, the algae *Botryochoccus* and *Pediastrum* reach their peak abundances in the core. This slough environment, indicated by a single sample, is replaced by sawgrass marsh, again indicated by a single sample (53 cm). The abundance of both algal forms and charcoal are decreased in this section.

At 43 cm depth, the environment is enigmatic; pollen is dominated by Chenopodiaceae-Amaranthaceae type. Willard et al. (2001) report high percentages of Chenopodiaceae-Amaranthaceae type at the edges of tree islands, an interpretation consistent with the existence of tree island indicators in the sample above this depth.

Increases in Polypodiaceae spores and occurrence of *Cephalanthus* and *Salix* pollen at 42 and 36 cm depth indicate development or expansion of a tree island community. This tree island deposit contains the earliest appearance of testate amoebae and high abundances of *Gleotrichia*.

The environment reverts back to sawgrass marsh by 31 cm depth, where *Sagittaria* pollen increases to 5% and Poaceae pollen reaches 12%, the highest abundance found among all samples in the three cores. Conditions seem to become continually drier towards the surface. The abundance of Polypodiaceae spores increases through this section. *Osmunda* is temporarily important (>35% at 20 and 14 cm) in the fern community, but the percentage of its spores decreases to trace amounts towards the surface of the core. This is similar to the decline of *Osmunda* in youngest sediments of the Ficus Hammock bayhead core.

Arboreal pollen constitutes <1% of the pollen sum during the initial phase of the modern tree island community. Increases are first seen in *Cephalanthus*, then *Salix*, followed by *Myrica* and *Chrysobalanus*. Increasing dryness also is indicated by the increase in fungal spores and fruiting bodies, although Sordariales ascospores are present in trace amounts.

Black Hammock. The lowermost samples (>120 cm depth) contains >4% pollen of *Cladium*, undifferentiated Cyperaceae (which could be *Cladium*) plus *Sagittaria* (Figure 5-35), thus meeting the threshold reported by Willard et al. (2001) for sawgrass marsh. However, the bottom sample is unique, with high proportions of *Pinus* pollen (~60%) and high abundance of algal type 128 and presence of Zygnemataceae spores (Figure 5-36). (*Pinus* pollen is abundant in the atmosphere and its relative importance is high when local pollen production is low.) These suggest an aquatic environment, and Poaceae pollen >5% may indicate a wetland with emergent plants. The presence of *Glomus* and other fungal spores probably indicate seasonal dryness. This is consistent with its origin in a marl, though one with slight enrichment in organic matter. This sample came from slightly above a date of 6280 BP (Figure 5-15) and may give the first reported paleovegetation data from the middle-Holocene-age marlland that preceded the peatland in the Everglades. Poaceae pollen is rare in any of the three cores, as is the presence of *Gleotrichia* in any deposit other than that from tree island ecosystems. The co-existence of this nitrogen-fixing cyanobacteria and Poaceae suggests a nutrient status different from that found in more recent sawgrass environments (i.e., a higher phosphorous/nitrogen ratio).

At 152 cm depth, Chenopodiaceae-Amaranthaceae type and *Pinus* pollen dominate (Figure 5-35). The level of pollen from emergent wetland plants is below the threshold for designation of sawgrass marsh, but this level was not designated as a discrete section. With the exception of *Botryococchus* and *Mougeotia*, abundance of most algal forms at 152 cm (Figure 5-36) is similar to the sawgrass marsh deposits above and below this.

An increase in *Nymphaea* pollen at 110 and 98 cm signals a slough environment (Figure 5-36). At 87 cm, *Nymphaea* pollen declines and Chenopodiaceae-Amaranthaceae type dominates the pollen spectra at >80% (Figure 5-35). Charcoal and algal forms all decrease at this depth. The origin of this sample is enigmatic. Willard et al. (2001) report high percentages of Chenopodiaceae-Amaranthaceae type at the edge of tree islands, but samples available do not indicate transition to a tree island environment. It is possible that a tree island deposit was nearby, but not directly sampled. Alternatively, the deposit could have been lost to fire, as charcoal abundances rise sharply in the next sample (Figure 5-36). Instead, the next sample (~76 cm) indicates return of a slough environment. The slough deposit continues up to 42 cm as indicated by >4% *Nymphaea* pollen. *Typha domingensis* and Poaceae pollen occur within this section, albeit at low percentages. Interestingly, the nitrogen-fixing *Gleotrichia* reappears at these same depths.

The next two samples (32 and 29 cm depth) possibly represent (using the modern plant community analogues) the edge or expansion of an existing tree island as Chenopodiaceae-Amaranthaceae type pollen dominates at 32 and 29 cm-depth. The minor presence of fern spores supports this interpretation. Algal forms and all other pollen taxa decline except *Osmunda* and Asteraceae-Tubuliflorae type.

A tree island community is suggested as the total percentage of fern spores becomes >20% by ~22 cm depth. As in the Gumbo Limbo and Ficus Bayhead cores, *Osmunda* spores decline towards the surface. The local arboreal pollen is first dominated by *Salix*, then *Cephalanthus* and *Myrica*, followed by *Chrysobalanus* pollen. In this section, algal abundances decrease and fungal forms increase towards the surface, indicating decreased soil moisture.

In the Black Hammock core, *Ambrosia* pollen type occurs above trace levels only within the tree island deposit. Its peak relative abundance occurs at 11 cm and it declines abruptly above this.

Ficus Hammock. Low pollen abundance and low pollen counts limit interpretations of this core. The number of fossil plant taxa is lower, as well as non-pollen microfossils. Neither slough nor sawgrass marsh is indicated by pollen and plant spores (Figure 5-39). The lower half of the core is dominated by ≥70% Chenopodiaceae-Amaranthaceae type. Above 80 cm depth, a tree island ecosystem is clearly indicated. Polypodiaceae fern spores are important throughout this section, but the importance of *Osmunda* is limited to ~32 to 50 cm depth. The first arboreal pollen to appear above trace amounts is from *Cephalanthus*, followed by *Salix* then *Myrica*. *Chrysobalanus* appears about the same depth as *Myrica*, but its abundance remains low, as does pollen of *Ilex*. What is interesting, however, is the increase in abundance of *Quercus* towards the top of the core. This is the highest proportion of *Quercus* observed in the three cores. This is a bit enigmatic, as oaks are not reportedly common at sites far in the Everglades interior. *Quercus*, is wind-pollinated and could be considered part of the regional background pollen “rain”, but if so this variation should appear in all three cores.

There are few algal forms recorded in this core (Figure 5-40). *Botryochoccus* is present throughout the core, but at low percentages. *Spirogyra* occurs in only two samples and Zygnema-type zygospores in five samples.

Although found in the tree island deposits of Black and Gumbo Limbo Hammocks, the cyanobacteria *Gleotrichia* was not found in the Ficus Hammock core. The mycorrhizal genus, *Glomus*, however, was found in greatest abundance of the three cores. Both Sordiales ascospores and undifferentiated fungal spores and fruiting bodies increase in abundance towards the surface of the core, reaching abundances that are 30 (Sordiales) and 60 (undifferentiated fungus) times higher. High abundance of fungal forms are normalized to the pollen count, thus actual concentrations may be low. The high proportion of fungal forms does support an assumption of dry conditions, explaining low algal counts. During periods of high water, wildlife are known to congregate on dry tree islands (Meshaka et al. 2002). Do they also use the flooded bayhead? If so their dung is probably the source of the abundant coprophilous Sordariales ascospores.

Ambrosia-type pollen makes a curious occurrence towards the surface of the tree island deposit. A single grain of *Ambrosia* type was found at 47 cm depth. Its abundance remains low, but peaks at 8.3 cm depth. Above this, it declines and no *Ambrosia*-type was counted in the surface sample.

The exceptionally dry conditions (amongst the samples in this study) probably enhanced decomposition of pollen and other organic constituents. This conclusion is supported by the observation of a predominance of amorphous organic matter in palynological preparations from the Ficus Hammock core.

Phosphorous in Tree Island Soils

Observations of the nitrogen-fixing *Gleotrichia* may help to explain the enigmatic soil nutrient status of hardwood hammock communities reported by Ross et al. (2002). They measured high levels of phosphorous in tree island soils, relative to surrounding areas. Because these levels are exceptional, they are being validated by analysis of external labs. Besides being a sampling artifact, Ross et al. (2002) posed three hypotheses to explain high phosphorous in tree island soils: 1) selective groundwater transport; 2) contributions from bird guano; or 3) selective loss of nitrogen as leaf litter decomposes. *Gleotrichia* presence is fairly restricted to deposits containing pollen of *Typha*, Poaceae, and particularly, tree island species at Gumbo Limbo and Black Hammocks. Higher concentrations of phosphorus are supported by the palynological study of the tree island soils, verifying that they are not an artifact.

A critical observation is that, within tree island deposits, the relative abundance of *Gleotrichia* is highest in the *lowermost* samples of these two surface tree island deposits. The presence of nitrogen-fixing bacteria in the earliest stages of the local tree island ecosystem suggests that increased P/N occurs very early in tree island development, and thus is not a result of a slow, cumulative process, such as selective groundwater transport. The decline in abundance of *Gleotrichia* as the tree island ages is further evidence negating the first hypothesis.

Pre-European Human Disturbance?

The appearance of *Ambrosia* type pollen within the surface tree island deposits of Black and Ficus Hammock cores is curious. Unless the tree island flora includes *Iva*, *Xanthium* or *Ambrosia*, then this probably indicates human disturbance. *Ambrosia* is a sun-loving terrestrial weed, and increases in its pollen are associated with land clearance (Brugham 1978). If land clearance is ephemeral (e.g., secondary succession is allowed to proceed), *Ambrosia* pollen declines (Chmura et al. 2001). Thus, the appearance of *Ambrosia* type pollen may be associated with European clearance of the natural landscape throughout southern Florida. However, *Ambrosia* pollen declines again towards the surface, inconsistent with the continued development of the region. An alternative explanation could be that the source of *Ambrosia* type pollen is *Iva*. Long and Lakela (1971) report at least one *Iva* (marsh elder) species (*I. microcephala*) to occur on disturbed and damp sites in southern Florida (plus, in the same tribe of Asteraceae, several species of *Melanthera* characteristic of wet freshwater sites). Smith (1992) reported, however, that North American Indians cultured *Iva* for consumption. In the Everglades, the only practical location for horticulture would be tree islands, but there mainly on the hammock portion. One of us (GLC) has collected reference material from *Iva annua* (the agricultural species) held in the National Herbarium, Smithsonian Institution, Washington, D.C., USA, and plans to compare this to the suspect grains in the tree island core.

Summary and Conclusions

Environmental Change

What is most interesting is that only in the Ficus Hammock core was change unidirectional, suggesting a general increase in elevation (or decrease in water levels). Paleoenvironmental change in the Gumbo Limbo (110 cm) and Black Hammock (205 cm) cores was not unidirectional. Both sites have experienced major ecological shifts, in the context of the Everglades system. If Shark Slough marshes, or at least the sloughs themselves, were formerly *Nymphaea*-dominated, one must keep in mind the possibility of some peat shifting by rafting of *Nymphaea* peat, which would cause major shifts in microfossil stratigraphy (the slough deposit wedged between two sections of sawgrass marsh at Gumbo Limbo Hammock is an example of a suspect stratigraphy). Alternatively, hydrological shifts may have led to that vegetational shifting in more normal manner. Problems or uncertainties of this sort, inherent in an initial investigation such as this one, can be resolved by more detailed study that correlates pollen stratigraphies from multiple cores on individual tree islands.

The occurrence of deposits representing tree island communities overlain by sawgrass marsh deposit (Gumbo Limbo) and, possibly, a microfossil assemblage characteristic of tree island edges overlain by a slough deposit (Black Hammock), suggest external (allogenic) forcing. These shifts suggest hydrological changes which could be driven by climatic change or decline in surface elevation after fires. Charcoal in all three cores indicates that fire has been common throughout the available history of the sites. Additional microscopic analysis of charcoal (as size fractions) may provide further insight into the role of fire.

Some indicators suggest that the surface tree island deposits of all three sites became gradually drier throughout the history of the deposit. Increase in pollen abundance of woody species to a large degree reflects the decreasing flood tolerance of the source vegetation that has been suggested by Ross et al. (2001a). *Cephalanthus* pollen appears first, followed by *Salix*, then *Myrica*, and finally *Chrysobalanus*. Although present in two cores, *Ilex* pollen remains in low abundance, and its first appearance does not align to its flood tolerance ranking. Increased abundance of fungal spores may also be an indicator of soil moisture, but studies of surface soils from a range of modern tree island vegetation zones are needed to test this theory.

Variation in nutrient status is also suggested by occasional appearance of the nitrogen-fixing *Gleotrichia* in deep section of Black Hammock and Gumbo Limbo. Co-occurrence of *Gleotrichia* with *Typha domingensis* and/or Poaceae pollen indicates increased phosphorous abundance at select times prior to European disturbance in the region.

Ecological Change During and Just Previous to the Drainage Era

The most dramatic finding is that the bayhead forests of the two typical, large two-component tree islands (Black and Gumbo Limbo Hammocks) occupy areas that were marsh throughout much of the peatland era, succeeding to forest only long after the peat marshes had arrived. Willard et al. (2002) found similar stratigraphy in tails of two two-component tree islands in WCA 3B just north of Northeast Shark Slough of ENP (note: their "Gumbo Limbo Island" is a different one than that investigated here). Kremer and Spackman (1981) found marsh peats at depths beneath shrub or forest peats in about half the cores from an elongated tree island in extreme southwestern Shark Slough. The main bodies of the tree islands may be much younger than the peat marshes and far younger than the nearby tree islands that likely existed on the raised hammock area. The latter existed perhaps as early as when the surroundings were of rockland marsh, prior to the marlland marsh. To verify this will require dating the base of tree island deposits from the hardwood hammock through the bayhead and bayhead swamp.

The recent nature of the tree islands raises many questions. Main among them is what triggered the succession to forest, and what shaped that island? There is limited evidence that succession involved shaping and initially raising (shallowing) of the tail area as a sawgrass strand. However, sawgrass pollen is not abundant immediately below the incipient stages of tree island, and pollen of other emergent marsh plants is abundant in places (e.g., *Sagittaria*). Another important finding is that *Nymphaea* was important in the marshes that now occupy the tree island site. This is in contrast to the marshes of today in which emergent plants are more important. An obvious question is, what vegetation predominated in Shark Slough at that time, in the areas that are still marsh? Was it deeper *Nymphaea* marsh, where perhaps flow and transport were facilitated relative to the more baffled marsh waters of today? Perhaps even flocculent production was greater.

The surface 10 cm of the profiles show distinct shifts in individual taxa. The assemblage changes are not large and the overall interpretation remains as tree island, but changes in individual taxa suggest some recent changes in the forest stands. The suggestions of very recent changes at Black Hammock's bayhead forest include an apparent shift from *Myrica* to *Chrysobalanus* among the shrubs, an increase in grasses, and a decrease in ferns with Polypodiaceae-type spores (Figure 5-35). Oddly, *Utricularia* (bladderworts) are indicated in this top layer. Grasses, *Utricularia*, and sedges suggest some reasonably direct sunlight at times during the day on the ground layer or water surface, thus an open canopy in the woody vegetation. An open canopy with such light-loving plants below, including *Utricularia*, is given as a characteristic of many bayhead tail forests in Shark Slough, termed "bayhead swamp forest" by Olmsted and Armentano (1997). The sun loving taxa tended to increase as *Salix* and *Typha* declined and *Myrica*/*Chrysobalanus* rose, suggesting a quite recent establishment of that typical condition here. To ascribe any changes here to drainage or water management is tenuous, because from 20-30 cm depth down to the top of the presumed ash layer, there is a suggestion that there was a long-term recovery from that extreme disturbance. Thus continued change rather than stability might be expected even without drainage or water management effects. The age of the zone below the surface 10 cm apparently had *Typha* and *Salix* among the dominants, either mixed together or locally segregated. *Typha* produces abundant wind-blown pollen, and it may not take a very large population to produce the abundance of pollen found here. In today's landscape *Typha* seems to occur mainly in patches rather than intermixed with other marsh plants, so a local dominance or co-dominance (e.g., with willow) is suggested. Both taxa are known frequently to succeed after disturbance, perhaps particularly after peat fire that deepens the returned water a bit and liberates trapped nutrients (presumably P). Any extremely local disturbance, accidentally encountered, where *Salix* and *Typha* might also have been common, such as an ancient alligator wallow, would likely not have persisted long (it also could be revealed by noncorrelation in multiple cores in a more intensive study). *Nymphaea* slough clearly occurred before the presumed severe peat fire, but remember that considerable record is lost in a peat burn and whether this "lost era" was of tree island, sawgrass, or slough peat is unknown.

Gumbo Limbo Hammock bayhead shows nearly the opposite shifts in the surface 10 cm (Figure 5-37). (This indicates the value in examining several seemingly typical tree islands in an initial study rather than more intensively studying just one example, though that is the obvious next step.) Polypodiaceae-type ferns increased dramatically and the decrease in sedge and *Sagittaria* may merely be in artificial (arithmetic) response to that. But an increase and then decrease in *Myrica* in these late times seems real (unexplainable merely by shifts in others). The dilution by regional pine input to traces suggests prolific pollen and spore production in the bayhead forest environment. (This was not, as is sometimes the case in the Everglades, merely by exceptional abundance of Cheno-Am pollen, for it too dropped noticeably.) The overall trends may be the further slow successional development and closing of the canopy of the bayhead forest.

More pronounced shifts occurred at the base or just prior to the surface 10-cm zone though. Pine pollen briefly peaked, as did Cheno-Am pollen, indicating lesser dilution by local pollen production and perhaps more open conditions. The proportion of *Osmunda* spores dropped precipitously, while Polypodiaceae-type fern spores notably declined. *Cephalanthus* pollen increased, as did sedges and *Sagittaria*, and apparently not just as arithmetic artifacts. A disturbance leading to more open vegetation is suspected, especially in view of the older trends that were temporarily reversed. The age is unknown, though at ca. 10 cm, it is at least feasibly within the drainage era or represents its start. But lowered water levels of themselves would be expected more to enhance tree growth and raise and close the canopy. Given no early historical era of high water to allow the alternative (i.e., tree-island "drowning" and opening of the canopy, as is seen today in southern parts of the water conservation areas), it is again tempting to interpret severe fire, but here without a visible ash layer. No charcoal-rich zone was seen here, but these are hard to note visibly in profiles of the unusually black peats of this area and typically are thin and often missed between discrete pollen samples. (A next step should be to examine the entire upper 20-30 cm at high resolution (i.e., 1-2 cm).

The recent history of Ficus Hammock represents a well-established tree island with several woody taxa all through this period, which may have been subject to some late changes. In its surface 10 cm, first an increase in *Salix* pollen and then a decline in *Salix* and increase in *Myrica* along with a perplexing, distinct rise in *Quercus* pollen at the top. The chance of *Quercus* actually growing here seems remote, though *Quercus* grows on another type of tree island to the southwest in Shark Slough (Olmsted and Armentano 1997). Isolated, locally rare species are seen on occasion on tree islands (e.g., pine and cabbage palm in the northeastern Everglades). A notable peak in charcoal occurs in the surface sample. A rise in pine and *Sagittaria* at ~10 cm depth may indicate some opening in the canopy, or may be an artifact of the decline in Polypodeaceae-type ferns spores. (The ecology of ferns on these tree islands remains largely unknown.)

Ficus Hammock exhibits a thicker upper deposit with a tree island-like pollen assemblage and probably shows what a bayhead sequence looks like without significant loss of peat record by fire. But even here, again at ca. 30 cm depth, is evidence of a pronounced shift: a distinct stage of abundant *Salix*. This is compatible with occurrence of a severe fire and likely some peat fire. However, this interpretation is complicated by the shift from distinctly mucky peat (below) to fibrous peat (above) at the same depth. Which best represents the control? Did the change in vegetation shift the nature of the sediment (did the onset of abundant *Salix* itself start to produce a more fibrous peat?) or did an external control (likely hydrologic) impose both changes?

Salix reportedly has succeeded burned out tree islands elsewhere. Could intense vegetation fire even without peat fire produce such late change to willow in Ficus Hammock before the final succession to the vegetation of today? Wax myrtle is fairly tolerant of above-ground fire (it has to be, as it is highly flammable), and even such trees as holly (*Ilex*) can recover by stump sprouting. More examination of fire ecology literature and inquiry among experienced observers is necessary here. It is possible that severe vegetation fire can so set back the existing trees to their stumps that *Salix* might gain a foothold between them, only much later to be out-competed by them.

In all three tree island profiles, among the strong evidence for vegetational change late in developmental times, but likely occurring before the drainage era, is a rise to importance of *Osmunda* and then a decline in importance by modern times. More information on fern distribution and ecology under southern Everglades conditions (and more reference spore material from important local genera and species) have strong potential for better understanding these longer term but late stage changes (if not modern shifts).

In summary, there were some readily detectable late stage pollen shifts (and thus by inference, some vegetation and environmental shifts) in the surface ca. 10 cm of sediment, some pronounced changes in the upper few 10s of centimeters below that. The longer term history is of tree island forest or at least open canopied bayhead swamp forest, *sensu* Olmstead and Armentano (1997), originating only long after the peat marshes arrived and replacing a peat marsh at the immediate site. The abundance of charcoal in the zones lying just below the surface layer with woody plant pollen common is very suggestive of sawgrass abundance prior to woody plant colonization. Finally, these marshes often through time contained appreciable to abundant *Nymphaea*, at least local to the coring sites.

Directions for Future Research

We have identified four possible directions for future paleoecological research:

(1) Interpretations of environmental change have been limited by the lack of modern analogues for different tree island communities. Future research should include the description of a pollen

and microfossil assemblage from surface soils of well-described (e.g., cover, dbh, canopy) vegetation units. This information will support future tree island studies and a second interpretation of the data obtained in this study.

(2) To detect recent changes, higher resolution samples are needed in the surface 20-30 cm. Samples should be collected sequentially, at 1 cm thickness. To make this high resolution sampling reasonable, actions must be taken to minimize core compaction.

(3) For finer-precision work, dating of bulk samples should be avoided to prevent the problem of contamination of younger roots into lower deposits. Selection of macro-remains of emergent plants (e.g., seeds of sedges and *Sagittaria*) for AMS dating would avoid such contamination (and in marls, avoid any problem associated with introduction of “old” carbon from dissolution of carbonates).

(4) Lead-210 and cesium-137 dating may be useful.

Biological Aspects

6

Vegetation Structure and Composition in Relation to the Hydrological and Soil Environments in Tree Islands of Shark Slough

Jay P. Sah

Introduction

Tree island vegetation in the Everglades has continuously been affected by management-oriented changes in water flow pattern (McPherson 1973, Alexander and Crook 1984, Higer and Kolipinski 1988, Heisler et al. 2002). The Water Conservation Areas (WCAs) have a long history of over-drainage and/or flooding, and their current hydrological regime differs from that for Shark Slough. Prolonged high water levels in WCA 2 and 3 due to impoundment and water management practices have been considered important factors in the decline in the number of tree islands in these areas (Schortemeyer 1980) and in the change in vegetation on the existing islands (Wetzel 2002). During the high water event of 1994-95, which caused extensive, prolonged flooding in the southern Everglades, Guerra (1997) observed widespread symptoms of flooding stress in tree species occurring on tree islands within WCA 2 and 3; in contrast, Jones et al. (1997) reported little effects on tree island vegetation in Shark Slough. In a study of plant communities on tree islands in WCA 2 and 3, Wetzel (2002) noted that, besides hydrology (and fire), there is little known about the importance of other environmental and biological factors that potentially affect tree island vegetation.

The typical, large tree island in Shark Slough consists of several different plant communities: tropical hardwood forest (“hammock”), bayhead forest, and bayhead swamp forest (Armentano et al. 2002). Several studies have described the composition of these forests (Davis 1943, Egler 1952, Loveless 1959, Olmsted et al. 1980, Craighead 1984, Olmsted and Loope 1984, Olmsted and Armentano 1997, Armentano et al. 2002), but few studies have documented how the vegetation is influenced by environmental factors, such as soil and hydrology. Armentano et al. (2002) concluded that species composition of tree islands in the slough is primarily determined by hydrology, but also recognized the need for studying the influence of soil characteristics on plant responses to hydrologic regimes.

Shark Slough tree islands are generally associated with a bedrock outcrop lying under the “head” of each island. Many of these islands also consist of a “tail” believed to be developed from the accumulation of peat downstream of the head. The various forest communities are adapted to the hydrologic regimes that vary with the elevation gradient existing primarily along the long axis of each island (Armentano et al. 2002). Soil characteristics on this type of tree island also vary owing to the differences in foundation of the “head” and “tail” portions and their associated vegetation (Mason and van der Valk 2002, Chapters 3 and 5 of this report). Variation in soil type, depth, and nutrients, in turn, are believed to affect vegetation composition and development, either directly or indirectly by influencing the responses of vegetation to the hydrologic regime (Duivenvoorden 1995, Ross et al. 2003, 2004).

Plant species growing along a narrow range of elevation gradient on Shark Slough tree islands vary in their tolerance to flooding (Armentano et al. 2002, Chapter 8 of this report) and are sensitive to changes in water levels. Therefore, tree islands have great potential to be used as indicators of hydrologic conditions, allowing managers to predict the responses of tree island vegetation to various hydrologic changes that are inevitable during restoration under the Comprehensive Everglades Restoration Plan (CERP). To realize this potential, however, it is important to study the variation in structure and composition of tree island plant communities in relation to varying conditions of hydrology, physical and chemical soil characteristics, and other environmental and biological factors.

Most vegetation studies of the greater Everglades have emphasized wetland vegetation (Davis 1943, Loveless 1959, Alexander and Crook 1984, McPherson 1973, Zaffke 1983). The few studies on tree island vegetation (e.g., Armentano 2002, Brandt et al. 2002) provide only a general description of plant composition and structure and lack in-depth analyses of vegetation:environment relationships. Some quantitative studies of tree island vegetation have been proposed or undertaken on tree islands within WCA 2 and 3 (van der Valk et al. 1998, Sklar et al. 2004). In addition, Wetzel (2002) and Heisler et al. (2002) have taken a quantitative approach in their studies of tree island vegetation in the WCAs. In view of the fact that Shark Slough tree island vegetation has not been the focus of any in-depth ecological research, the objectives of this study were (1) to describe the structure and composition of major plant communities within several Shark Slough tree islands, (2) to identify major environmental factors that underlie the patterns seen, (3) to examine the association of the structural patterns of these plant communities with recent hydrologic conditions, (4) to determine the consistency of these relationships among various islands, (5) to determine water level optima for major woody tree and shrub species and their seedlings occurring on tree islands, and (6) to compare the productivity of the various tree island plant communities using litter production studies.

Methods

Vegetation Sampling

Vegetation sampling in three tree islands, Black Hammock (BL), Gumbo Limbo Hammock (GL) and Satinleaf Hammock (SL), included a one-time assessment of vegetation structure and composition along four transects and in three permanent plots. One transect followed the long (north-south, or N-S) axis of the tree island; three other transects were perpendicular to the long transect (one traversed the "head" and two the tail) (Figure 6-1). One permanent plot was established in each of three plant communities on each tree island: hardwood hammock, bayhead, and bayhead swamp (Figure 6-2). In addition, one non-forested plot was established downstream of the bayhead swamp forest in the tail of GL.

Sampling Along Transects. Vegetation sampling protocols were as follows: (1) tree basal area and size structure were determined by species at 10 m intervals (5 m intervals within and immediately adjacent to the hardwood hammock) by recording the density of trees in 5-cm diameter classes within belts of 2 m width (for stems 1-10 cm DBH), 4 m width (for stems 10-25 cm DBH), and 10 m width (stems >25 cm DBH) surrounding the center line of the transect; (2) maximum height and cover class of trees and vines were estimated by species within a plot of 2 m radius around each transect point; (3) cover class of herbs and shrubs were estimated by species within a plot of 1 m radius at each transect point. Cover classes for (2) and (3) were: 1, 0-1%; 2, 1-4%; 3, 4-16%; 4, 16-33%; 5, 33-66%; and 6, >66%.

Sampling in Permanent Plots. In the late summer of 2001, permanent plots of 25 x 25 m, 20 x 20 m, and 15 x 15 m were established in the hardwood hammock, bayhead, and bayhead swamp forests, respectively, on each of the study three islands (Figure 6-2). (The permanent plot installed in the hardwood hammock of BL was 20 x 20 m; the permanent plot installed in the tail of GL was 15 x 15 m and established in November 2002.) Each plot was gridded into 5 x 5 m cells, and vegetation sampling addressed tree, sapling, shrub, and herb strata separately within these units in a nested design. In the tree stratum (stems >5 cm DBH), we tagged each individual and recorded its species, location (W-E and S-N coordinates, ±0.5 m), total height (±0.1 m), DBH (±0.1 cm), and number of stems (for multi-trunked individuals). In the sapling stratum (trees 1-5 cm DBH), we recorded the density of individuals in two diameter classes (1-3 cm, 3-5 cm) in each cell. For the shrub stratum (stems >1 meter tall and <1 cm DBH, including all vines and lianas), we made visual estimates of the shoot cover (in six classes, i.e., 1, 0-1%; 2, 1-4%; 3, 4-16%; 4, 16-33%; 5, 33-66%; and 6, >66%) of species overlapping a circular 3.14 m^2 (1 m radius) plot in the center of each cell. For individuals in the herb stratum (<1 meter height), we estimated species cover in the 3.14 m^2 plot using the cover classes described above, and counted tree seedlings rooted within a circular 1 m^2 plot (0.57 m radius) centered at the same point, distinguishing stems of three height classes (<30 cm, 30-60 cm, 60-100 cm). The seedling density estimates were repeated at 3-6 month intervals between June 2001 and October 2003 (Table 6-1).

Table 6-1. Sampling frequency for estimates of seedling density in permanent plots for various plant communities at three tree island sites. HH, hardwood hammock; BH, bayhead; BS, bayhead swamp; T, tail.

Sampling Month and Year	Black Hammock			Gumbo Limbo				Satinleaf		
	HH	BH	BS	HH	BH	BS	T	HH	BH	BS
June 2001								x	x	x
September 2001								x	x	x
December 2001	x	x	x	x	x	x		x	x	x
April 2002								x	x	x
July 2002	x	x	x	x	x	x		x	x	x
October/November 2002	x	x	x	x	x	x	x	x	x	x
July/August 2003	x	x	x	x	x	x	x	x		
October 2003								x		

The nested sampling of canopy strata described above was supplemented by a vertical line intercept method whose intent was to describe overall canopy structure. We recorded the species and height interval(s), in 1 m increments, of each tree crown that intercepted a cylinder of 30 cm radius centered on a level height pole extended upward from the midpoint of each cell. When several conspecific individuals intercepted the cylinder within the same height interval, the species was recorded once only. At the stand level, the data were summarized in a crown density profile (CDP). The CDP was constructed by calculating, for each 1 m height interval, the percent occupancy among all sample points (i.e., cylinders). With few exceptions, the grid spacing of 5 m was sufficient and the same large tree was not sampled in adjacent plots.

Litter Production

The productivity of tree island hardwood hammock, bayhead and bayhead swamp forest communities was assessed in term of litter production. To assess spatial and temporal variation in litter production, litter traps were constructed by attaching standard window screening to a wooden frame according to the following specifications: the trap was 0.6 meters on a side, with a base approximately 40 cm above the ground in the hardwood hammock plots and approximately 80 cm above the ground in bayhead and bayhead swamp plots, and a basket depth of 20 cm. Trap locations were determined according to a stratified random selection process. Eleven traps were established in the hardwood hammock plots, seven traps in the bayhead plots, and 5 traps in the bayhead swamp plots, resulting in a sampling intensity of at least 0.5% of the plot area in each plant community.

Traps were installed in SL on June 15, 2001, and in GL and BL on December 17, 2001. Debris was collected from the litter traps approximately quarterly during the year (except for the last collection which was done after five months), depending on access. Litter from each trap was separated into three fractions (leaves, woody fragments, and reproductive parts) which were dried in an oven and weighed.

The 2001-02 winter collections from the SL bayhead plot were lost in transport and unavailable for analysis. In addition, several litter traps sustained serious damage from animal activity, probably feral hogs. Six of the 11 traps in the Gumbo Limbo hardwood hammock were destroyed during the first quarter (the missing data was corrected by calculating litter production per m^2 sampled during each period). The remaining five traps were destroyed soon afterward, and litter collection was discontinued in this plot.

Data Analysis

Vegetation Structure and Composition

Moving Split-Window Method. To identify discontinuities in plant community structure along a transect, we used the moving split-window method first introduced by Whitaker (1960) and developed further by others (Ludwig and Cornelius 1987, Wierenga et al. 1987). This method involves the calculation of dissimilarity between two halves of a window, where the window contains data from a fixed block of contiguous sampling units, followed by movement of the window one unit further along the transect, and repetition of the process. After trying window sizes between 2 and 12, we settled on a window of 6 sampling units, because it seemed to produce the best definition in the dissimilarity peaks. We calculated Bray-Curtis dissimilarity (Bray and Curtis 1957) based on species cover at the six sampling units on either side of the window. In a separate analysis, species were grouped according to their life-forms (i.e., trees, shrubs, graminoids, forbs, ferns, vines, seedlings). The mean cover of these groups at each sampling point was then used to calculate Bray-Curtis dissimilarity, which was later used to explore discontinuity in community structure.

NMS Ordination. To examine the relationships among tree island plant communities in a visual and quantitative manner, we ordinated their relativized species abundances using non-metric multidimensional scaling (NMS) (Kruskal 1964). The NMS procedure involves an iterative search to position sites along a limited number of axes such that the among-site dissimilarities in vegetation composition are replicated as much as possible (McCune and Grace 2002). The discrepancy between the site x site dissimilarity matrix (when the individual elements are *ranked* from most dissimilar to least dissimilar), and its representation in reduced-dimensional space, is measured as "stress." Bray-Curtis dissimilarity was used in the analyses. The NMS analysis was done using PC-ORD software (McCune and Mefford 1999). Species richness, evenness and Shannon diversity index (H') values were calculated for each vegetation zone using the method outlined in the PC-ORD statistical package.

Litter Production. Two-way analysis of variance (ANOVA) was used to determine the differences in litter production among tree islands and plant communities. Since litter production data for GL hardwood hammock was available only for the winter of 2001-02, one-way ANOVA was used on those data. Repeated measures ANOVA was conducted to analyze seasonal variation in litter production.

Vegetation:environment Relationships

Correspondence Analysis. Deterended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were used to analyze vegetation:environment relationships. DCA is a multivariate indirect gradient analysis technique, and is used to visualize the species organization along environmental gradients, leaving environmental interpretation to a subsequent step (Hill and Gauch 1980). CCA is a 'direct gradient analysis method', and is best suited to community data sets in which species responses to environments are unimodal and the important underlying environmental variables have been measured (ter Braak 1987). Response variables were species cover at 138 sites arranged along transects on three tree islands. Environmental variables were elevation, hydroperiod, mean annual water level, soil depth, pH, electrical conductivity (EC), organic matter, and total carbon (TC), nitrogen (TN), phosphorus (TP) and carbonate (TCO_3). Hydroperiod and mean water level was averaged over seven years preceding the vegetation sampling. The period of seven year was chosen because it produced the best fit model when weighted average (WA) regression models were developed (for details see next sub-section) using different time periods, from 1 to 15 years preceding sampling. Data for the soil variables were the same as those described in Chapter 3.

CCA was also used to determine the influence of hydrologic regimes and canopy structures on the understory vegetation. For this analysis, response variables were species abundances in the understory in permanent plots and the explanatory variables were elevation, hydroperiod, mean water level, soil depth, tree basal area, canopy openness, and percentage of direct light transmitted through canopy. The forward selection option in CCA was used to select the environmental variables that were important in explaining the variability in species data. In the forward selection, we used the automatic selection option in which environmental variables are progressively added to the model (ter Braak 1987). At each step, the statistical significance of the variable was judged by Monte Carlo permutation test (499 permutations) (ter Braak and Smilauer 2002). The permutation tests were performed also to test the overall hypothesis that there is no relationship between species data and environmental data. Analysis of variance (ANOVA) followed by Bonferroni multiple comparison tests ($\alpha = 0.05$) was used to determine whether individual environmental variables differed significantly among vegetation types and islands.

Weighted Averaging and Calibration. To determine hydrological niches of plant species of Shark Slough tree islands, we used weighted averaging (WA) regression. WA regression and calibration is a two-step sequence in which (1) species optima and tolerances (an expression of dispersion around the optimum) for individual, ecologically significant environmental variables are calculated from species abundances across a range of sites for which the environmental variable is known (training data set), and (2) these optima are utilized in order to infer the level of the environmental variable in data sets in which environmental variable is unknown, but species composition is known (calibration data set). These steps are weighted averaging regression and calibration, respectively (Birks et al. 1990). We used the C^2 program of Juggins (2003) to calculate species optima and tolerances for hydroperiod.

We evaluated four alternative WA inference models in conjunction with the species relationships enumerated above. These models used different weighting parameters (tolerance-weighting or not) and methods of “deshrinking” the estimates (classical or inverse). In WA regression, deshrinking is needed to correct for contraction in the range of inferred hydroperiods associated with the double-averaging sequence outlined in the last paragraph. We used the root mean square error of prediction (RMSEP) of 100 bootstrapped estimates from the training data set to compare among the models, selecting the model which minimized RMSEP.

Finally, we applied the best WA model to calibration data sets (i.e., species abundance data for other tree islands). Here the hydrologic record of the sites is already well-known, but dynamics in the vegetation-inferred estimates hydroperiod may shed some light on the responsiveness of the plant communities to annual or longer-term hydrologic variation.

Results

Vegetation Structure and Composition

Tree Island Flora. A total of 128 vascular plant species, belonging to 66 families, were identified in three tree islands. Poaceae, Cyperaceae, Asteraceae, Bromeliaceae, Fabaceae and Vitaceae had the greatest number (≥ 5) of species. There were 21 tree species, 8 shrubs, 26 graminoids, 41 forbs, 15 vines, 10 ferns, 6 epiphytes, and one parasitic species (Appendix 6-1**)**. Of the 128 species, 116 were recorded from the sampling units established along transects and within the permanent plots, and 12 were recorded from outside the sampling units, but from the tree islands. GL had the highest number of species (91), and BL and SL had 69 species each. Fifty-one taxa occurred in only one of the three tree islands (BL, 7; GL, 30; SL, 14). The higher number of species for GL was probably due to a greater sampling area resulting from its larger relative size.

Plant Communities Along Transects. Vegetation composition varied along the N-S transects of the tree islands. In general, four plant communities were distinguishable along these transects on each island (Figure 6-3). The tropical hardwood forest plant community occupied the upstream portion of tree islands, characterized by the presence of tropical hardwood hammock species. This forest had a canopy generally 7-10 m tall and occupied a 60-100 m segment of the transect. GL had the largest hardwood hammock area of the three tree islands. The next section along the N-S transect was the bayhead forest plant community characterized by bayhead species. The forest canopy height was about 4-7 m and occupied a 100-700 m segment of the transect. The bayhead forest of GL was the largest of the three tree islands and was more heterogeneous in composition as depicted by fluctuations in dissimilarities between adjacent segments of samples along the transect (Figure 6-3). The bayhead swamp forest plant community, with a canopy 2-4 m tall, occupied the distal portions of each N-S transect. A fourth plant community – sawgrass (*Cladium jamaicense*) and/or spikerush (*Eleocharis cellulosa*) marsh - occupied a small portion of the ends of transects.

Plant communities along the N-S transects were also distinguishable based on mean cover of species belonging to the same life-form (Figure 6-4). The peaks representing higher Bray-Curtis dissimilarity between adjacent segments of samples in moving-split windows were identical in both species and life-form abundance data. However, the patterns were not the same in all three tree islands. The life-forms along the N-S transect in BL were more uniform than in GL and SL. As a result, plant communities were not distinguishable based on life-form cover (Figure 6-4A). The life-forms used for the analysis were trees, shrubs, graminoids, forbs, vines, ferns and seedlings. In general, the tropical hardwood hammocks of all three sites were characterized by tall trees (>80% cover). The major tree species were *Bursera simaruba*, *Celtis laevigata, Eugenia axillaris, Ficus aurea,* and *Sideroxylon foetidissimum.* The understory of these forests was very sparse, represented by mainly seedlings of the species present in the canopy. Vegetation in the bayhead forests was more diverse in life-forms compared to hardwood hammocks, comprising mainly trees, vines, ferns, and a few seedlings. Major tree species were *Annona glabra*, *Salix caroliniana, Myrica cerifera, Chrysobalanus icaco,* and *Magnolia virginiana*. The understory of these forests was characterized by a thick growth of tall ferns, such as *Acrostichum danaeifolium, Blechunum serrulatum* and *Thelypteris interrupta*. Only a few species (e.g., *Chrysobalanus icaco*) were abundant in both hardwood hammock and bayhead forest communities.

Tree cover decreased towards the lower end of the bayhead forests and was less than 5% in the adjacent bayhead swamp forests, where low shrubs and forbs were most abundant (Figure 6-5). *Cephalanthus occidentalis* was the major shrub in the bayhead swamp forests of all three tree islands, though its individuals were mostly less than 1 m in height. Dominant forbs were *Bacopa* *caroliniana, Peltandra virginica, Pontederia cordata,* and *Utricularia foliosa*, but their relative abundance differed among tree islands. Graminoid cover increased towards the distal end of the transects and was the highest in marsh, where sawgrass constituted >80% of the total plant cover. In general, species richness and diversity were higher in bayhead and bayhead swamp forests than in hardwood hammocks and marshes (Table 6-2).

NMS ordination analysis of N-S transect sample plots from the same plant community revealed that a plant community on one island was closer to the same community from other tree islands compared to neighboring plant communities within the same tree island (Figure 6-6).

Plant communities identified along the N-S transects were strongly associated with elevation. Hardwood hammocks were located at the highest elevation, with bayheads, bayhead swamps and marshes occupying the decreasing elevation gradient. Canopy heights in all three tree islands also exhibited a strong positive association with surface elevation (Figure 6-7). Hardwood hammocks that occupied the head of the island had the tallest canopies, followed by bayhead forest, and finally bayhead swamp forest. GL had taller trees, especially in the hardwood hammock and bayhead forests, compared to BL and SL (Figure 6-7). However, canopy height of the bayhead swamp forest was shorter in GL than in the other two tree islands.

Table 6-2. Mean species richness, species diversity and evenness in different plant communities along transects of tree islands. HH, hardwood hammock; BH, bayhead; BS, bayhead swamp; M, marsh.

Tree Island and Plant Community	Species Richness	Evenness	Species Diversity (Shannon-Wiener)
Black Hammock			
HH	4.9	0.680	0.940
BH	8.6	0.597	1.261
BS	9.8	0.646	1.448
M	3.6	0.264	0.390
Gumbo Limbo			
HH	6.2	0.673	1.123
BH	10.0	0.652	1.477
BS	9.1	0.641	1.379
M	3.5	0.305	0.435
Satinleaf			
HH	5.2	0.675	1.087
BH	8.9	0.628	1.359
BS	6.1	0.577	1.013
M	3.7	0.310	0.430

Vegetation Structure in Permanent Plots. A detailed account of community structure was derived from the vegetation data collected in permanent plots established within the hardwood hammock, bayhead and bayhead swamp forests of all three tree islands. A total of 75 plant taxa were identified within these plots, including the "tail" plot established at GL (Appendix 6-2). GL had the highest number of species; however, when the "tail" plot at GL was excluded, the number of species recorded in the permanent plots of all tree islands was approximately the same (i.e., BL, 46; GL and SL, 45 each). Of the 75 taxa, 27 occurred in only one of the three sites (i.e., SL, 11; GL, 9; BL, 7). BL shared 33 species with GL, and 31 with SL, whereas GL shared only 27 species with SL.

Total plant species present in the three main permanent plots were hardwood hammock (27), bayhead (37), and bayhead swamp (46). The bayhead swamp in BL was the richest of all permanent plots. Combining data from all three tree islands, the bayhead forest plots shared 15 species with the hardwood hammock plots and 26 with the bayhead swamp plots, but only eight were present in both. Some taxa present in the hardwood hammock plots, usually associated with depressions, were common in the bayhead or bayhead swamp plots. Similarly, seedlings of a few hardwood hammock species were present on higher ground in the bayhead swamp plots. Species richness data from the permanent plots supported the findings from the transect sampling: plant species diversity in all three tree islands was highest in the wetter forest types (Figure 6-8). However, these differences were influenced by differences in sample sizes resulting from differences in sample areas; sample areas decreased from hardwood hammock (625 m^2; in Black Hammock 400 m^2) to bayhead (400 m^2) to bayhead swamp (225 m^2). Sampling at equal intensity would only have accentuated differences among forest types. Finally, species numbers in permanent plots on each tree island underestimated the total flora present on these islands by about 51.7 to 73.0%, as the species encountered in transect sampling alone on BL, GL and SL were 63, 87, and 63, respectively.

Community structure in the three forest types differed fundamentally in both understory and canopy layers. The hardwood hammock understory of BL was more densely covered (>50%) and dominated by mainly tree seedlings and saplings compared to the other two sites (Figure 6-9A). In GL and SL, hardwood hammock understory was sparsely (<25%) covered. In GL, tree seedlings and a forb species, *Rivina humilis*, were equally dominant, and in SL, vines were common in the lower strata (Figure 6-9B,C). The bayhead forest understory in the three tree islands was characterized by a thick growth of tall ferns, which were much denser in GL and BL than in SL. In the bayhead of BL, tree seedlings and saplings were also abundant (Figure 6-9A). Shrubs, forbs, and graminoids were important in the densely vegetated lower strata of the bayhead swamp plots. In part, the evident increase in life-form diversity from hammock through bayhead to bayhead swamp (Figure 6-9**)** may be driven by a concomitant decrease in upper canopy development along this same sequence (Figure 6-10). Maximum canopy height determined from the vertical line intercept surveys was 11-12 m in the hardwood hammock, 7-8 m in the bayhead, and 3-4 m in the bayhead swamp. In the hardwood hammocks of BL and GL, crown densities were relatively more uniform (between 3 to 10 m) compared to SL where maximum crown density was 4-6 m. Crown density profiles (Figure 6-10) also indicated maximum crown density at 3-5 m in the bayhead plots and 2-3 m in the bayhead swamp plots. We suspect that the canopy depths illustrated in these profiles (deep in hardwood hammock, intermediate in bayhead, thin in bayhead swamp) create very different understory light environments in these three forests and have apparent effects on vegetation at lower strata.

The woody, structural component of the nine stands described above was partitioned among 22 tree and shrub species (Appendix 6-2), each possessing its own ecological characteristics and occupying a different position in the existing forest. In the hardwood hammock of all three tree islands, *Bursera simaruba* was the dominant species in the upper forest canopy, though a tree of *Ficus aurea* was the largest (DBH = 62 cm; height = 11.7 m) single tree in BL (Figure 6-11). *Celtis laevigata* and *Sideroxylon foetidissimum* were important in the midstory, while *Eugenia axillaris* was abundant in the understory. In SL, however, *S. foetidissimum* was absent in the sub-canopy layer, but *Chrysophyllum oliviforme* was present. In the wet periphery of the hardwood hammocks of BL and SL, medium sized trees (5-30 cm DBH) of *Chrysobalanus icaco* were also common in the understory.

The largest trees in the bayhead forest plots were *Salix caroliniana*, but *Magnolia virginiana* occupied a similar position in the highest strata of the bayhead forest canopy in GL and SL (Figure 6-11). *M. virginiana* was not present within the bayhead plot of BL. *Annona glabra* was the most abundant small tree. *Chrysobalanus icaco* was common in the bayhead plots of BL and SL but scattered in GL. Small trees of *Ilex cassine* and *Myrica cerifera* were abundant in the understory within bayhead plots of GL and SL, respectively.

Forest structure in the bayhead swamp was extremely simple in all three sites. At a maximum height of only 3-4 m, the upper canopy stratum of this forest was occupied by saplings less than 5 cm in diameter (Figure 6-11). In BL, *A. glabra* and *M. cerifera* were abundant in the upper canopy layer, while *S. caroliniana* was abundant in GL. In SL, the tallest single tree was an individual tree of *M. cerifera*, but *A. glabra* and *M. virginiana* had the highest densities in the sapling sizes. Normally a tall shrub, the height of *C. occidentalis* sometimes exceeded 1 m in the plots.

Spatial Variation in Permanent Plots. The horizontal patterns of trees found in the hardwood hammocks are illustrated in Figures 6-12 to 6-14. The distribution of stems in SL was more patchy (CV = 93.4% for tree density) than BL and GL (CV = 68.4 and 62.3%, respectively). In BL, however, most of the large multi-trunked trees of *B. simaruba* and *C. laevigata* were also clumped together within a 10 m^2 area at the southeast corner of the plot (Figure 6-12A). In SL, 10 of 25 cells of the plot contained only one or no rooted tree. The patchy distribution of trees in the hammocks of BL and SL caused a greater variation in canopy openness (CV = 14.5% and 18.6%, respectively) and percent of direct light transmitted to understory (CV = 28.3% and 22.3%, respectively) compared to GL (CV = 8.0% for canopy openness, CV = 17.7% for direct light transmitted). In GL, large trees of *B. simaruba* and *C. laevigata* were rooted in different parts of the hammock (Figure 6-13A). The individuals of *E. axillaris* were also scattered. In SL, however, there were occurrences of several large, multi-trunked *B. simaruba* individuals interspersed with small *E. axillaris* trees (Figure 6-14A). *C. laevigata* stems were restricted to the western edge of the plot, and *C. oliviforme* and *C. icaco* to the eastern side. The large canopy gap near the center of the plots in both BL and SL hammocks was narrowed somewhat by the asymmetrical growth of adjacent crowns, but this is not apparent in those figures which indicate only the rooting positions of the trees.

In the understory of the hardwood hammock plots, *E. axillaris* seedlings were uniformly distributed in all three tree islands, especially BL (Figure 6-12B). Although the center of the hammocks had a relatively flat surface, seedlings of upper canopy dominant species were affected by microtopography and understory environment. For example, seedling density of *C. laevigata* in GL (Figure 6-13B) and *B. simaruba* in SL (Figure 6-14B) had significant positive correlation with elevation ($p = 0.02$ and $p = 0.03$, respectively). In contrast, seedling densities of both *C. icaco* and *C. oliviforme* in SL ($p = 0.03$ and $p < 0.01$) and *C. icaco* in BL ($p = 0.01$) were relatively higher at lower elevation.

Microtopography in the bayhead plots was sometimes quite striking, with the larger trees frequently occupying (and helping to form) local peaks. As the result, the bayhead plots in all three tree islands included large openings occupied primarily by ferns (*Acrostichum danaeifolium*, *Blechnum serrulatum* and *Thelypteris interrupta*) and shrub-sized *A. glabra* and *C. icaco*. In GL, a *Ficus aurea* tree was exceptionally large (Figure 6-15A). In this tree island, other stems also were larger and more patchily distributed than in SL bayhead (Figure 6-15B). However, as in the hammock, multi-stemmed individuals in bayhead plots of all three sites were common but did not necessarily comprise the largest trees in the stands.

Tree Seedling Dynamics. In the hardwood hammock plots, seedling populations were much higher in BL ($>10^5$ ha^{-1}) than in GL and SL (Figure 6-16). In all three tree islands, *E. axillaris* comprised more than 80% of the total seedlings, and with a minor decrease in the early wet season, its population remained almost constant throughout the study period. A small population of *C. icaco* appeared in the hammock of BL in December 2001 but was not observed in the wet seasons of 2002 and 2003 (Figure 6-16A). In GL, however, a small population of *C. icaco* was observed only in the early wet season of 2003 (Figure 6-16B). In SL, *C. icaco* seedlings remained relatively constant with minor peaks in April 2002 and December 2003 (Figure 6-16C). In GL, a small population of *C. laevigata* seedlings was present in the wet seasons of 2002 and 2003. In June 2001, *B. simaruba* seedlings were abundant in the hammock of SL, mostly at higher elevations, but were not observed in GL and BL. Its population, however, dropped to zero by September of that year and was not observed during the samplings in 2002 and 2003.

Tree seedlings were less plentiful in the bayhead than in the hardwood hammock plots, especially in GL where the seedling density was 2-3 times less than in BL and SL (Figure 6-17) In the bayhead of GL, 85% of the seedling populations were comprised of *A. glabra*, while *C. icaco* and *M. virginiana* were co-dominant with *A. glabra* in BL and SL, respectively. SL had a more diverse bayhead seedling flora than BL and GL. *A. glabra* exhibited a strong seasonal variation in seedling density, especially in SL where the samplings continued for two complete years. In this tree island, *A. glabra* density peaked in dry or early wet seasons, such as June 2001 and April 2001. Similarly, in GL, *A. glabra* seedling densities were higher in the early wet season (July) than in the late wet season (October). In BL, however, the seasonal peak of *A. glabra* seedlings in the bayhead appeared in July 2002 and was not observed the following year. In contrast, *C. icaco* seedling density remained constant in BL throughout the study period. Seedling density was very low (<1500 seedlings/ha) in GL. In SL, however, *C. icaco* seedling density was moderate and higher in the wet season compared to the dry season. In this tree island, *M. virginiana, M. cerifera* and *Persea borbonia* exhibited strong seasonal peaks, in June 2001 and/or April 2002.

Very few tree seedlings were present in bayhead swamp forest plots of BL and GL. Total seedling density in SL was much higher than the other two sites (Figure 6-18). In the bayhead swamp of SL, the density of *A. glabra* reached a maximum (~600,000 seedlings/ha) in April 2002, and the density of this population never fell below 50,000/ha. September and December were generally periods of minimum seedling density in the tree islands. *A. glabra* seedling density exhibited a strong seasonal pattern also in GL, where it was observed only during the early wet season. In BL, however, the seasonal pattern was somewhat unclear, as the *A. glabra* density peaked in December 2001 and was lower in July 2002 than in September of the same year. In contrast, a small population of *C. icaco* seedlings remained constant throughout the study period in this tree island. In GL, the seedling density of *Salix caroliniana* was fairly high during the wet seasons.

Forest Dynamics. In forests, the size structure of trees provides an indication of the forest status and its development. The density of tree stems was plotted against size classes for hammocks, bayheads and bayhead swamps of the three tree islands. In hammocks, the density decreased with increasing size, providing a reasonable fit to the negative exponential distribution (Figure 6-19). However, not all species had the similar trend. For example, in BL and GL, *B. simaruba*, *C. laevigata* and *S. foetidissimum* were abundant in large size classes, but had a very small number of recruitments. In contrast, in SL, *B. simaruba* seedling density was high in small size classes, and the density gradually decreased with increasing size. This species was not well-represented in the sapling layer of the SL hammock, indicating that the high density of *B. simaruba* seedlings was seasonal and seedling mortality rate for this species was very high. In all three tree islands, the density of *E. axillaris* seedlings was high in small size classes, indicating its dominance in the lower stratum. *Chysobalanus icaco* and *Chrysophyllum oliviforme* seedling densities were low in general and roughly decreased with an increase in size classes.

In bayhead forest plots of BL and SL, the density of tree stems decreased with increasing size (Figure 6-20). In GL, however, stem density in small tree size classes was higher than saplings. In BL, both *A. glabra* and *C. icaco* were evenly distributed in the seedling layer, whereas *A. glabra* was dominant in the tree layer (Figure 6-20A). However, the sapling layer in this tree island was dominated by *C. icaco*, indicating that the species composition in the upper canopy will change within the next few years. In GL, the upper canopy was very diverse and composed mainly of *A. glabra*, *I. cassine*, *M. virginiana* and *S. caroliniana*. However, *I. cassine* and *M. viginiana* were absent in both sapling and seedling layers, while *M. cerifera* was dominant in the sapling layer (Figure 6-20B). In SL, the stem densities of almost all species decreased with increasing size, demonstrating that species composition of the tree layer in the bayhead forest plot of this tree island will not change significantly.

In the bayhead swamp forest plots of all three tree islands, woody plant composition was very simple, dominated by mainly *A. glabra*. Other associated species were *M. cerifera* in BL, *S. caroliniana* in GL, and *M. virginiana* in SL (Figure 6-21). In the latter two tree islands, the other species were found in only the lower strata. In GL, *A. glabra* was dominant in the seedling layer, although *S. caroliniana* formed more than 80% of the canopy in the sapling layer. Similarly, in SL, *M. virginiana* was co-dominant in the sapling layer, but was absent in seedling populations. In BL, the tree size structure did not provide a reasonable fit to the negative exponential distribution, as the total sapling density was much higher than seedlings.

Litter Production

Mean litter production in the tree island plant communities varied from 1,439 kg/ha/yr in the SL bayhead swamp to 10,879 kg/ha/yr in the SL hardwood hammock (Table 6.3). For all three tree islands, the rate of litter production was higher in hardwood hammocks than in the other two communities, and it was 3-4 times higher in bayhead than in bayhead swamp.

Table 6.3. Mean litter production in different plant communities of three Shark Slough tree islands.

Tree Island	Mean Litter Production (kg/ha/yr ± 1 S.D.)		
	Hardwood Hammock	Bayhead	Bayhead Swamp
Black Hammock	10621 ± 6703	6673 ± 3713	1835 ± 1200
Gumbo Limbo Hammock	7789 ± 1703	7457 ± 5477	2082 ± 1452
Satinleaf Hammock	10879 ± 3860	7400 ± 3650	1439 ± 1185

For a season when litter production data were available for a community type in all three tree islands, the effects of tree islands were non-significant for all community types. For example, in the hardwood hammock community where litter production data was available for all tree islands only for winter 2001-02, mean litter production did not differ significantly (one-way ANOVA, $F_{2,23} = 3.39$, $p = 0.051$) among tree islands, though the mean litter production in GL was slightly lower than in BL and SL. In the bayhead and bayhead swamp communities of the three tree islands, litter production data were available for four seasons (spring, summer, fall, and winter of 2002). For these two communities, litter production did not differ among tree islands (Table 6-4). However, litter production differed significantly (two-way ANOVA; $p < 0.01$) between two plant communities, bayhead and bayhead swamps. The interaction between tree island and community types was also non-significant.

Table 6.4. F and *p*-values in the two-way analysis of variance (ANOVA) of litter production in two communities, bayhead and bayhead swamp, of three tree islands during four different seasons.

Source	Spring 2002		Summer 2002		Fall 2002		Winter 2002-03	
	F	*p*	F	*p*	F	*p*	F	*p*
Island	0.52	0.602	0.95	0.400	0.13	0.881	0.79	0.464
Community	41.05	0.000	23.15	0.000	17.71	0.000	53.06	0.000
Island*Community	3.18	0.560	0.24	0.790	0.69	0.510	2.61	0.090

Since tree islands had non-significant effects on litter production, data from all three sites were pooled (Figure 6-22) and repeated-ANOVA was used to analyze seasonal variation in litter production and differences in litter production among community types. Because repeated measures analyses require balanced samples, data for only five seasons was used and the conservative Greenhouse-Geisser approximation for evaluating F-tests was considered. Seasons had significant effects ($F_{4,\ 172} = 7.27$, $p < 0.001$) on litter production in the plant communities. However, multiple mean comparisons (Bonferroni test) for individual community type showed that effects of season on litter production were not significant for bayhead swamp. For hardwood hammock, however, litter production was significantly ($p < 0.05$) higher in the summer and winter seasons than in spring and fall (Figure 6-22). For bayhead, mean litter production was the highest in the summer season (29.4 kg/ha/day), followed by winter (19.5 kg/ha/day). Litter production in hardwood hammock and bayhead did not differ between spring and fall seasons, and production was low during these seasons. This pattern differed from bayhead swamp, where litter production peaked in the fall and was lowest during winter.

In all three plant communities, leaves were the dominant component (>75%) of litter. The mean proportion of woody fragments (stems, bark) varied between 9.1% in SL bayhead swamp and 20.9% in SL hardwood hammock. In all three tree islands, the hardwood hammock had the highest percentage of woody debris in the litter. For the bayhead community, woody components comprised up to 13-15% of the total litter. Approximately 1-6% of the litter comprised reproductive parts, including flowers, fruits and seeds. Tree island plant communities did not reveal any fixed patterns in terms of percentage of reproductive parts of total litter.

Vegetation:Environment Relationships

DCA ordination of sampling points along transects revealed a strong gradient (1st axis score > 8 standard deviation) in species composition on each tree island (Figure 6-23). This gradient in species composition represented variation in elevation which had a significant correlation ($p < 0.001$) with the first axis ordination scores for those tree islands (Table 6-5). In BL and GL, sites were more uniform in vegetation composition at high elevation. In contrast, sites at high elevation in SL slightly differed in species composition, confirming the patchy distribution of hammock species (Figure 6-14A). In GL, a gap between the hammock and bayhead indicated a sharp drop in elevation. Sites located at the middle elevation of this tree island were widely spread on Axis 2, indicating the presence of a heterogeneous community in bayhead and bayhead swamp forests. When an ordination of species data from all three tree islands was performed together, the gradient in species composition along the first axis did not change (Figure 6-24). The groups of sites comprising different vegetation structure separated along the elevation gradients (eigenvalue, λ, of the axis 1 = 0.912) with some overlaps. However, the sampling points, especially within the bayheads and bayhead swamps from different tree islands, were grouped separately along the second axis (eigenvalue $\lambda = 0.492$), indicating the influence of other factors, probably related to soil, on the plant communities.

Elevation optima and tolerances for all vascular plants present in more than three plots along the sampling transects are listed in Appendix 6-3. The ranking of elevation optima for species present on all three tree islands did not differ (Friedman Test: $\chi^2 = 0.278$, df = 2, p = 0.87) among the three sites. For example, when pairs of optima for the common species among these islands were plotted, a strong correlation between species behaviors emerged (Figure 6-25). However, most points falling above the 1:1 line (Figure 6-25A) indicated that BL elevation optima tended to be a few centimeters less than SL optima. In contrast, most points below the 1:1 line (Figure 6-25B,C) indicated that GL elevation optima were less than both BL and SL optima. This apparent discrepancy is at least in part attributable to regional variation in water levels; long-term average water level at hydrological monitoring station G-620, about 1 km from SL, is about 5.6 cm, 8.7 cm higher than at P33 and NP203, the closest water level recorders to BL and GL, respectively. Water level differences among these stage recorders are probably due to variation in regional topography and water management practices in the WCAs and the southern Everglades. Water levels at the stage recorders were used to calculate hydroperiods for these tree islands. Thus, hydroperiod optima, which will be described in the following section for all three tree islands, have a similar pattern to elevation optima.

Table 6-5. Eigenvalues of first two axes and coefficients (r) for correlations between elevation and Axis 1 scores of detrended correspondence analysis (DCA) of species abundance data collected along transects on three Shark Slough tree islands.

Tree Island	Eigenvalues (λ)		Correlation between Axis-1 Scores and Elevation	
	Axis-1	Axis-2	r	p-value
Black Hammock	0.874	0.399	0.811	<0.001
Gumbo Limbo	0.976	0.419	0.875	<0.001
Satinleaf	0.920	0.505	0.853	<0.001

CCA analysis was used to determine a relationship between species cover and 11 environmental variables measured at 138 sampling sites along sampling transects of the three tree islands. The environmental variables were elevation (ELEV), mean annual water level (WL), hydroperiod (HYD), soil depth (SDEP), pH, organic matter (OM), EC, and soil TN, TP, TC and TCO_3 (Table 6-6). The CCA results revealed a strong relationship between species composition and environment variables as evidenced by significant eigenvalue (λ) (Monte-Carlo test, p = 0.01) for the first three axes (Table 6-7). Axis 1 represented the combination of hydrological variables and elevation, as they are strongly correlated (Table 6-8). Soil characteristics, such as pH, EC, OM, TC, TN and TP were also correlated with Axis 1. Soil pH, EC and TP were highest in the hammocks and decreased with a decrease in elevation, whereas OM, TN and TC showed an opposite trend. The forward selection option in CCA was used to select the environmental variables that were significant (Monte Carlo test; 449 permutations) in explaining the variation in species data. Three soil variables (EC, TC and TP) were not significant (Table 6-7), thus subsequent analysis was performed with only eight environmental variables. This changed the vegetation:environment correlation and eigenvalues for the first three axes in CCA only slightly.

On the first axis of CCA, hammocks were well separated from bayhead, bayhead swamp and marsh sites. Sites comprising similar vegetation types but from different islands were also separated on axes 2 and 3, with which TCO_3 and soil depth, respectively, were strongly correlated (Table 6-7). Hammock sites from the three tree islands were well spread along the second axis, mostly due to variation in TCO_3 (Figure 6-26A). TCO_3 in the hammock soils of SL was the highest of all sites (Table 6-6). Mean soil depths in wets sites of GL (i.e., bayhead and bayhead swamp forests), grouped in the lower right corner of Figure 6-26B, were significantly higher (ANOVA; $F_{2,88} = 43.3$, Bonferroni test, $p < 0.01$) than wet sites of BL and SL.

Table 6-6. Mean (± S.D.) values of environmental variables used in CCA to determine vegetation:environment relationships in plant communities on three Shark Slough tree islands. HH, hardwood hammock; BH, bayhead; BS, bayhead swamp; M, marsh.

Tree Island and Plant Community	Elevation (m)	7-yr Mean Hydroperiod (days)	7-yr Mean Water Level (m)	Soil Depth (cm)	pH	EC	OM (%	TN (%)	TP (%)	TC (%)	CO_3 (%)	Canopy OpennesS (%)
Black Hammock												
HH	2.320 ± 0.143	0 ± 0	-0.781 ± 0.145	33.9 ± 11.3	7.92 ± 0.23	526 ± 128	30.3 ± 3.5	1.33 ± 0.11	4.36 ± 1.18	17.83 ± 2.16	11.73 ± 2.09	12.8 ± 1.8
BH	1.546 ± 0.114	180 ± 15	-0.020 ± 0.026	63.2 ± 24.8	6.50 ± 0.64	308 ± 86	73.9 ± 16.2	2.45 ± 0.77	1.55 ± 2.42	36.79 ± 10.88	4.27 ± 3.11	13.6 ± 7.3
BS	1.397 ± 0.077	254 ± 26	0.102 ± 0.038	76.7 ± 48.3	5.85 ± 0.56	266 ± 56	83.2 ± 4.5	3.11 ± 0.42	0.07 ± 0.01	42.89 ± 5.21	5.01 ± 4.01	29.5 ± 7.9
M	1.363 ± 0.062	322 ± 34	0.203 ± 0.062	24.6 ± 20.1	6.70 ± 0.36	376 ± 111	61.4 ± 17.4	2.51 ± 0.66	0.06 ± 0.02	34.81 ± 8.99	9.57 ± 7.13	
Gumbo Limbo												
HH	2.006 ± 0.121	0 ± 0	-0.557 ± 0.063	36.2 ± 16.2	7.47 ± 0.58	432 ± 110	22.9 ± 3.8	1.13 ± 0.39	5.96 ± 2.34	15.11 ± 4.47	7.82 ± 3.37	13.8 ± 1.1
BH	1.358 ± 0.118	198 ± 28	0.003 ± 0.052	111.2 ± 23.4	6.06 ± 0.62	243 ± 101	73.8 ± 21.7	3.04 ± 0.58	0.15 ± 0.14	44.07 ± 8.08	8.13 ± 6.69	17.1 ± 5.6
BS	1.234 ± 0.034	327 ± 5	0.264 ± 0.014	115.1 ± 25.0	6.04 ± 0.30	229 ± 58	74.4 ± 19.3	3.52 ± 0.27	0.53 ± 1.62	47.01 ± 1.09	9.78 ± 6.11	51.3 ± 8.6
M	1.112 ± 0.039	362 ± 2	0.418 ± 0.039	90.7 ± 20.8	6.48 ± 0.56	232 ± 55	72.9 ± 22.3	3.79 ± 0.34	0.09 ± 0.14	48.30 ± 2.38	9.35 ± 6.59	
Satinleaf												
HH	2.163 ± 0.105	0 ± 0	-0.587 ± 0.071	29.7 ± 9.8	7.74 ± 0.24	356 ± 61	27.6 ± 3.6	0.99 ± 0.21	5.82 ± 1.81	16.43 ± 2.24	14.32 ± 6.60	10.9 ± 2.0
BH	1.653 ± 0.191	206 ± 27	0.042 ± 0.054	38.1 ± 27.4	7.22 ± 0.59	301 ± 98	55.4 ± 21.6	2.20 ± 0.82	1.21 ± 1.57	30.86 ± 11.82	8.05 ± 5.92	13.2 ± 3.3
BS	1.446 ± 0.091	283 ± 28	0.176 ±0.043	51.8 ± 24.5	6.38 ± 0.45	184 ± 30	72.0 ± 8.4	3.24 ± 0.02	0.06 ± 0.01	45.89 ± 0.31	10.39 ± 3.37	24.6 ± 5.1
M	1.386 ± 0.054	331 ± 26	0.282 ± 0.054	55.9 ± 29.5	6.78 ± 0.42	174 ± 22	73.7 ± 5.7	3.07 ± 0.29	0.09 ± 0.05	41.87 ± 4.53	8.50 ± 5.80	

Hydrology and soil characteristics were relatively more important in explaining variation (50%) in species data at a coarser scale (i.e., at the scale of vegetation zones). CCA analysis of species cover, measured within permanent plots in the hardwood hammock, bayhead and bayhead swamp plant communities, and their relationship with three major environmental variables revealed that mean water level, a surrogate of elevation or hydroperiod, explained most of the variation (24.7%) in species data. Soil depth and TCO_3 together also explained some variation (24.8%). While differences in species composition between dry and wet sites were explicit (segregated on Axis 1), the differences between bayhead and bayhead swamp were unclear (Figure 6-27). The hammock of SL, with a relatively high amount of soil TCO_3, was somewhat different from the other two hammocks. Among the wet sites, soil depth was important in determining plant community composition.

Hardwood hammocks have not been completely inundated for many years, and their hydrological regimes differ from that of bayheads and bayhead swamps. CCA was performed for hammocks and wet sites (i.e., bayhead, bayhead swamp, marsh) separately. Water level was not the primary factor explaining the variation in species data among hammocks of the three tree islands (Figure 6-28). Instead, TCO_3 was strongly correlated ($r = 0.716$) to the first axis of CCA ($\lambda=0.496$). The eigenvalues of the 2nd and 3rd axes were 0.197 and 0.145, respectively, and were not significant. In wet sites, however, hydroperiod was still the important gradient (Figure 6-29), though not as strong as it was when both hammocks and wet sites were included in the analysis. The eigenvalues of the first two axes were 0.575 and 0.412, and hydroperiod had a significant correlation with the first axis ($r = -0.808$, $p < 0.01$).

CCA analysis of the relationship between species composition in the herb layer and environment included tree canopy cover as an additional environmental variable. Eigenvalues and the percentage of variance in species data explained by environment variables were slightly higher, but the overall pattern of ordination did not change, as the elevation gradient along axis 1 resulted in the separation of hammocks from other vegetation types. To explore the variation within similar plant communities among tree islands, subsequent analysis was performed on upland (i.e., hammocks) and swamp (i.e., bayhead, bayhead swamp, marsh) sites separately.

Ground vegetation within hardwood hammocks of the three tree islands was primarily related to mean ground water level and canopy cover, as evidenced by their significant correlation with CCA axis 1 (Monte-Carlo test; $p < 0.05$). Results of randomization tests further revealed that soil characteristics, such as soil depth, OM, TCO_3, TC, TN and TP were not significant in explaining variation in ground vegetation within the hammocks. The evidence for the importance of water level and canopy structure in determining ground vegetation was further supported from the data collected more intensively within permanent plots (Figure 6-30). In CCA analysis of such data, the first two axes were significantly correlated with water level and canopy openness, respectively (Table 6-9). Hammocks in GL and BL were more open than SL, and mean ground water level in BL was about 20 cm lower than in the other two sites. The relationship of total tree basal area with CCA axis 3 was not significant (Monte-Carlo test; $p = 0.14$), indicating that plants in the herb layer, which was primarily composed of tree seedlings, were not growing close to large trees. In the bayhead and bayhead swamps, ground vegetation was strongly influenced by canopy cover, as indicated by its significant correlation with the first CCA axis (Figure 6-30). Water level and soil depth were other significant variables. GL sites with deeper soils were well segregated (see bottom right quarter of Figure 6-31) from the other tree islands, indicating that ground vegetation in wet sites of GL differed in composition from those in BL and SL.

Table 6-7. Results of canonical correspondence analysis (CCA) of species cover and environmental variables measured at 138 sites along transects on three Shark Slough tree islands.

CCA Models	Axis-1	Axis-2	Axis-3
Model 1 (11 environmental variables)			
Eigenvalue	0.860	0.401	0.357
Species:environment Pearson correlation	0.969	0.801	0.740
% of variance in species data explained	6.8	3.2	2.8
% of variance in species:environment relationship	34.5	16.1	14.4
p-value (Monte-Carlo test; 99 permutations)	0.01	0.01	0.01
Model 2 (8 environmental variables)			
Eigenvalue	0.857	0.394	0.333
Species:environment Pearson correlation	0.967	0.798	0.723
% of variance in species data explained	6.8	3.1	2.7
% of variance in species:environment relationship	38.5	17.7	15.0
p-value (Monte-Carlo test; 99 permutations)	0.01	0.01	0.01
Interset-correlations			
Elevation (ELEV)	-0.908	0.124	0.083
Water level (WL)	0.932	-0.059	-0.047
Hydroperiod (HYD)	0.939	-0.164	-0.022
Soil depth (SDEP)	0.647	-0.132	-0.431
Total Carbonate (CO_3)	-0.116	0.301	-0.034
Organic matter (OM)	0.851	-0.042	-0.131
Total nitrogen (TN)	0.858	-0.155	-0.021
Soil pH	-0.690	0.171	0.218

Species Hydroperiod Optima and Tolerances. WA regression models were developed and evaluated by comparing the mean of the bootstrapped estimates of hydroperiod along the four transects on each individual tree island with the observed hydroperiod. When the hydroperiod was calculated across different time periods (i.e., for the year preceding vegetation sampling), and as mean annual values of the 2 to 15 year periods preceding sampling were evaluated, the results were not consistent among tree islands. However, the seven year period preceding vegetation sampling yielded the best model for GL and BL and the second best model for SL (Figure 6-32). In general, the best model, with minimum RMSEP and high R^2, was the one in which species impact was weighted on the basis of tolerance, and in which the inverse method of deshrinking the site estimates was employed.

Table 6-8. Correlation coefficients among environmental variables measured at 138 points along transects on three Shark Slough tree islands.

Variable	Elevation	Soil Depth	pH	EC	OM	CO_3	TN	TC	TP	Hydroperiod
Soil Depth	-0.643									
pH	0.766	-0.686								
EC	0.616	-0.485	0.525							
OM	-0.780	0.570	-0.740	-0.645						
CO_3	0.203	-0.109	0.325	0.138	-0.422					
TN	-0.875	0.679	-0.779	-0.647	0.844	-0.276				
TC	-0.875	0.700	-0.798	-0.677	0.883	-0.241	0.969			
TP	0.798	-0.558	0.684	0.539	-0.770	0.109	-0.773	-0.806		
Hydroperiod	-0.963	0.635	-0.765	-0.622	0.795	-0.204	0.895	0.885	-0.792	
Water Level	-0.994	0.611	-0.752	-0.641	0.788	-0.185	0.873	0.878	-0.804	0.969

SL yielded the best model for the relationship between species data and seven year mean hydroperiod (Figure 6-33). WA regression models were also developed from sampling points along transects on all three tree islands taken together. When inferred hydroperiods for those points were plotted against observed hydroperiod averaged over the seven year period preceding vegetation sampling, a strong correlation (R^2 = 0.85) was found (Figure 6-34). However, most sampling points on GL falling below the 1:1 line indicated that inferred hydroperiods were underestimated. This was apparent when we developed a model from species and hydroperiod data for BL and SL and applied it to species data from GL, and vice versa (Figure 6-35), indicating that species on GL are adapted to longer hydroperiods than BL and SL.

Species hydroperiod optima and tolerances were calculated from the vegetation and hydrology information collected along the four transects of each tree island (Appendix 6-3). For the species common to all three sites, species ranks based on their optima were not significantly different (Friedman Rank test; $\chi^2 = 0.541$, df = 2, p = 0.76); however, the species absolute hydroperiod optima significantly differed among tree islands ($\chi^2 = 0.541$, $p < 0.001$). The mean optimum hydroperiod for those species was 281, 253 and 217 days, respectively, for GL, BL and SL. This apparent discrepancy is at least in part attributable to the location of tree islands and the water level used to calculate hydroperiod. GL, located in the middle of Shark Slough, had a longer hydroperiod and higher annual mean water level than BL and SL (Table 6-6).

Table 6-9. Results of canonical correspondence analysis (CCA) of herb layer species cover and environmental variables measured within permanent plots on three Shark Slough tree islands.

CCA Models	Axis-1	Axis-2	Axis-3
Model 2 (8 environmental variables)			
Eigenvalue	0.419	0.131	0.028
Species:environment Pearson correlation	0.807	0.515	0.262
% of variance in species data explained	12.3	3.9	0.8
% of variance in species:environment relationship	72.6	22.6	4.8
p-value (Monte-Carlo test; 99 permutations)	0.02	0.04	0.11
Interset-correlations			
Water level (WL)	-0.771	-0.122	-0.046
Canopy openness (CANOP)	-0.314	0.473	0.018
Basal Area (BA)	0.330	-0.116	-0.231

Tree and Tree Seedling Optimum Hydroperiods

Optimum hydroperiods and water levels for woody species are presented in Figures 6-36 and 6-37. Woody species common to the bayhead and bayhead swamp forests increased in flood tolerance in the order *Sambucus canadensis* < *Chrysobalanus icaco* < *Persea borbonia* < *Magnolia virginiana* < *Myrica cerifera* < *Salix caroliniana* < *Annona glabra* < *Ilex cassine*. *C. icaco* and *S. canadensis,* which had intermediate hydroperiod optima, appear to be transitional between bayhead and hardwood hammock, as their water level optima are slightly below the surface. Among the upland species, tolerance to the higher ground water levels increased in the order *Sideroxylon foetidissimum* < *Coccoloba diversifolia* < *Eugenia axillaris* < *Bursera simaruba* < *Celtis laevigata* < *Chrysophyllum oliviforme* < *Solanum erianthum* < *Simarouba glauca* < *Myrsine floridana* and *Ficus aurea*. Tree seedlings had similar rankings in terms of species optimum hydroperiod and mean annual water level. However, the absolute optimum hydroperiod and water level of tree seedlings, especially of swamp forest species, were significantly higher than actual trees (Figures 6-36 and 6-37), most notably *C. icaco* and *S. caroliniana*. These two species can withstand hydroperiods two to three months longer and mean water levels 10 to 13 cm higher in the seedling stage compared to the tree stage. The much higher hydroperiod and water level optima for *Ficus aurea* seedlings compared to tree optima were probably due to a few surviving seedlings confined to very small area in the bayhead of GL. Among the upland species, only *Bursera simaruba* seedlings had a optimum hydroperiod longer than five days; however, its mean water level optimum of -33.4 cm indicates its intolerance to flooding.

Discussion

Shark Slough tree islands exhibit a more or less regular spatial pattern with respect to species composition. Data collected along the N-S transects of the three study tree islands illustrates how closely vegetation composition and structure is related to variation in topography, hydrology and soil characteristics. In general, vegetation occurring along soil moisture (hydrologic) gradients can be grouped into various 'zones', depending on the extent of soil saturation or inundation (Larson et al. 1981, Patrick et al. 1981). The tropical hardwood hammock, bayhead, bayhead swamp, and tall sawgrass marsh plant communities correspond to the "zones" of tree island vegetation. Vegetation characteristics of the three Shark Slough tree islands, considered for detailed study, are in accordance with the patterns described by Loveless (1959) and others (e.g., Sklar et al. 2004) for fixed tree islands in the central and southern Everglades. Like a typical tree island in the slough, the three study tree islands are tear-drop shaped and consist of a tropical hardwood (hammock) forest on higher ground at the upstream end, with a gradual shift to low stature vegetation (i.e., bayhead, bayhead swamp and tall sawgrass marsh) towards the "tail" of the island. Hammocks, composed of tall trees rooted deeply in the limestone "head" of the bedrock outcrop, are adapted to the drier conditions created and lower, ground water levels. Vegetation in bayhead and bayhead swamps, rich in shrubs and ferns, grow on peat-accumulated soil and are adapted to prolonged flooding conditions. Tall sawgrass with minor woody components dominate the tail region of the tree island.

Within a tree island, transition from one plant community (vegetation zone) to another is not always obvious. While the transition between hammock and bayhead was apparent in the study tree islands, the transition between bayhead and bayhead swamp was subtle and difficult to ascertain, especially at Satinleaf (Figure 6-1). This is because plant species such as *Annona glabra*, *Salix caroliniana, Myrica cerifera,* and *Magnolia virginiana,* which dominate the bayhead, also occur in bayhead swamp, though growth is stunted in the latter. An analysis that incorporates both species cover and structural components may help delineate these two zones. In this study, however, the combination of maximum tree height with either species or life-form cover measured at each sampling point did not affect the result, indicating that plant communities that occur along a small gradient are indistinct. Species occurring along a hydrologic gradient usually overlap in their occurrence due to the influence of soils and other environmental factors and their interactions with the water regime (Harper 1977, Larson et al. 1981).

Shark Slough tree islands are rich in their variety of plant communities and species, since they harbor both upland and wetland species. Species diversity is greater in bayhead and bayhead swamp forests than in hardwood hammocks and sawgrass marsh. The relatively high species diversity in bayhead forest may be due to an increase in topographic heterogeneity resulting from localized mounds formed around uprooted trees and fallen wood debris (see Chapter 5 of this report). Researchers have suggested that species richness can be used as a measure of tree island performance in relation to hydrological changes (Heisler et al. 2002), though it may not be considered the best indicator of overall tree island health (Sklar et al. 2004).

Gumbo Limbo showed higher species richness than either Black Hammock or Satinleaf, probably a result of its larger sampling area. The three study sites were different in terms of the size of their hammocks and length of their tails. The relatively longer tail and wider bayhead and bayhead swamp forests in Gumbo Limbo were probably related to the size of its "head" and location of the tree island. For fixed tree islands, two hypotheses, namely hydrodynamic and chemo-hydrodynamic, have been proposed to explain the formation of their tails (Sklar and van der Valk 2002). In both hypotheses, the role of the tree island "head" has been emphasized, whether in the accumulation of peat in the lee of the head by water currents (hydrodynamic) and/or the release of nutrients from the head into surrounding marshes (chemo-hydrodynamic). In both circumstances, it is most likely that more peat would accumulate behind a larger and nutrient-rich head. Though the hardwood hammock of Gumbo Limo is larger than Black Hammock and Satinleaf, mean total nitrogen and total phosphorus did not differ among tree islands, and mean organic matter was the lowest in Gumbo Limbo (see Chapter 3 of this report). Where a hydrologic gradient is established due to topographic variation, water flow plays an important role in determining soil nutrients, litter and sediment transport, and ultimately vegetation composition (Frye and Quinn 1979). Flow pattern depends on the water level, a function of topographic variation within the slough (Riscassi and Schaffranek 2002). In general, flow velocity decreases along a gradient from the center of the slough to its margins. Tree islands located in the central slough are subjected to high water level and flow velocity, and thus may tend to be longer with extended hydrologic and soil nutrient gradients. The analyses of directionality and longest vector of Shark Slough tree islands reveals that those located in the central slough are longer than in other regions (see Chapter 2 of this report).

In the Shark Slough tree islands, above-ground biomass production was highest in hardwood hammocks, moderate in bayheads, and lowest in bayhead swamps. Biomass production rates in the three hardwood hammock forests (10661 kg/ha/yr) can be compared to rates obtained from hardwood hammocks in other south Florida sites. For instance, Ross et al. (1992) found that fine litter production ranged from 6030 to 6200 kg/ha/yr in three stands in the most productive upland forest type in the Florida Keys. These annual values are well below the values we obtained for tropical hardwood hammocks in any of the three tree islands, but the values are close to the litter production in bayhead forests. However, comparable annual litter production from the bayhead swamp communities (1439 to 2082 kg/ha/yr) was considerably less than the values observed for any of the three Florida Keys rockland hammocks. Mean annual litterfall in the hardwood hammocks of the three tree island sites in Shark Slough is higher than several tropical deciduous forests (Martinez-Yrizar and Sarukhan 1990, Table 4).

Variation in structure and composition of plant communities within Shark Slough tree islands is directly or indirectly related to the surface elevation, which reveals a definite gradient along the long axis of the islands. On these tree islands, elevation as a significant predictor of variation in species composition is a consequence of its strong correlation with hydrology, an important variable in influencing community structure on tree islands in the slough environment (Armentano et al. 2002, Heisler et al. 2002, Wetzel 2002, Sklar et al. 2004). Plant communities that develop along a hydrologic gradient are influenced by periodic events of extreme changes in hydrological pattern. A strong correlation between current vegetation (sampled in 2001-02) and the seven year mean water level implies that tree island vegetation was affected by the prolonged flooding event of 1994-95, though trees on Shark Slough tree islands within Everglades National Park did not show signs of serious damage during or after the flood (Jones et al. 1997).

Soil nutrient gradients can also be strongly correlated with topographic moisture gradients (Frye and Quinn 1979, Lyon and Sagers 1998). Where that occurs, vegetation develops in response to how soil nutrients influence the responses of plant communities to the hydrologic regime (Duivenvoorden 1995). In hardwood hammocks of tree islands, where mean water level is mostly below the ground surface, vegetation is composed of primarily tropical hardwood tree species. These forests are highly productive, and their composition is influenced by ground water level, edaphic factors, and disturbances, including fire. Variation in vegetation composition in hammocks of the three study tree islands is attributed to differences in water level and soil nutrients. For example, the higher basal areas of *Celtis laevigata* in Gumbo Limbo and *Chrysophyllum oliviforme* in Satinleaf compared to Black Hammock may be related to higher mean ground water levels in the hammocks of the former two. On some floodplains, *C. laevigata* is dominant in areas with high ground water levels (Wood and Wood 1988). The significant correlation of soil carbonate with the 2nd axis of CCA (Figure 6-30) suggests a relationship between vegetation composition and total carbonate in Satinleaf hammock, a relationship not seen in the other two tree islands. How total carbonate influences tree island vegetation is not well understood; however, its role in phosphorus biogeochemical cycling is important (see Chapter 3 of this report). Satinleaf hammock has the highest number of tree species of the three study tree islands. While local site history may have played a role in the higher species richness, another reason could be the proximity of Satinleaf to areas impacted by human activities (i.e., the Shark Valley Tram Road in Everglades National Park).

When vegetation in different strata respond to the same topographic-hydrologic gradient, the herb layer can also be influenced by other factors, such as canopy cover in the upper strata (Bell 1974) and habitat disturbances (Mathooko and Kariuki 2000). In this study, canopy cover showed a significant influence on the ground vegetation in hammocks, and bayhead and bayhead swamp forests (Figures 6-30 and 6-31). While canopy cover co-varied with hydrological gradient in bayhead and bayhead swamps, it was influenced by tree size distribution in hardwood hammocks. Although trees are patchily distributed in the hammock of Satinleaf, the canopy has a relatively small opening due to the asymmetrical growth of crowns of large trees. In contrast, the canopy of the hammock in Gumbo Limbo is relatively more open despite the uniform distribution of trees. The mean ground cover in Satinleaf was 5.8%, much less than that in

Gumbo Limbo and Black Hammock (24.8% and 26.5%, respectively). Ground vegetation in hammocks was mostly composed of tree seedlings. In the months when all three tree islands were sampled simultaneously (Figure 6-19), the lowest density of seedlings was found in Satinleaf and this may be due to the denser canopy found there compared to the other two sites.

The herb layer in the hardwood hammocks differed among tree islands. Species composition in this layer at Gumbo Limbo hammock differed from Black Hammock and Satinleaf. This difference may have been influenced by the microclimates associated with the tree canopies, and possibly by the activities of feral pigs. Feral pigs (*Sus scrofa*) affect vegetation composition directly by eating plants and, indirectly, by digging into the soil (Hoeck 1984). Although research has recorded the presence of feral pigs on tree islands in Everglades National Park and the Water Conservation Areas (Layne 1984, Jones et al. 1997), there is a lack of literature on the effects of feral pigs on vegetation in the Everglades. Feral pigs, however, have been considered one of principal agents of soil disturbance, leading to altered vegetation in various ecosystems, such as coastal prairies in California (Kotanen 1995), island ecosystems in the Galapagos Archipelago (Schofeld 1989), and montane forests in the Hawaiian Islands (Spatz and Mueller-Dombois 1975, Aplet et al. 1991). There were signs of soil disturbance by *S. scrofa* in Gumbo Limbo hammock, where feral pigs were sighted on several occasions during our field surveys.

In ecosystems where water is not a limiting factor, other environmental factors such as light, competition, and soil type appear to be important in determining community composition (Voight and Mohlenbrock 1964). In the bayhead and bayhead swamps of the study tree islands, canopy cover was the most significant factor in explaining the variation in ground vegetation. Soil depth was another important variable related to the differences in bayhead and bayhead swamp vegetation among sites. In the bayhead and bayhead swamp forests of Gumbo Limbo, soils were deeper, probably because of bedrock depressions and deposits of organic matter. In Gumbo Limbo, mean bedrock elevations in the bayhead and bayhead swamp forests were 0.39 and -0.04 m, respectively, values about 0.6 to 0.9 m lower than those in Black Hammock and Satinleaf. Soils in wet portions of the tree islands were more organic (see Chapter 3 of this report); deep organic soils help to hold water for longer periods and contain high amounts of soil nutrients. This may be the reason for the ability of Gumbo Limbo bayhead and bayhead swamp forest sites to support highly flood-tolerant species, and to differ in their species composition compared to the other two sites. Mean cover of *A. glabra* and *S. caroliniana*, both adapted to high water levels, were greater in the upper canopy of the bayhead and bayhead swamp forests of Gumbo Limbo than in Black Hammock and Satinleaf.

Species:environment relationships may vary with the tree life-stage (Stohlgren et al. 1998) and are scale dependent (Wiser et al. 1996, Ehrenfeld et al. 1997,Vetaas and Chaudhary 1998, Drewa and Bradfield 2000). The nested hierarchical framework used for vegetation sampling in this study provided a way to examine the variability in species:environment relationships at different scales. In this study, the percentage of variation in species data explained by environmental variables was greater at the level of the entire vegetation zone (49.5%) than at the level of sampling plots along transects (9.9%). At the vegetation zone level, hydrology and organic matter were important variables within the tree islands, while hydrology, total carbonate and soil depth were significant among tree islands. At the transect plot level, other variables, such as elevation, soil pH and TN, were also significant. The reasons for this may be the scale-related variability in both environmental and biological factors (Reed et al. 1993, Ehrenfeld et al. 1997, Vetaas and Chaudhary 1998, Drewa and Bradfield 2000). The higher percentage of variation found at the level of the vegetation zone implies a coarser scaling of environmental conditions within tree islands. This observation is consistent with the recognition of four main vegetation zones along a hydrologic gradient. Within the study tree islands, vegetation composition is consistently correlated with elevation and associated variables, such as hydrology and soil nutrients, but its relationship to soil depth and total carbonate varies among sites. Furthermore, some factors, especially biological, such as the interactions among plant individuals, can contribute to some of the small scale variation seen in species composition, but are not represented among measured environmental variables (Ehrenfeld et al. 1997). For the herb layer, when canopy cover was included among the environmental variables, the relatively high percentage of variation in species data was explained by the first two CCA axes. The interpretation of our results may have limited implications as it is based on the one time collection of data at only three tree islands. In a system like tree islands, the degree of environmental gradients may change with time, meaning that a temporal dimension should also be considered when dealing with vegetation:environment relationships.

Productivity in tree island forest communities varies along hydrologic gradients. Megonigal et al. (1997) found that productivity in wet plots (water level >0 cm) was less than in dry plots (water level 0 to <60 cm) in hardwood bottomland forests of the southeastern United States. In general, flooding is considered a stress if the productivity of a forest composed of highly flood-tolerant trees species is lower than the nearby upland forest composed of trees adapted to drier conditions (Sharitz and Mitsch 1993). The current study also showed that above-ground production in tree islands is higher in dry sites than in wet sites. The reason may be due to flooding stress in trees growing in the bayhead and bayhead swamp communities.

Litter production in tree island plant communities showed seasonal variation to some extent; however, seasonality was more obscure with increasing hydroperiod. Tree island litterfall dynamics is mostly regulated by leaf shedding, since leaf material constituted the major portion of litter in these sites. Researchers have recognized the importance of soil moisture in leaf shedding (Lugo et al. 1978, Reich and Borchert 1984, Martinez-Yrizar and Sarukhan 1990). In general, trees growing in sites with low soil moisture content shed their leaves soon after the end of the wet season, while trees growing in sites with high soil moisture content drop their leaves later in the dry season (Martinez-Yrizar and Sarukhan 1990). Litter production in the hardwood hammock communities, areas which remain dry and are rarely flooded, was highest in the summer (mid-July to mid-October), corresponding to the wet season in southern Florida. However, the high litter production in hammocks during the winter season contradicts the findings of Martinez-Yrizar and Sarukhan (1990) for tropical deciduous forests; the reason for this may be linked to differences in species composition.

Plant species growing along the tree island hydrological gradient differ in flooding tolerance (Larson et al. 1981), though the reason for these differences may not always be the same. For example, the absence of upland species in areas subject to seasonal flooding is not always due to the lack of flood tolerance in those species (Lopez and Kursar 1999). In tree islands of Shark Slough, species appear to be distributed according to their differential flood tolerances. Based on the degree of tolerance, which is measured in terms of the ability to survive, grow and reproduce, plant species can be arbitrarily divided into several categories: very tolerant, tolerant, moderately tolerant and intolerant (McKevlin et al. 1998). In the current study, we focused on the occurrence of species along hydrological gradients, and do not have quantitative information on the flood tolerance characteristics of these species (however, see Chapter 8 of this report). Our ranking of species derived from hydroperiod and water level optima, however, clearly reveal that *Sideroxylon foetidissimum, Coccoloba diversifolia, Eugenia axillaris, Bursera simaruba, Celtis laevigata, Chrysophyllum oliviforme, Solanum erianthum, Simarouba glauca,, Myrsine floridana* and *Ficus aurea* occur on high ground and can be categorized as flood intolerant species as they have optimum hydroperiods <60 days (Figure 6-36). *Sambucus canadensis* and *Chrysobalanus icaco,* revealing hydroperiod optima between 60 and 150 days, are intolerant to moderately tolerant. The ranking of these species along water level optima coincides with those described by Armentano et al. (2002). The differences in their ground water level optima implies that management induced changes in water levels for prolonged periods in the Shark Slough could shift the dominance among these species within the hammocks of tree islands.

Tree islands, which are continuously flooded during the growing season, show species occurrences that are related to adaptive flood-tolerance characteristics. *Persea borbonia, Magnolia virginiana, Myrica cerifera, Salix caroliniana, Annona glabra,* and *Ilex cassine* have hydroperiod optima >180 days and are moderately tolerant to tolerant (Figure 6-36). Researchers have categorized some of these species based on their flood tolerances. For example, McKnight et al. (1981) reported that *P. borbonia* is moderately tolerant to tolerant, and Hook (1984) reported that *M. virginiana* is moderately tolerant. From this study, *M. cerifera, S. caroliniana*, *A. glabra*, and *I. cassine* are flood tolerant and reveal water level optima of 10 to 25 cm. The effect of flooding on these species has not been quantified. However, studies show that *M. cerifera* can tolerate short-term freshwater flooding (Tolliver et al. 1987) and willows (*Salix*) may die with prolonged (>3 yrs) flooding (Pereira and Kozlowski 1977). *A. glabra* grows in very wet environments and was once dominant along the south shore of Lake Okeechobee (Davis 1943). Although *I. cassine* has been found invading wet areas of south central Florida (Landman and Menges 1999), other species of *Ilex* are weakly tolerant to flooding (McKnight et al. 1981). In this study, the high water level optimum of *I. cassine* (the highest of all the species) is based on the occurrence of only a few individuals in bayhead forests of Gumbo Limbo and Satinleaf tree islands. The results of our shadehouse experiment on flood tolerances of trees common to Everglades tree islands (see Chapter 8 of this report) showed only moderate tolerance to flooding in this species.

Flood tolerance in plants depends on species, age, water quality, and duration and time of flooding (Kozlowski 1982). Therefore, in seasonally flooded wetlands, developing seedlings, saplings, and mature adults may vary in their degree of tolerance to inundation and soil saturation (Larson et al. 1981). In general, flooding tolerance increases with age and size up to tree maturity (Gill 1970, Kozlowski 1982). In many species, while mature trees can withstand flooding for several days, seedlings of the same species may be killed within few days after inundation. In such species, seedlings usually get established during dry periods and mature to the stage where they become able to survive subsequent flooding (Huffman and Forsythe 1981). In this study, however, seedlings of a few upland and many wetland tree species showed higher tolerances than the mature trees of the same species (Figures 6-36 and 6-37). The much higher hydroperiod optimum of *F. aurea* seedlings compared to mature trees is because *F. aurea* seeds usually germinate in moist conditions on some host plant or fallen wood; when the host plant later dies, *Ficus* continues to live. In the current study, the presence of a few seedlings of *F. aurea* growing on locally high spots in bayhead swamps yielded a high flood tolerance value. In some species, seedlings germinate on saturated soil and survive shallow flooding. Seeds of willows can even germinate in water; however, when seedlings are submerged or if flooding continues until late in the growing season, they die back (Kozlowski 1982). Though seedlings of a species in different populations may vary in their responses to flooding depending on their genotypes (Hook et al. 1987), our results were somewhat biased due to sampling schedules. Because two tree islands were accessible by only air boat when water levels in the slough were sufficiently high, most of the vegetation sampling was done in the fall (wet season). During that period, woody plant seedlings that had emerged during the preceding dry season were still present. Many of those seedlings would die by the end of the wet season, as we recorded for Satinleaf (Figures 6-20 and 6-21), a site only accessible during the spring. A detailed study of seedling population dynamics involving repeated sampling in different seasons would be needed to test the hypothesis that flood tolerances of seedlings are lower than for mature trees of the same species.

In general, the plant communities of Shark Slough tree islands occur along a continuum, from marsh to upland forest. Since vegetation zones on these islands are primarily determined by hydrologic gradients, changes in hydrology, including both water depth and duration of inundation, are more likely to affect the composition and aerial extent of the various zones. In the past, such changes occurred owing to variation in the climatic regime and natural water flows over a period of hundreds of years (see Chapter 5 of this report). The effects of these factors will be more pronounced in the bayhead portions of tree islands which are adapted to alternating periods of wet and dry conditions caused by increases and decreases in water levels. In the tropical hardwood hammocks of tree islands, areas which have rarely flooded in the past and are unlikely to be flooded under hydrologic changes predicted under CERP, vegetation composition will respond to changes in ground water levels.

7

Notes and Observations on the Use of Tree Island Habitat by Wildlife

Pablo L. Ruiz

Introduction

Animals are a significant component of the Everglades ecosystem and occupy a full range of trophic levels. Except for a few well-studied species (e.g., Cape Sable Seaside Sparrow, Whitetail Deer, Florida Panther, American alligator), little is known about the relationship between wildlife and vegetation communities of the Everglades. Few studies have documented wildlife in Everglades tree islands, although the recent papers by Gaines et al. (2002) and Meshaka et al. (2002) are noteworthy.

Though not part of the original scope of work for the current project, an annotated list of wildlife species was created from anecdotal information derived from three years of observations in three tree islands in Shark Slough: Black Hammock (BL), Gumbo Limbo Hammock (GL), and Satinleaf Hammock (SL).

Results and Discussion

Table 7-1 lists the animal species observed, and the tree island forest communities they were associated with, by class. Only observed, living animals were included; bones, scat, and other animal signs were not used as a basis to list a species. The sections that follow describe each of the six classes of animals in greater detail.

Class Amphibia

The only member of this class observed using tree island habitat was *Hyla cinerea* (Green Treefrog). This charismatic, 3-6 cm long green frog was found throughout our study area, where it hid predominately in ½” and ¾” diameter PVC pipes used to mark our vegetation sampling plots. In some cases, more than one individual could be seen within the cavity of the pipes.

Class Arachnida

The only member of this class observed using tree island habitat was *Nephala clavipes* (Golden Orb Spider). Observations of *N. clavipes* were largely restricted to the hardwood hammock community of all three tree islands, with one observation in the bayhead forest community of GL (Table 7-1). Overall, *N. clavipes* was most abundant in BL.

Table 7-1. The observed wildlife of Satinleaf, Black Hammock, and Gumbo Limbo tree islands.

Class	Species Name	Common Name	Tree Island Plant Community		
			Hammock	Bayhead	Bayhead Swamp
Amphibia	*Hyla cinerea*	Green Treefrog	*	*	*
Arachnida	*Nephala clavipes*	Golden Orb Spider	*	*	
Aves	*Agelaius phoeniceus*	Red-winged Blackbird	*	*	*
	Aramus guarauna	Limpkin			*
	Buteo lineatus	Red-shouldered Hawk	*		*
	Cardinalis cardinalis	Northern Cardinal	*	*	
	Cathartes atratus	Black Vulture	*		
	Cathartes aura	Turkey Vulture	*		
	Dendroica palmarum	Palm Warbler	*		
	Geothlypis trichas	Common Yellowthroat		*	*
	Mniotilta varia	Black-and-white Warbler	*		
	Polioptila caerulea	Blue-gray Gnatcatcher	*		
	Quiscalus quiscula	Common Grackle	*	*	*
	Setophaga ruticilla	American Redstart	*		
	Strix varia	Barred Owl	*		
Insecta	*Agraulis vanillae*	Gulf Fritillaries			*
	Camponotus sp.	Carpenter Ant	*	*	*
	Danaus gilippus	Queen Butterfly			*
	Heliconius charithonius	Zebra Longwing Butterfly			*
	Papilio cresphontes	Giant Swallowtail		*	*
Mammalia	*Odocoileus virginianus*	Whitetail Deer	*		
	Sus scrofa	Feral Pig	*	*	
Reptilia	*Alligator mississipiensis*	American Alligator	*	*	*
	Anolis carolinensis	Green Anole		*	*
	Elaphe obsoleta rossalleni	Yellow Rat Snake		*	
	Eumeces inexpectatus	Southeastern five-lined skink	*	*	
	Farancia abacura abacura	Eastern Mud Snake	*		
	Nerodia taxispilota	Brown Water Snake		*	
	Opheodrys aestivus carinatus	Florida Rough Green Snake			*
	Sistrurus miliarius barbouri	Dusky Pygmy Rattlesnake	*	*	
	Thamnophis sauritus sackenii	Peninsula Ribbon Snake			*

Class Aves

Species diversity in this class was the highest with 13 individual species. Of these, the Common Grackle (*Quiscalus quiscula*) was the most frequently encountered and, by far, had the largest number of individuals observed at any given time regardless of season. Observation frequencies for all other species, however, varied throughout the year, with most observations taking place in late fall or winter. This was particularly true for *Dendroica palmarum* (Palm Warbler), *Geothlypis trichas* (Common Yellowthroat), *Mniotilta varia* (Black-and-white Warbler), *Polioptila caerulea* (Blue-gray Gnatcatcher) and *Setophaga ruticilla* (American Redstart). Of these, *G. trichas* was the most commonly encountered species.

The portions of tree islands utilized by birds varied among species (Table 7-1). Most species were observed exclusively in the hammock forest communities of the tree islands studied. However, two species were encountered in all three tree island forest types, *Agelaius phoeniceus* (Red-winged Blackbird) and *Quiscalus quiscula.*

Bird nests were rarely encountered. However, *Buteo lineatus* (Red-shouldered Hawk) was observed nesting in the hardwood hammock forest of BL in 2001. Small oval nests constructed of plant material on small shrubs were occasionally encountered in the bayhead swamp forest of all three tree islands. Unfortunately, we were unable to determine the species responsible for the construction of these nests because, at time of observation, all nests were abandoned.

Class Insecta

The most frequently encountered member of this class was the mosquito. However, mosquito numbers varied both among the three tree islands and among the tree island forest communities. In response to increased marsh water levels, mosquito numbers generally decreased first in the bayhead swamp community, then the bayhead community, and finally the hardwood hammock forest.

Ants, as a group, were well represented within the three tree island community types. We were unable to identify most of these species. However, we were able to identify one ant species to genus, *Camponotus* (commonly know as Carpenter ants). We found *Camponotus* nesting within dying or dead tree branches or trunks in all three tree island forest communities.

Butterflies, in general, were observed in the bayhead and bayhead swamp forests of the tree islands studied. Of the four species listed in Table 7-1, the Queen butterfly (*Danaus gilippus*) was the most abundant. This species was frequently spotted visiting the flowers of *Sarcostemma clausum* (Jacq.) Roem. & Schult. (White Twinevine) of the family Asclepiadaceae in the bayhead swamp community of our tree islands. The Giant Swallowtail (*Papilio cresphontes*) was the only butterfly species observed to frequent the bayhead forest of these tree islands.

Class Mammalia

Mammal observations were limited to two species, *Odocoileus virginianus* (Whitetail Deer) and *Sus scrofa* (Feral Pig), the latter an introduced domesticated pig with an indiscriminate diet that includes plants and fruits (e.g., *Annona glabra* L. or Pond Apple), eggs, snakes, insects, small mammals, roots, and tubers. Moreover, because of its diet and destructive nature, *S. scrofa* is a serious problem for tree island ecosystem health. Fortunately, sightings of *S. scrofa* were limited to the hardwood hammock and bayhead forest communities of GL.

Class Reptilia

After birds, this class showed the highest diversity of species observed but was probably the least frequently observed group of species. Overall, the use of tree island forest communities by this group varied greatly, with most species preferring the bayhead forest. However, the use of multiple habitats by a species was common.

The use of the hardwood hammock forest as a nesting site for several species, most notably turtles, was evident from the observation of eggs and/or egg shell fragments. Turtles are not included in Table 7-1, however, because no living animals were actually seen. *Farancia abacura abacura* (Eastern Mud Snake) was also observed guarding a nest in the hardwood hammock forest of GL.

After the Green Anole (*Anolis carolinensis*), the most frequently encountered species was *Sistrurus miliarius barbouri* (Dusky Pygmy Rattlesnake). This 38-79 cm long venomous snake was very common in the hardwood hammock forest community of GL, where up to five individuals were observed in a single day. This species was also observed in SL on one or two different occasions. Despite its ominous name, we found the Dusky Pigmy Rattlesnake to be shy and non-threatening.

Conclusions

Without question, the tree islands of Shark Slough are an important habitat resource for the wildlife of the Everglades. Tree islands act as refugia for wildlife – they provide high ground, food, roosting, and a nesting site for many species. This is clearly the case for the marsh rice rat (*Oryzomys palustris*) and the hispid cotton rat (*Sigmodon hispidus*) (Gaines et al. 2002), as well as some if not all of the species cataloged in this section. However, much remains unknown about the biological needs and habitat requirements of many of these species and the role of tree islands. Furthermore, as the Everglades restoration plans unfold, it is important that biologists, resource managers, and policy makers take into account not just how restoration efforts will impact or improve the vegetative component of the Everglades, but how the restoration might impact the wildlife that appears tightly bound to the tree island habitat. This, however, is a daunting task because of the lack of information available about the diversity of wildlife that populates the tree island communities of the Everglades.

Experimental

8

Responses of Tree Island Tree Species to Simulated Hydrologic Regimes: A Shadehouse Study

David T. Jones, Jay P. Sah, Michael S. Ross, Steven F. Oberbauer, Bernice Hwang and Krish Jayachandran

Introduction

Tree islands are one of the most sensitive components of the Everglades landscape to changes in regional hydrology. Extremes in marsh water levels, resulting from water management practices in the Everglades, can have serious consequences for biodiversity and biogeochemical processes in islands (Loveless 1959, Craighead 1971, 1984, McPherson 1973, Alexander and Crook 1984, Brandt et al. 2000). Prolonged periods of high water may adversely affect the condition of tree islands via death or dieback in flood-intolerant species. Similarly, persistent low water may create conditions of extreme fire risk, during which tree islands may be catastrophically damaged.

The loss of tree islands and their associated historical, cultural and biological values have raised awareness of the fragility of these habitats and stimulated a resurgence of interest in their study and preservation. Maintaining and/or restoring the health of tree islands (and other Everglades habitats) are components of the Comprehensive Everglades Restoration Plan (CERP), a multi-agency project designed to restore and enhance the freshwater resources and natural environments of southern Florida (USACE 1999). Consequently, there is a need within CERP for tools to assess the health of tree islands, and to relate these measures to the hydrologic regime to which they are exposed. Flood response and other ecophysiological characteristics of tree island species are a critical element in the formulation of these performance measures.

While responses of tree island communities to hydrologic conditions throughout the Everglades have received some attention (Loveless 1959, Craighead 1971, 1984, McPherson 1973, Alexander and Crook 1984, Brandt et al. 2000), the responses of constituent tree species are not well documented. Guerra (1997) and Jones et al. (1997) evaluated tree island vegetation in the southern Everglades after a period of prolonged high water in 1994-95 and noted its effects on individual tree and shrub species. Conner et al. (2002) reviewed flood tolerance in ten common tree island species based on flood impact studies conducted largely in bottomland forests in other parts of the southern United States. In the only reported greenhouse study, Gunderson et al. (1988) examined the effects of a range of hydrologic conditions, including flooding, on seedling growth and morphology in five Everglades tree island species. None of these studies attempted to assess physiological responses of plants, and, between the latter two, only three upland (hardwood hammock) forest species were examined compared to nine swamp forest species. In order to gain insight into species responses in the field, a controlled study combining morphological and physiological measurements on a broad range of hydric and mesic tree island species growing under different hydrologic regimes is needed.

Studies in other ecosystems have successfully used morphological (e.g., root and stem biomass, height, stem diameter, leaf area, comparative anatomy) and physiological parameters (e.g., chlorophyll fluorescence, leaf water potential, relative water content, gas exchange, stomatal conductance) to elucidate tree responses to water stress induced by flooding and drought (Regehr et al. 1975, Pereira and Kozlowski 1977, Ögren and Öquist 1985, Ewing 1996, Schmull and Thomas 2000, Anderson and Pezeshki 2001, Davanso et al. 2002). Previous studies have shown that flooding to or above the soil surface may result in a range of adverse responses, from diminished growth and photosynthesis to death, in seedlings and saplings (Keeley 1979, Pezeshki and Chambers 1986, Ewing 1996, Lopez and Kursar 1999, Schmull and Thomas 2000, Davanso et al. 2002) and trees (Broadfoot and Williston 1973, Harms et al. 1980, Vu and Yelenosky 1991, Ewing 1996, McKevlin 1998). Fernandez et al. (1999) concluded that a decrease in photosynthetic rate and leaf conductance may be related to reduced flood tolerance.

The objectives of our study were threefold. First, we compared growth and physiological responses in 12 common tree island species subjected to three realistic hydrologic regimes (i.e., high, low, and no flood) under controlled conditions in a shadehouse. Tree height, basal stem diameter, crown volume, plant condition, and mortality were used to assess growth and survival, while stomatal conductance, chlorophyll fluorescence, and leaf relative water content were measured to assess physiological performance. Second, we determined the timing and sequence of adverse growth and physiological responses for each species, to elucidate common patterns in these responses among species. Third, we compared the relative flood tolerances of the species tested in the shadehouse to their observed distribution along the hydrologic gradient in tree islands under natural conditions.

We hypothesized that increased flooding would adversely affect the growth and physiological activity of plant species adapted to tree islands. We predicted that the adverse responses would be more pronounced and occur earlier in the tropical hardwood forest tree species compared to the swamp forest species, and the greatest effects would be seen under conditions of high flood rather than low or no flood. We also expected that relative flood tolerances of the species tested in the shadehouse would reflect their observed distribution along the hydrologic gradient in tree islands under natural conditions.

Methods

Species Studied

The names and distributions of the 12 tree species used in this study are listed in Table 8-1. Plant species are referred hereafter by their genus name. Seven swamp forest species were selected, all temperate in origin, except *Annona* and *Chrysobalanus*, which are largely tropical. In southern Florida, these species prefer wet habitats and are common elements of the seasonally flooded portions of tree islands. The remaining five upland forest species are broadly distributed in the American tropics, with southern Florida at the northern limit of their ranges. Within the Everglades, they can be found in the most elevated portions of the tree islands, commonly referred to as hardwood hammocks, as well as in other mesic forest sites. All 12 species are evergreen, with the exception of *Salix* (deciduous), and *Annona* and *Bursera* (semi-deciduous) (Tomlinson 1980).

Table 8-1. List of species and their distributions. Species are grouped by their habitat preference in southern Florida.

Species[1]	Family	Distribution[2,3]
	Swamp Forest Species	
Annona glabra L.	Annonaceae	West Africa, southern Florida, West Indies, Mexico to South America
Chrysobalanus icaco L.	Chrysobalanaceae	West Africa, West Indies, Mexico to South America, southern Florida
Ilex cassine L.	Aquifoliaceae	Virginia to southern Florida, Cuba, Bahama Islands
Magnolia virginiana L.	Magnoliaceae	eastern U.S. from Massachusetts to southern Florida
Myrica cerifera L.	Myricaceae	Bermuda, Greater Antilles, Central America, eastern U.S. from New Jersey to southern Florida
Persea borbonia L.	Lauraceae	Gulf and Atlantic States of U.S.
Salix caroliniana Michx.	Salicaceae	southeastern U.S. from Virginia to southern Florida, Cuba
	Upland Forest Species	
Bursera simaruba (L.) Sarg.	Burseraceae	West Indies, southern Florida, Mexico to northern South America
Coccoloba diversifolia Jacq.	Polygonaceae	West Indies, southern Florida
Eugenia axillaris (Sw.) Willd.	Myrtaceae	southern Florida, Bermuda, West Indies, Central America
Sideroxylon foetidissimum Jacq.	Sapotaceae	West Indies, Mexico, Belize, southern Florida
Simarouba glauca DC.	Simaroubaceae	West Indies, Central America, southern Florida

[1] Wunderlin (1998), [2] Little (1978), [3] Tomlinson (1980)

Plant Acquisition and Experimental Design

During May and June of 2001, a minimum of 100 recently emerged seedlings of each species were collected from tree islands in Shark Slough, Everglades National Park, Florida. Seedlings were transferred to 5 cm peat pots containing commercial organic potting soil and placed in a glasshouse. After approximately eight weeks, the young plants were transferred to 26.5 L plastic pots containing a commercially available garden soil (pH 6.4, 32% total carbon) and raised in a temporary shadehouse where they remained until the end of the experiment. The shadehouse was a steel-framed structure, 3.4 m high, whose top was covered with a woven, synthetic shadecloth that provided 50% full sun. In early March of 2002, three weeks before the experiment commenced, healthy plants selected for the study were treated with a systemic insecticide, Marathon® 1% Granular (Olympic Horticultural Products Co., Mainland, PA, USA), and a controlled release fertilizer, Osmocote® PLUS 15-9-12 (Scotts-Sierra Horticultural Products Co., Marysville, OH, USA), according to label directions.

Each species was subjected to three flooding treatments for 25 weeks: high flood (HF), low flood (LF), and no flood (NF). The experimental design was randomized complete block, with 12 species and 3 treatment combinations represented twice in each of four blocks for a total of 288 plants. Plants were stratified among the three treatments according to height and randomly placed within blocks. The blocks were self-rising, inflatable swimming pools (Intex Easy Set™, Intex Recreation Corp., Long Beach, CA, USA), 4.6 m in diameter, placed in the shadehouse. Pots subjected to HF and LF, representing realistic hydrologic regimes found at the lower and higher ends, respectively, of the tree island swamp forest environmental gradient, were maintained in each pool at the relative heights of 6.8 and 33.9 cm, respectively. These heights included a 6.8 cm deep layer of rocks added to the bottom of each pot to prevent tipping during periodic high winds. HF pots were placed on the floor of the pools, while LF pots were placed on pedestals (inverted plastic pots) at the designated height. Pots subjected to NF, representing the hydrologic regime found in the relatively higher tropical hardwood forest of tree islands, were maintained at a height of 63.8 cm (with rock layer). The relative heights of the three treatments were determined from topographic surveys conducted along the elevation gradient of a typical tree island in Shark Slough (M. Ross, unpublished data).

Water levels, equal in all pools, varied over the course of the experiment to mimic variation in mean weekly water depths from the years 1990 through 1999 as recorded by U.S. Geological Survey (USGS) groundwater hydrostation G620 located in Shark Slough. This station was chosen as a source of water depth data because of its proximity to the tree island selected for the topographic survey described above. Before the pools were filled with water, pots assigned to treatments HF and LF were topped off with enough garden soil to bring the final soil depth to 26.7 cm. Nylon mesh was then placed across the soil surface of each pot and secured with wire to prevent soil loss due to accidental tipping. Pots were arranged in the pools, and the pools were filled with piped water (pH 7.7) to the appropriate level.

The experiment began on April 7, 2002, which coincided with the beginning of the growing season in southern Florida. Every seven days thereafter, water levels were adjusted by adding or removing water according to the experimental weekly water depth schedule (Figure 8-1). Following this schedule, under HF, water levels exceeded the bottoms of pots on day 1 and reached the soil surface at week 10. Under LF, the bottoms of pots first encountered the rising water at week 10 and the soil surface would have been inundated at week 28 had the experiment not been concluded before that date (see below). Because pots would not be subjected to any flooding under NF, they were placed outside and around the pools. Under NF, plants required regular watering, while all others were watered by hand whenever the soil surface appeared dry, especially in the earlier weeks of the experiment when water levels were low. For logistical reasons associated with rapid growth in several species x treatment combinations (e.g., competition among individuals for light, outgrowing the shadehouse), the experiment was terminated after 25 weeks of treatment.

Mortality and Plant Condition

Plant condition was determined by subjectively assessing each individual tree using several criteria and assigning an overall numerical score. The criteria used were proportion of live to old stems and foliage, new shoot growth and leaf expansion, leaf coloration (green versus yellowing), leaf turgidity, and occurrence of pests and disease (e.g., gall formation and other damage by insects). Numerical scores ranged from '1' (representing a near dead individual) to '5' (representing a healthy individual); dead individuals were assigned a value of '0'. Plant condition was the only measurement used in this study in which all individuals were assessed weekly. Mean condition of surviving individuals was calculated weekly for each species and treatment, and mortality was tracked on the same interval. Plants that appeared dead were kept in their pools and observed for several more weeks until their status (dead or alive) could be ascertained; dead trees were then removed from the block.

Growth Measurements

Height, basal diameter, and crown volume of all individuals were measured during the week prior to treatment (week 0), then at 6, 12, 18, and 24 weeks after initiation of the experiment. Height from the top of the soil in each pot to the highest point of the tree (not always the apical meristem) was recorded to the nearest cm. Diameter was measured using a plastic dial caliper to the nearest tenth of a millimeter. In most cases, trees produced a single stem that was measured at a point approximately 2 cm above the soil surface. For individual trees that produced multiple stems arising at or near soil level, as in *Myrica* and *Salix*, the most vigorous stem was selected for measurement. To ensure that each stem was measured at the same place, red paint was applied in a narrow band around the stem at the point of measurement. Crown volume was estimated by modeling the tree crown as a series of conic frustums of 10 cm height and terminal cones of smaller height (Figure 8-2). Crown volumes of individuals with crown depths of at least 30 cm were measured by taking crown width measurements at intervals of 10 cm along the stem and totaling the volume of each conic frustum (Figure 8-2a); volumes of conic frustums were then summed to estimate total crown volume. For individuals with crown depths of less than 30 cm, lengths of the basal and widest portions of the crowns, their perpendicular widths, and their distance to crown tops were measured (Figure 8-2b). Volumes of the conic frustum and cone were then summed to estimate total crown volume.

Physiological Measurements

Stomatal conductance, chlorophyll fluorescence, and leaf relative water content were measured, at weeks 3, 6, 12, 18, and 24. Four individuals from each species-treatment combination (one from each pool) were selected for the measurements. Measurements were conducted in the shadehouse on young, fully expanded, intact leaves. We attempted to standardize measurements by taking data under sunny, dry conditions, between the hours of 0900 and 1500, whenever possible. A different leaf was selected for each sampling week.

Conductance provides a sensitive physiological indicator of stress (Sojka 1992). A LI-1600 steady state porometer (LI-COR Biosciences, Lincoln, NE, USA) was used to measure conductance to water vapor. Attached leaves were inserted in the porometer and measured after 60 s. Fluorescence has been widely used to monitor changes in the photosynthetic activity of terrestrial plants subjected to environmental stresses (reviewed by Renger and Schreiber 1986). Fluorescence yield, expressed in terms of the ratio of variable fluorescence to maximal fluorescence (F_v/F_m), an indicator of the photochemical efficiency of photosystem II (PSII), was measured using an OS1-FL pulse modulated chlorophyll fluorometer (Opti-Sciences, Inc., Tyngsboro, MA, USA). Leaves were dark-adapted for 10 min before measurement. Relative water content is a robust indicator of plant water status for comparison of species (Lawlor and Cornic 2002) and is a less destructive method than leaf water potential. Two 6 mm diameter discs were punched from a leaf and immediately weighed to obtain fresh weight (fw). Discs were then wrapped in saturated paper toweling and kept in small, sealed petri dishes in the lab at room temperature for 16-20 h and reweighed after blotting dry to obtain saturated weight (sw). Discs were then placed in an oven at 60 ^{o} C for 24 h and reweighed to obtain the dry weight (dw). Relative water content was calculated using the formula of J. Čatský (in Slavík 1974):

$$\text{Relative water content (\%)} = (fw-dw)/(sw-dw) \times 100.$$

Statistical Analyses

A split-plot design approach was used to analyze the main effects of species, hydrologic treatment, and time. In standard repeated measures ANOVA, which resembles multivariate analysis of variance (MANOVA), a single missing value causes the entire subject to be omitted from analysis in a listwise deletion procedure. When missing values are common, split-plot ANOVA is an effective alternative approach to analyze repeated measures data (Maceina et al. 1994). In our study, missing values resulted primarily from the mortality of individual plants. In addition, on several occasions, physiological data could not be collected because of equipment malfunction, or in the aftermath of leaf shedding events or herbivore outbreaks that affected several species; these were considered to be random events for the purpose of data analysis.

In preliminary analyses, the effect of Block (the four pools) on all six parameters was found to be non-significant; replicates for each species-treatment combination were therefore pooled together for subsequent analyses. An initial examination of the data also revealed that measurements of stomatal conductance during week 6 were anomalously high across all treatments, and many of these values were identified as statistical outliers. We eliminated this sampling period entirely from the analysis of variance in stomatal conductance. For all dependent variables, when ‘F’ tests for main effects in the split-plot ANOVA were found to be significant, multiple comparison tests among treatments were conducted for each species-week combination, using the Fisher’s least significant difference (LSD).

Trends in plant growth and physiology were examined in more detail in four taxa that represented groups of species with similar response to the three treatments. To define these groupings, we used agglomerative cluster analysis (Goodall 1973), with Euclidean distance used as a dissimilarity measure and Ward’s linkage method of calculating relation among species. Analysis was performed on six composite variables obtained by applying Principal Component

Analysis (PCA) to response data collected throughout the experiment. Data included species periodic means for all three morphological variables, stomatal conductance, chlorophyll fluorescence and overall plant condition, and week of occurrence of first mortality. Responses to the HF and LF treatments were standardized by dividing mean periodic values for each species by their values under the NF treatment.

For each of the four representative species, coefficients of response curves generated by individual plants were analyzed to test whether treatments differed in response patterns over time (Meredith and Stehman 1991; Carlton and Bazzaz 1998). For each individual, linear, quadratic and cubic coefficients of response curves were obtained by calculating weighted sums of the repeated measurements, using the relevant contrast coefficients as the weights (Gurevitch and Chester 1986). Contrast coefficients for morphological variables were obtained from Keppel (1973: Table C-2). For physiological variables, which were measured at unequal intervals, linear and quadratic coefficients were calculated using methods described in Keppel (1973). Treatment effects on the response curve coefficients were then assessed by one-way ANOVA. In these analyses, quadratic and cubic terms represent U-shaped and S-shaped temporal trends, respectively (Gurevitch and Chester 1986).

Results

Flooding treatment had significant ($p < 0.001$) effects on height, basal diameter and crown volume of the twelve plant species considered over the 25 week study period (Table 8-2). In eight of 12 species, mean height, basal diameter and crown volume were greater in LF than in HF and NF treatments. Physiological response of plants showed mixed results, however. Chlorophyll fluorescence differed significantly ($p < 0.001$) among species and treatments, while stomatal conductance only differed among species. Relative water content differed significantly among species but showed only a marginal treatment effect ($p = 0.049$). A significant species x treatment interaction was observed for all parameters except relative water content, and all morphological and physiological parameters were affected by Time (Table 8-2).

The cluster analysis produced four groups of species at the 50% information remaining level (Figure 8-3): two groups of swamp forest species, one group of upland forest species, and an intermediate group combining both swamp and upland species. The swamp species group of *Annona* and *Salix* (Swamp Group 1) was sister to a second, larger swamp group comprising *Myrica*, *Chrysobalanus*, *Magnolia*, and *Ilex* (Swamp Group 2). Four upland species, *Coccoloba*, *Bursera*, *Simarouba*, and *Sideroxylon*, formed a single group (Upland Group). The fifth upland species, *Eugenia*, combined with the swamp species *Persea* in a grouping (Intermediate Group) that was most closely aligned with the Upland Group. The results that follow are presented in terms of these groups.

Tree Mortality

Under HF, all four species of the Upland Group and *Eugenia* of the Intermediate Group showed mortalities of between 50 and 100%, while *Magnolia* and *Ilex* of Swamp Group 2 and *Persea* of the Intermediate Group showed mortalities of between 25 and 40% (Table 8-3). Seven of these species first exhibited losses of individuals between weeks 13 and 16 (only *Sideroxylon* showed some mortality at week 13) under this treatment. Mortality was not observed in *Eugenia* until week 19, the latest for any species.

Table 8-2. F-statistics from split-plot ANOVA for repeated measures data testing morphological and physiological responses to three hydrologic treatments in twelve species. Number of repeated measures (t) = 5 and number of replicates per species x treatment combination (n) = 8 for height (HT), basal diameter (BD), and crown volume (CV); t = 5 & n = 4 for chlorophyll fluorescence (CF) and relative water content (RWC); and t = 4 and n = 4 for stomatal conductance (SC). * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$

Source	HT	BD	CV	SC	CF	RWC
Species	79.7***	177.9***	50.7***	14.7***	12.0***	10.7***
Treatment	19.9***	13.1***	30.1***	5.8**	59.7***	3.8*
Species*Treatment	2.5***	2.9***	3.3***	2.8***	5.2***	0.3
PlantID (Species*Treatment)	5.8***	5.8***	2.5***	1.4*	0.9	1.0
Time	966.8***	818.6***	297.1***	20.7***	28.4***	35.3***
Species*Time	21.3***	50.7***	21.1***	4.7***	2.8***	1.1
Treatment*Time	35.0***	22.1***	30.8***	9.3***	8.7***	0.7
Species*Treatment*Time	3.2***	5.6***	3.4***	1.9***	1.9***	1.0

Only *Simarouba*, *Sideroxylon*, and *Bursera* of the Upland Group showed some mortality under LF (Table 8-3); these species had the highest mortality under HF as well. Under LF, *Simarouba* and *Bursera* exhibited their earliest mortalities at weeks 15 and 17, respectively, values comparable to the first mortalities seen in the majority of species under HF. The single mortality seen in *Sideroxylon* occurred at week 24.

Four species, *Annona* and *Salix* (Swamp Group 1) and *Myrica* and *Chrysobalanus* (Swamp Group 2), did not experience any mortality under HF and LF. No mortality occurred in any species under NF.

Plant Condition

Most species showed an increase in plant condition under HF within the first eight weeks, followed by a period of no change, then a decline (Figure 8-4). Compared to the Upland and Intermediate Groups, both Swamp Groups were generally less adversely affected in terms of the onset and rate of decline in plant condition under HF. Small declines were observed as late as weeks 22 and 18 in *Annona* and *Salix*, respectively. Greater declines were seen in *Myrica*, *Chrysobalanus*, and *Magnolia* of Swamp Group 2 and *Eugenia* and *Persea* of the Intermediate Group, commencing at weeks 19, 14, 12, 13, and 11, respectively. *Ilex* of Swamp Group 2 performed as poorly as the upland species, experiencing a steady decline in condition as early as week 10. All four species of the Upland Group experienced the largest cumulative declines. The onset of declining condition in these species occurred at weeks 9-10, when water levels first inundated the soil surface in pots. Yellowing of leaves (widespread in *Magnolia*), leaf fall (notable in *Ilex* and *Simarouba*), and insect herbivory (various species, most notably *Coccoloba*, *Persea*, and *Salix*) were the prevalent health problems affecting ratings under this treatment.

Figure 8-3. Tree mortality after 25 weeks of experimental treatments. Values are percentage of dead individuals. Numbers in parentheses are week of earliest mortality observed. Species are arranged from highest to lowest mortality under the high flood treatment.

Species	Mortality (%) by Treatment		
	High Flood	Low Flood	No Flood
Simarouba glauca	100(15)	25 (15)	-
Sideroxylon foetidissimum	100 (13)	13 (24)	-
Bursera simaruba	75 (15)	50 (17)	-
Coccoloba diversifolia	50 (14)	-	-
Eugenia axillaris	50 (19)	-	-
Magnolia virginiana	38 (16)	-	-
Ilex cassine	25 (16)	-	-
Persea borbonia	25 (16)	-	-
Annona glabra	-	-	-
Chrysobalanus icaco	-	-	-
Myrica cerifera	-	-	-
Salix caroliniana	-	-	-

Under LF, some species experienced a decline in mean ratings over time (Figure 8-4). Compared to HF, the onset of these declines occurred earlier in *Magnolia*, at the same time in *Annona* and *Bursera*, and later in *Coccoloba*, *Eugenia*, *Sideroxylon*, and *Simarouba*. Among the remaining species, all of which were from the two swamp groups, with the exception of *Persea*, mean condition under LF either increased or did not change over time. Herbivory was the most commonly observed health problem affecting plant condition under this treatment.

Growth Responses

Crown volume, tree height and basal diameter responses were similar, therefore only the former are presented here (Figure 8-5). Crown volumes in *Annona* (Figure 8-5a) and *Salix* of Swamp Group 1 increased throughout the study under all three treatments. In *Annona*, the treatments elicited significantly different linear (p = 0.001) and quadratic (p = 0.025) growth trends (Table 8-4). In this species, crown volumes did not differ among the three treatments through the first 12 weeks, but there was an acceleration of growth under LF after week 12 (week 18 in *Salix*), resulting in a difference in growth trends under LF and the other two treatments (Table 8-4). At the end of the study, crown volumes in *Annona* under HF and NF did not differ significantly.

Table 8-4. Summary of ANNOVA results showing linear and quadratic trends in treatment effects (df = 2) on crown volume and stomatal conductance in four species.

Species	Crown volume					Stomatal conductance				
	df (error)	Linear		Quadratic		df (error)	Linear		Quadratic	
		F	*p*	F	*p*		F	*p*	F	*p*
Annona	21	9.77	0.001	4.40	0.025	8	3.59	0.077	0.95	0.427
Bursera	11	6.76	0.012	1.81	0.209	3	2.01	0.280	9.83	0.048
Chrysobalanus	21	7.33	0.004	8.04	0.003	8	7.92	0.013	1.24	0.339
Persea	19	6.27	0.008	7.37	0.004	9	6.42	0.019	0.84	0.463

Chrysobalanus, representing Swamp Group 2, was similar to *Annona* in its crown volume response, although linear growth trends under both LF and NF were significantly (LSD pairwise tests, $p < 0.05$) greater than under HF (Figure 8-5b). Crown volume under LF and NF continued to increase after week 12, when growth under HF started to slow down, resulting as well in a significantly different quadratic trend. At the end of the study, crown volume in *Chrysobalanus* under NF did not differ significantly from HF or LF. Among the remaining species in Swamp Group 2, *Magnolia* and *Myrica* exhibited similar growth trends to *Chrysobalanus*. *Ilex* differed, however, experiencing a decline in crown volume under HF after week 12.

Crown volumes in *Persea*, representing the Intermediate Group, increased throughout the study under all three treatments, except for a decline under HF after week 18 (Figure 8-5c). Differences in linear and quadratic trends among treatments were highly significant in this species (Table 8-4). The growth trend was similar (roughly linear) under LF and NF, with slight acceleration starting at weeks 12 and 6, respectively. Under HF, the growth trend was quadratic (U-shaped), due to an increase in crown volume through week 18, followed by a decrease. As in Swamp Group 2, crown volumes under LF and NF in *Persea* (and *Eugenia*, also of the Intermediate Group) did not differ throughout the study.

Representing the Upland Group, *Bursera* showed an increase in crown volumes under LF and NF throughout the study, but experienced a decrease under HF after week 6 (Figure 8-5d). In this species, the linear growth trend differed significantly ($p = 0.012$) among treatments. However, despite an apparent distinction in growth trends among three treatments – an upward trend under LF and NF and an inverted-U shaped trend under HF (Figure 8-5d) - the quadratic terms did not differ significantly ($p = 0.209$) among treatments, in part because of low statistical power due to mortality and loss of replication (only three individuals of *Bursera* survived under both HF and LF). The remaining species of this group (*Coccoloba*, *Sideroxylon*, *Simarouba*) showed similar responses. Like Swamp Group 2 and the Intermediate Group, crown volumes under LF and NF in the Upland Group did not differ throughout the study.

Physiological Responses

Mean leaf relative water content and chlorophyll fluorescence responses were similar among all species and showed little or no change throughout the study. Among the physiological parameters, only stomatal conductance responses are presented here (Figure 8-6). In *Annona*, representing Swamp Group 1, mean stomatal conductance decreased under HF and NF over the study period, while under LF, it peaked at week 12 before declining (Figure 8-6a). Mean stomatal conductance under LF at week 12 was significantly higher than HF and NF. However, neither the linear nor the quadratic trends differed significantly among treatments. Stomatal conductance values under HF for *Salix* were the highest of all species after week 3.

In *Chrysobalanus*, representing Swamp Group 2, mean stomatal conductance varied broadly over the study period, with the linear trend differing significantly among the treatments (Table 8-4). Mean stomatal conductance was lowest under HF at week 18. In contrast, conductance was highest under LF and NF during week 18, and declined thereafter (Figure 8-6b). *Ilex* and *Magnolia* showed similar responses, though the decline under HF occurred earlier, at week 12, in the latter species. Stomatal conductance under HF for *Myrica* was the highest of all species in Swamp Group 2 after week 12 and was slightly greater than *Salix* of Swamp Group 1 at week 24.

Persea (Figure 8-6c) and *Eugenia* of the Intermediate Group were most similar to Swamp Group 2, with mean stomatal conductance under HF significantly lower than under LF and NF. Trend analysis in *Persea* indicated that only the linear term differed significantly among treatments. At week 3, mean stomatal conductance did not differ among treatments; differences first became evident at week 12, and were apparent at weeks 18 and 24.

Bursera (Figure 8-6d) of the Upland Group showed the lowest stomatal conductance values under HF of any species during weeks 12 through 24. In this species, stomatal conductance under NF declined from week 3 through week 24. At week 3, stomatal conductance under LF was significantly lower than under HF or NF (LSD test; $p < 0.003$ and 0.001, respectively), but peaked under this treatment during week 12 before declining. By the end of the experiment, there was no significant difference in stomatal conductance among treatments. Analysis indicated no difference in the linear trend, but a significant difference in the quadratic trend among treatments. The responses of *Sideroxylon*, *Coccoloba*, and *Simarouba* to the HF treatments were similar to *Bursera* (i.e., an early, precipitous decline in stomatal conductance), but in these species, both LF and NF declined slowly or remained stable throughout.

Discussion

Species Responses

Woody plants respond to the effects of soil flooding in a variety of ways, ranging from improved growth to death (Gill 1970, Kozlowski 1982, Kozlowski et al. 1991, Kozlowski and Pallardy 2002). In this study, flooding of the soil surface generally resulted in a reduction of tree growth and physiological function in most of the species tested. These declines, however, were usually more pronounced and occurred earlier in the upland forest species than in the swamp forest species.

Growth Responses. Annona, Myrica, and *Salix* were least affected by flooding, as evidenced by their complete survival, continuous increase in size (in all three parameters), and maintenance of plant condition even under HF throughout the study. The remaining swamp species *Chrysobalanus*, *Ilex, Magnolia*, and *Persea* were less flood tolerant and showed similar responses. In comparison to their swamp forest associates, the latter three species suffered some mortality; however, all four species experienced an early and sharp decline in overall plant condition (though the declines were gradual and generally occurred after soil surface inundation), and exhibited a reduction in growth, as early as week 12. Growth was poorest in *Persea,* suggesting its relative intolerance to flooding and supporting its segregation from the other swamp species in the cluster analysis. It is noteworthy that one individual each of *Annona* and *Magnolia* flowered under HF during the study.

Responses of the five upland forest species to HF were relatively homogeneous, though *Eugenia* clearly showed higher flood tolerance, supporting its segregation from the other upland species in the cluster analysis. With the exception of *Eugenia*, each upland species showed a decline (precipitous in *Sideroxylon*, *Simarouba*, and *Bursera*) in overall condition well before inundation of the soil surface at week 10. *Sideroxylon* and *Simarouba* did not survive to the end of the study under this treatment, despite considerable growth during the first 12 weeks. Of the three surviving upland species, *Bursera* and *Coccoloba* were most adversely affected by HF, suffering high mortality and showing low growth. *Eugenia* was least affected; initial mortality in this species did not occur until week 19, the latest of any swamp or upland species, and overall condition declined only after the soil surface became flooded. Despite total submergence of its stems and leaves under HF by the last week of the study, *Eugenia* showed the greatest cumulative growth in crown volume (and height) relative to control of any of the upland species.

Though species were not examined for specific adaptations in the current study, the formation of adventitious roots was observed in the seven swamp forest species growing under HF; they did not form in any of the upland species. Adventitious root formation is known to occur in a large number of flood-tolerant species (Hosner and Boyce 1962, Gill 1970, Kozlowski et al. 1991, Vartapetian and Jackson 1997). Several authors have suggested that differential flood tolerance among species is determined by the presence of structural (and metabolic) adaptations to anoxia (Gill 1970, Kozlowski 1982, Armstrong et al. 1994, Vartapetian and Jackson 1997, McKevlin et al. 1998), and the presence of adventitious roots may account in part for the differences seen among species in the current study. Various woody and herbaceous wetland species are also known to develop aerenchyma tissue in response to flooded conditions (Smirnoff and Crawford 1983, Kozlowski et al. 1991, Vartapetian and Jackson 1997); *Annona* characteristically forms aerenchyma in its roots and lower trunk (Zotz et al. 1997), as does *Salix* (Jackson and Attwood 1996). *Salix* roots and stems can also develop hypertrophied lenticels, which facilitate oxygen absorption and transport in plant tissues (Pereira and Kozlowski 1977, Jackson and Attwood 1996). Gunderson et al. (1988) did not observe an increase in lenticel formation in seedlings of *Chrysobalanus*, *Ilex*, or *Myrica* after 90 days of flooding, though all three species formed adventitious roots.

The lower survival and relatively poor growth seen under HF in the upland species studied were not unexpected, given that they are not found in regularly inundated sites. These and many other important tropical species occurring in upland sites of the region are adapted to seasonally-dry conditions and commonly inhabit thin soils that form directly on limestone (Armentano et al. 2002). Consequently, they are potentially exposed to seasonal drought, although in southern Florida, some may be rooted in ground water. Whether the ability to tolerate or avoid drought among upland tree species is related to the ability to tolerate shoot water stress induced by soil anoxia is not certain. In a study of tropical dry forest trees, Brodribb et al. (2003) found that *Bursera simaruba,* a species that responds to drought in southern Florida by shedding its leaves and avoiding drought, was especially vulnerable to xylem cavitation (hence reduced water conductivity). We found *B. simaruba* to be extremely sensitive to flooding. Specific information on the drought tolerance of the other upland species in our study, however, is lacking. Our findings are in marked contrast to a similar study involving seedlings of three upland tropical tree species subjected to an experimental flooding regime. In that study, Lopez and Kursar (1999) reported no mortality or visible leaf damage after 90 days of inundation, and concluded that most tropical tree species are relatively tolerant of flooding, yet do not become established in inundated habitats.

The intermediate hydrological conditions (LF), in which rising flood water first contacted the soil at week 12 and never inundated the surface, resulted in enhanced growth compared to high flood in almost all species, as evidenced by significantly different linear trends among treatments and higher linear coefficients under LF compared to HF in the four representative species (Table 8-4 and Figure 8-5). Despite mortality observed in the most flood-sensitive species (*Bursera*, *Simarouba*, *Sideroxylon*) under LF, surviving individuals of these species showed substantial growth by the end of the study as well. Enhancement of growth under saturated conditions in comparison to moist, well-drained conditions has been reported for several bottomland hardwood forest species in the southern Unites States (Hosner and Boyce 1962). Flooding is known to accelerate tree growth under certain conditions, when timing and duration are not injurious (Kozlowski 1982, Kozlowski and Pallardy 2002). Broadfoot and Williston (1973) reported a large increase in growth of trees next to reservoirs with rising water levels in Florida and Alabama, and in bottomland hardwoods of the southern United States subjected to temporary increases in the water table during the latter part of the growing season.

Physiological Responses. The study species showed fewer differences in physiological response compared to tree growth. In particular, relative water content exhibited non-significant species x treatment, species x time, and treatment x time interactions. In general, neither relative water content nor chlorophyll fluorescence responses differentiated flood-tolerant and flood-intolerant species in the current study.

Studies using relative water content as a measure of flood stress in plants are lacking; however, this parameter has been used extensively to study the effects of drought and salinity in important agricultural species (Teulat et al. 1997, Liu and Stutzel 2002, Rivelli et al. 2002). F_v/F_m has been used to quantify the effects of a range of environmental stresses on trees, including high and low temperatures, water deficit, salinity, disease, air pollution, nutrient deficiency, herbicide damage, and ultraviolet radiation (Mohammed et al. 1995). However, in the only reported study using F_v/F_m to assess plant responses under flooded conditions, Smith and Moss (1998) found that this technique was not able to detect flood stress in a group of herbaceous plants, despite decreases in growth and stomatal conductance. Mohammed et al. (1995) noted that other fluorescence parameters may be more sensitive to stress conditions under certain situations, responding before F_v/F_m, which may eventually be affected.

Stomatal conductance responses appeared to be a better predictor of flood stress under HF than relative water content or chlorophyll fluorescence. Stomatal conductance has been correlated to photosynthetic rate, gas exchange, growth, and mortality in other studies on flood-stressed plants (Regehr et al. 1975, Vu and Yelenosky 1991, Sojka 1992, Klimeξova 1994, Smith and Moss 1998). In contrast to Lopez and Kursar (1999), who reported no sharp declines in stomatal conductance in three upland tree species in Panama during 90 days of inundation, the five upland species we studied showed drastic declines in stomatal conductance over time, especially under the high flood condition. Depression of stomatal conductance under HF was reflected in the significant difference in linear (*Persea*) or quadratic (*Bursera*) trends among treatments (Table 8-4), supporting our hypothesis that flooding would diminish physiological activity. The mixed responses in the swamp species were probably due to their differential tolerance to flooding. In less tolerant swamp species, represented by *Chrysobalanus*, high flood caused a significant decrease in stomatal conductance. McKevlin et al. (1998) also observed decreases in stomatal conductance in both flood-tolerant and intolerant species growing in saturated soil. Other flood-tolerant swamp species (*Annona*, *Salix*, and *Myrica*), however, showed no reduction or a gradual decline with or without some recovery of performance by the end of the study. These responses support observations that flood-tolerant species that develop morphological adaptations, such as adventitious roots, are able to maintain stomatal conductance or regain it after flooding (Kozlowski 1984, Pezeshki and Chambers 1986, Sojka 1992, McKevlin et al. 1998).

Timing and Sequence of Responses

Our ability to link the commencement of the declines in growth to those in physiological response is limited by the frequency of our observations, which were usually at six week intervals. Thus, for species in which the onset of diminished growth and physiology (i.e., the point of departure of responses under HF from LF and NF) appeared during the same time interval, we are unable to determine which adverse response preceded the other. The upland species *Bursera*, for example, experienced a significant reduction in stomatal conductance sometime between weeks 3 and 12, while crown volume began to decline sometime between weeks 6 and 12. It is likewise difficult to relate the onset of adverse plant responses to hydrological conditions, in particular to the time when the soil surface became completely inundated under HF, at week 10. However, the precipitous drop in plant condition in *Bursera* was more precisely determined (i.e., between weeks 8 and 10), suggesting a link between declining plant vigor in this species and rising flood water during the two weeks prior to inundation of the soil surface.

Similar difficulties in elucidating a sequence of responses arise as well in *Chrysobalanus* and *Persea*, both swamp forest species, though the onset of the declines they experienced occurred later than *Bursera* (i.e., sometime between weeks 12 and 18, after inundation of the soil surface). These observations suggest a delay in the expression of adverse responses among swamp species compared to upland species. The results of the study support this conclusion, the notable exception being *Eugenia* (the most flood tolerant of the upland species studied), which behaved like a swamp species in terms of the timing of its responses. *Annona* was the only species that did not experience a decline in crown volume and stomatal conductance responses over time, which may be expected for a highly flood-tolerant species.

Annona, *Bursera*, *Chrysobalanus*, and *Persea* are not representative of the remaining species within their respective cluster groups, in terms of the patterns of adverse responses discussed above. There were no clear patterns in the sequential expression of these responses either within or among groups. It is noteworthy that the onset of declines in crown volume and stomatal conductance did not occur during the same interval in three species: stomatal conductances declined *before* crown volumes in *Ilex*, *Magnolia* and *Eugenia*. Stomatal closure was among the earliest responses in tree species exposed to flooding in one of the few studies reporting on the timing and sequence of adverse responses in plants (Pereira and Kozlowski 1977).

The onset of declines in height and basal diameter generally corresponded with declines in crown volume for most species, which is expected considering the close structural and developmental relationships among these three growth parameters. In contrast, the onset of the declines in chlorophyll fluorescence did not coincide with those of stomatal conductance for any of the 12 species (relative water content showed no changes over time for any species); declines in stomatal conductance preceded those in chlorophyll fluorescence in the majority of species. This agrees with the findings of Brodribb and Holbrook (2003) who reported that stomatal closure, resulting from xylem cavitation in leaf veins, preceded loss of chlorophyll fluorescence (and leaf turgor) in four tropical species (including one of our test species, *Simarouba glauca*) subjected to water stress.

Flood Tolerances: Shadehouse and Tree Island Compared

Did the responses of the 12 species to experimental flooding in the shadehouse agree with their distribution along the hydrologic gradient in tree islands under natural conditions? To answer this, we averaged the standardized means (i.e., ratio of HF to NF) for all growth, physiological and plant condition variables at week 24 for each species and used these values to rank the species under shadehouse conditions. For tree islands, we averaged mean water level optima calculated for each species from three tree island sites in Shark Slough and used these values to infer species rankings under natural field conditions. A comparison of these rankings is shown below:

	Shadehouse	Tree Island
highest tolerance	*Annona glabra*	*Annona glabra*
	Myrica cerifera	*Myrica cerifera*
↓	*Salix caroliniana*	*Salix caroliniana*
	Chrysobalanus icaco	*Magnolia virginiana*
	Magnolia virginiana	*Ilex cassine*
	Ilex cassine	*Persea borbonia*
	Persea borbonia	*Chrysobalanus icaco*
	Eugenia axillaris	*Simarouba glauca*
	Coccoloba diversifolia	*Bursera simaruba*
	Bursera simaruba	*Eugenia axillaris*
lowest tolerance	*Simarouba glauca*	*Coccoloba diversifolia*
	Sideroxylon foetidissimum	*Sideroxylon foetidissimum*

The comparison suggests that the responses of the 12 species after 24 weeks of simulated flooding roughly mimic their hydrologic niche in southern Everglades tree islands. The seven swamp species ranked highest (i.e., most tolerant) in both lists, followed by the five upland species. Age and size of plants, as well as water quality, factors known to affect flood tolerance in plants (Gill 1970, Kozlowski et al. 1991), may have accounted for some of the differences between shadehouse and tree island. Whereas shadehouse plants were grown to a certain age and size under similar environmental conditions before being subjected to flood treatment, individuals of the same species growing under natural field conditions responded over multiple years to a highly variable set of environmental factors, beginning at a much earlier developmental stage.

The differences seen may not be significant ecologically, especially since the rankings of the 12 species also varied slightly among the three tree island sites under natural field conditions (Ross et al. 2004). Plasticity in adaptation of tree island species to hydrological conditions may explain the overlapping variations in flood tolerances of these species. In the only other study that compared flood responses in Everglades tree island species under controlled conditions, Gunderson et al. (1988) exposed seedlings of five species to 90 days of inundation. They found the order of flood tolerance in three of the species tested to be *Myrica* > *Ilex* > *Chrysobalanus.* This agrees with the rankings of these species under the natural conditions of a tree island seen above, but differs from the rankings under the current shadehouse study. In one of the few studies examining tree responses to inundation under natural conditions in the Everglades, Guerra (1997) surveyed 12 tree islands in Water Conservation Area 3A, just north of Everglades National Park, after a prolonged flooding event in 1994-1995, and inferred flood tolerances from tree mortality data in several species. Flood tolerance in four of the species tested was *Chrysobalanus* > *Salix* > *Magnolia* > *Persea*. These relative tolerances are in agreement with both shadehouse and tree island species rankings, except for the placement of *Chrysobalanus*.

The results of this study are consistent with our current understanding of the ecology of the 12 species tested. In southern Florida, *Bursera*, *Coccoloba*, *Eugenia*, *Sideroxylon* and *Simarouba* are common elements of the rarely inundated, mesic tropical hardwood hammocks found in tree islands of the Everglades and in coastal areas as far south as the Florida Keys (Craighead 1971, Tomlinson 1980, Armentano et al. 2002). All of these species are typically major canopy trees, with the exception of *Eugenia* which usually grows as a small understory tree (Haehle and Brookwell 1999). *Annona, Chrysobalanus, Ilex, Magnolia, Myrica, Persea,* and *Salix* are found in a wide variety of hydric sites throughout the Everglades (Long and Lakela 1976, Godfrey and Wooten 1981, Conner et al. 2002). All are common components of the swamp forests associated with tree islands, *Annona* and *Salix* occupying the lowest end of the hydrologic gradients in these forests.

With the relative flood tolerances of the species tested in our study corresponding generally to their observed distribution along the hammock-bayhead swamp forest continuum in tree islands, we may expect parallel responses to water management. This knowledge may eventually allow early warning of flooding stress in tree islands. With restoration plans under CERP anticipating modifications in hydrologic conditions throughout the Everglades, predicting responses of tree island species to these changes becomes critical. Extrapolated to the natural setting of a tree island, the results of this study suggest that increasing water depths and durations may have a beneficial yet temporary effect on most hammock species, and that soil surface inundation will hasten reduction in tree growth, and eventually, death. The more flood intolerant species of the surrounding swamp forest (*Persea*, *Magnolia*, *Ilex*) can be expected to respond similarly, though the onset of reduced growth, and possibly death, would be delayed. We terminated our study before it was determined how the most flood tolerant swamp species (*Annona*, *Salix*, *Myrica*) would respond to increasingly higher and longer flood waters.

Knowledge of relative species tolerances, together with ancillary information such as genotypic variation (McKevlin et al. 1998), particularly in species distributed along a soil moisture gradient (Keeley 1979), will become important in selecting suitable species to include in projects aimed at restoring destroyed or degraded tree islands and creating new ones, a CERP objective. For example, Wallace et al. (1996) assessed flood tolerance and seedling growth and survival under varying soil conditions and developed guidelines for the use of nine tree species in wetland restoration and creation in Florida. Several of the species reported in our study have never been evaluated for flood tolerance until now. Coupled with other studies, this information can serve as a guide for the restoration of desired hydrologic regimes that will not adversely affect tree islands.

Synthesis

9

Tree Islands as Elements in the "Ridge and Slough" Mosaic

Michael S. Ross

Shark Slough tree islands have been influenced by the same uneven environmental history that has affected other Everglades wetland communities. The taming of the Everglades through the Central and Southern Florida (C&SF) Project was largely completed during the decades of the 1950s through the 1970s, leaving many regulated compartments where there had been one unbounded ecosystem. Water management in each compartment was a compromise between local agency and user objectives and the multi-purpose demands for the C&SF project as a whole, which emphasized regional drainage and water supply over environmental needs. Thus tree islands in different portions of the Everglades were exposed to radically different hydrologic conditions, i.e., excessive flooding in one area, insufficient water in the next, with these roles often changing from year to year depending on climate or sudden shifts in management priorities. Superimposed on the background gradients in tree island character that existed even before the water management era, the Balkanization of water conditions in the Everglades has presented resource managers in different reaches of the system with radically different issues in their efforts to ensure continued tree island health. In turn, the local context in which tree islands are "managed" has colored the popular as well as the scientific views that have emerged from each area. Nevertheless, in the central Everglades drainage basin, the role of tree islands as fundamental components in a well-integrated wetland landscape is common throughout.

The research described in this *Final Report* was collected in Shark Slough, ENP, a regulated but unconfined compartment whose water supply is satisfied by groundwater flow, direct rainfall, and periodic diversions of surface water from the regional system to the north. Water exits Shark Slough by evapotranspiration and by draining freely into Florida Bay and the Gulf of Mexico, as it always has. In addition, water may drain back into the canal system to the east, at the expense of the marl prairies which flank the slough on that side. As described in Chapter 1, water delivery from the four S-12 structures along Tamiami Trail is regulated individually. Since the wet season of 2000, regulatory schedules for these structures have called for the westernmost to be closed for substantially longer than the structures east of the Shark Valley tram road. This distributional pattern has resulted in different seasonal patterns in the hydrology of marshes on the east and west sides of Shark Slough, which influence the tree islands found in these areas accordingly.

Tree island science is not yet at the point where the ecological effects of such fine-scale seasonal differences in hydrology can be confidently predicted. One issue is that tree island hydrology is also influenced by current ecosystem function and legacies of the past. Irregularities in the soil surface created by ancient treefalls and animal activities cause water to pool in some microhabitats, and drain rapidly from others. Large volumes of water remain in the peat sediments once floodwaters have dropped below the surface, leading to complex exchanges between saturated and unsaturated water bodies. One of the most significant results in Chapter 1 is the diurnal pattern observed in tree island water tables during periods when they have dropped below the sediment surface and the surrounding marsh remains flooded. Under these conditions, on days without significant rainfall, the water surface in tree island wells typically exhibit a rapid daytime drop, followed by a partial nighttime recovery. The resultant cumulative daily decline is roughly the same as that observed in the adjacent marsh. Several mechanisms could be contributing to this pattern. For one, evapotranspiration (ET), which is maximum or entirely restricted to daylight hours, may be more rapid in a slightly elevated, well-aerated, highly productive forest ecosystem than in a flooded marsh with relatively anaerobic soils and reduced conductive leaf surface. Local water table gradients created by variable daytime ET would be corrected at night by water movement along the saturated-unsaturated interface. Moreover, the local water table gradients need not result from variable ET among wetland communities. Even if the volume of water evaporated or transpired from the surface of the water table is uniform across all marsh communities, the water table will drop more rapidly in unflooded than flooded soils, since in the former case water does not occupy the entire soil volume. In either case, the process suggests a net movement of water toward the tree islands from adjacent landscape elements.

By geologic standards, most wetlands are relatively ephemeral and short-lived, and the Everglades is no exception. In Shark Slough wetlands on both sides of Tamiami Trail, calcareous marsh sediments began to form 6000-7000 years ago, and peat-forming conditions were widespread by ~4500 BP (Chapter 5). Pollen and macroscopic evidence from several of the flagship tree islands we studied - Gumbo Limbo and Black Hammocks - indicate that the tails of the current tree islands passed through a long period under sawgrass marsh or slough vegetation cover before succeeding to forest. Because of a hiatus in the sediment record due to an extensive disturbance, presumably a fire, the timing of the onset of woody plant dominance is uncertain, though it seems that these areas were continuously forested during most of the last millennium. The chapter's paleological interpretation of these tree islands as the product of a prolonged, non-linear successional process, albeit one subject to long-term climatic variation as well as significant local and region-wide disturbances, is an important result that should be incorporated into our considerations about management or restoration.

In Shark Slough, the drainage route for most of the Everglades fresh water, these islands are fixed on and downstream of prominent outcrops that today may extend a meter or more above the surrounding limestone. As described in Chapter 2, these two-phased (i.e., comprised of "relictual" heads and "sedimentary" tails; Chapter 5), teardrop-shaped forest complexes point roughly southeast, as do the similarly elongated strands of tall sawgrass that occur nearby (Figure 2-20). This orientation is remarkably uniform within local landscapes, as well as from place to place in the ENP portions of Shark Slough (Figure 2-22). Except in Northeast Shark Slough, the orientation of landforms closely parallels the predominant direction of regional flow vectors (Sherry Mitchell-Bruker, ENP hydrologist, personal communication). In considering mechanisms potentially responsible for the development and maintenance of the "ridge and slough" landscape, as it has come to be known, it is hard to imagine one that does not involve the effects of moving water. The case for the central role of flow in shaping this landscape is bolstered by the analysis in Chapter 5 of tree island sediments, which include a high proportion of fine materials (organic, calcareous, and siliceous) that appear to have originated elsewhere.

Within the ridge and slough landscape, tree islands play many important functional roles. One of the most significant is the provision of habitat for animals, some of which complete their life cycles there and others that range more widely, using the tree islands for specific activities, e.g., feeding, nesting, or roosting (Chapter 7). In either case, faunal populations may respond to the number and distribution of tree islands in the landscape as much as to specific characteristics of the islands. Utilization patterns are likely to be very seasonal, with raised hardwood hammock environments becoming especially important as refuges during high water periods. In turn, concentrated animal use may alter ecosystem structure and function (e.g., the potential impacts of hogs on understory composition in Gumbo Limbo hammock, discussed in Chapter 6, or of birds on soil nutrient concentrations, described in Chapter 3). Because of their isolation in the landscape, tree island plant communities may be especially sensitive to the roles of animals in specialized functions such as seed dispersal or pollination. Despite a few recent contributions (Gaines et al. 20002, Meshaka et al. 2002), more is unknown than known regarding the relationships between animals and Everglades tree islands.

In some sense, vegetation patterning within Shark Slough tree islands resembles patterns in the marshes that surround them (Ross et al. 2003). As Chapter 6 illustrates, species composition is largely arranged along a single strong gradient, which is usually represented in our analyses by hydrologic measures such as hydroperiod or mean water level. In fact, when we examined the influence of hydrology on 12 tree island tree species, we found that their response under controlled conditions closely matched their hydrologic niche in the field (Chapter 8). Nevertheless, thorough examination of the tree island environment reveals that hydrology is in fact one aspect of multi-factorial environmental complex that also includes nutrient availability (Chapter 3), canopy openness or light availability (Chapter 6), and possibly temperature and other climatic variables (Chapter 4). Fundamentally, the gradient within individual islands is characterized by an increase in aboveground biomass and cover with decreasing hydroperiod and increasing phosphorus availability (discussed below). The gradient is also one in which the turnover in plant species and functional groups is rapid. In moving upgradient from the most frequently flooded tree island communities to the least flood-prone, species richness and cover in the herb layer decreases, while canopy height and the cover of trees and increases. Whereas the most elevated forests in the Shark Slough tree islands share many characteristics with the hardwood hammocks of the Florida Keys, the composition of the wet forests grade smoothly into the marsh assemblages of the slough. The wet forests in fact share many species with the marl prairies that flank Shark Slough, which have a similar hydrologic regime but grow on different substrate.

The relationship of nutrients to hydrology in Shark Slough tree islands deserves further comment. The high concentrations of phosphorus in hardwood hammock soils (Chapter 3) seem astonishing until viewed within the context of soils in other portions of the tree islands, or in adjacent marsh communities. Figure 9-1A indicates that concentrations of total P as high as 5000 ppm in hardwood hammock soils, which are rarely flooded, represent the culmination of a long gradient beginning with phosphorus concentrations of about 10 ppm in the soils of the most persistently flooded community, the spikerush marsh. This pattern of increasing P (and decreasing N) with decreasing flood frequency is paralleled in soil pore waters with respect to the most available (i.e., dissolved inorganic) forms of phosphorus and nitrogen (Figure 9-1B). Finally, plant response to this very strong nutrient gradient is illustrated in Figure 9-2. Leaf N:P ratios of widespread ridge and slough species show a general decrease from spikerush marsh through hardwood hammock. Recent literature has shown leaf N:P to be a good indicator of the nature of nutrient limitation in wetland plants, with molar ratios >36 signifying P limitation, ratios <31 indicating N limitation, and ratios of 31-36 indicative of co-limitation by both nutrients (Bedford et al. 1999, Koerselman and Meuleman 1996). Of the three species tested, only *Eleocharis cellulosa*, the dominant plant of the most P-limited community, seemed to be insensitive to the soil and pore water gradient. These data suggest that in the heart of the Everglades, microsites in which nitrogen is the limiting nutrient co-exist in close proximity to much more extensive marshes whose nature is largely defined by their unproductive, P-limited soils. Moreover, the landscapes in which these disparate elements are integrated show signs of stability over past centuries or millennia, though their ability to resist significant and sudden changes in flow regimes or water quality are probably very slight (e.g., Science Coordination Team 2003).

The mechanism by which the complex ridge and slough landscape structure has developed and been maintained over many centuries on a predominantly organic substrate is of great interest for wetland scientists and relevance for Everglades restoration. Recently, several research groups have pointed out that autogenic processes involving the effects of initially small differences in soil drainage on the balance between plant production and decomposition contribute to this developmental process (Givnish and Volin 2003, Ross et al. 2003). The N and P patterns summarized in Figures 9-1 and 9-2 suggest that (1) temporal and spatial variation in nutrient availability play important roles in this feedback system, and (2) these feedbacks may become accentuated at the point in successional development when woody vegetation becomes dominant over marsh species. What causes phosphorus to accumulate in tree islands? Is it simply through hydrologically-induced effects on nutrient cycling processes? Or are transport processes involved, either through animal activities (Chapter 7), or through local flow gradients, perhaps created by ET-driven spatial heterogeneity in the water table (Chapter 2)? Rietkerk et al. (2004) recently showed that spatial variation in transpiration can lead to nutrient and vegetation patterning in northern bogs, but their models produced a landscape in which the ridges ran perpendicular to flow direction, as they do in most boreal peatlands. Seemingly, flowing surface water flow plays a different and more significant role in shaping the Everglades landscape than it does in these ecosystems.

Figure 9-3 modifies our earlier model (Ross et al. 2003) to reflect the importance of nutrient availability along with hydrology in landscape development in the ridge and slough. Tree islands are very much a part of this landscape, and can probably best be protected by managing for the health of the landscape as a whole, i.e., by providing water quantity, quality and flow in the amounts and at the timing necessary to produce the habitat variation that characterized the pre-development Everglades. While even this simplified equation contains too many unknowns to solve at this stage in the infancy of Everglades landscape science, it points out a direction for further inquiry and practice.

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Appendices

Appendix 5-1

Generalized Core Descriptions

Original detailed descriptions were drawn and are somewhat generalized here. Zone thicknesses given are uncorrected for slight compression (corrections are made to final figures). Many strata or zone boundaries are gradual or transitional and an approximate visual center is given, thus the frequent use of "ca." for circa or approximately. The question marks are for more interpretative identifications of mostly minor constituents or for inferences. Some interpretations are fairly certain (e.g., bone fragments, charcoal, ash materials). Color is when wet.

Satinleaf Hammock

SL1 Hammock

Peaty Muck (degraded organic, not mineral): near black (5YR 2.5/1), firm, not slick, much of fine organic material ("fines"), with many small fragments (bone?): ca. 18 cm (7 in)

Mineral Sediment: carbonate-rich?, medium grey (Gley1 5/N), very firm and dense, not cemented, not slick; contains at least one large limestone pebble and several "hammock" snails: ca. 33 cm (13 in)

Peaty Muck: (as above), many small bone (?) fragments in upper part, and larger fragment and piece of turtle plate in middle and lower part respectively, and some intermixing with zone below near base: ca. 50 (19.5 in)

Granular Debris: variable including brown light colors, loose, light weight, some is bone: ca. 5 cm (2 in)

SL2 Hammock

Muck: black (5YR 2.5/1), dense, much is organic, medium fine grained, not slick, much lighter colored fragments in lower half (bone?): ca. 18 cm (7 in)

Mineral Sediment: grey (Gley1 6/6 [5/5?]), probably carbonate rich, relatively fine grained but finely gritty, not marl, with two limestone pebbles at mid-depth: ca. 27 cm (10.5 in)

SL-BHS Bayhead

Peat: almost black (10YR2/1), fines common (peaty), (transitional at bottom to below layer): ca. 13 cm (5 in)

Peaty Muck: black (10YR2/1), slick, sticky, fines black: ca. 50 cm (19.5 in)

Silty Sand or Sandy Silt: brown (10YR4/6), ca. 6 cm (2.5 in)

Appendix 5-1 (continued)

SL4 Bayhead

Peat: very dark brown, considerable fines (peaty, dark brown): ca. 9 cm (3.5 in)

Mucky Peat: nearly black (slightly brownish), not very slick (fines may be organic), (lower boundary fairly distinct) : ca. 23 cm (9 in)

Peaty Muck: near black, fairly slick: ca. 24 cm (9.5 in)

Black Hammock

BH1 Hammock

Forest Humus: very dark brown (10YR2/2), granular, fine, with turtle plate (?) fragment and "hammock" snail shell toward bottom: ca. 10 cm (4 in)

"Soil": greyer (Gley1 4/N), more mineral-rich than above, many small brown fragments (bone?): ca. 6 cm (2.5 in)

Mineral Sediment: dark grey (Gley1 4/N), carbonate? many small brown fragments (bone?) in upper half: ca. 14 cm (5.5 in)

Mineral Sediment: (as above), but partially cemented (though cut by knife), lighter color, grey (Gley1 6/N), upper boundary fairly distinct: ca. 6 cm (2.5 in)

BH-BH1 145m Bayhead

Peat: nearly black (5YR 2.5/1), fines present: ca. 25 cm (10 in)

*Transitional with above, and similar, but with substantial fines (very dark brown): ca. 8 cm (3 in)

Similar, but with abundant granular material (charcoal?): ca. 2.5 cm (1 in)

Mineral Sediment: marl-like, ash?, fine, orange (10YR6/6, or 10YR5/3 where more organic matter is intermixed): ca. 2.5 cm (1 in)

Peaty Muck (top ca. 2 cm with granular material as above the mineral layer): near black (10YR2.5/1), fines slick and black (much mineral?), grades into lower layer: ca. 36 cm (14 in)

Mucky Peat (marly?), grades into lower` layer: ca. 13 cm (5 in)

Marly Peat or Muck, grey (Gley1 4/N), with fine grit: ca. 4 cm (1.5 in)

Appendix 5-1 (continued)

BH-BHS 450m Bayhead

Peat: very dark brown (10YR2/2), fines present, woody root toward bottom, bottom boundary distinct: ca. 25 cm (10 in)

Muck: black (10YR2/1), fine, with very granular coarse material (ash?): ca. 4 cm (1.75 in)

Mineral Sediment: Marl-like, ash? brown (by organic matter) (10YR6/3), a few granular hard components: ca. 4 cm (1.5 in)

Muck: (as above): ca. 4 cm (1.5 in)

Peat: very dark brown (10YR2/2) finely fibrous, much denser than top layer, bottom ca. two-thirds with more large fibers (sawgrass?, waterlily?), fines abundant in lower ca. half (dark brown, peaty?), no wood noted:, grades indistinctly into layer below: ca. 67 cm (26.5 in)

Mucky Peat (indistinct boundaries): nearly black (5YR2.5/1), fines fairly slick (possibly organic), grades into layer below: ca. 18 (7 in)

Peat: (as second layer up): ca. 9 cm (3.5 in)

Mucky (Marly?) Peat: near black (5YR2.5/1), with numerous fine fragments of freshwater snail shells (more abundant with depth): ca. 15 cm (6 in)

Peaty Marl (upper boundary arbitrary): 5YR2.5/2, abundant fragments of freshwater snail shells (some complete): ca. 11 cm (4.5 in)

Marl

*Stained with organic matter (10YR4/2, 10YR5/2, 10YR3/0), shell fragments (as above), lower boundary distinct: ca. 23 cm (9.25 in)

*Little organic staining (2.5YR7/2), shell fragments (as above), lower boundary fairly distinct: ca. 12 cm (4.75 in)

*Typical, (2.5YR7/2, 2.5 YR6/2), shell fragments (as above): ca. 32 cm (12.5 in)

*Greyer (2.5YR6/1): ca. 6 cm (2.5 in)

(rock occurred ca. 13 cm [5 in] below)

Appendix 5-1 (continued)

Gumbo Limbo Hammock

GL1 Hammock

Muck "Soil": very dark grey to near black ((5YR2.5/1), granular with gritty material and fines, organic and mineral rich, "hammock" snail shells at midlevel, many small brown fragments in lower ca. one-half (bone?): ca. 24 cm (9.5 in)

Mineral Sediment: grey (Gley1 5/N), finer and firmer than above layer, probably carbonate in part, with a large marine shell land small brown fragments (bone?) at ca. one-third depth and a large rock fragment and small brown fragments at ca. two-thirds depth: ca. 17 cm (6.5 in)

GL2 Hammock Edge

Peaty "Soil": dark greyish-brown (10YR3/2), woody roots at several levels, pebble (?) toward bottom: ca. 15 cm (5.75 in)

Mineral "Soil": dark brownish-grey (10YR4/2, 10YR4/1), distinct cementation (widely but there localized, but some may be pebbles): ca. 20 cm (7.75 in)

*As above (10YR4/2) but loose (uncemented), with pot sherd at midlevel and large pebble near base: ca. 11 cm (4.25 in)

Granular Sediment (coarse sand size): very dark grey or near black (Gley1 2.5/N), mineral dominated, organic rich, with small brown fragments throughout (bone?), distinct scattered tiny white specks (sand?), some dark fines present, with a large stained pebble at the top and a pot sherd ca. 7 cm (2.75 in) down: ca. 51 cm (20 in)

Carbonate Debris: grey to dark grey with organics (Gley1 7/2, Gley1 4/N), coarse, gritty or sandy, includes white specks, large pebbles at top and midlevel and many small rock fragments: ca. 10 cm (4 in)

Mucky Debris: very dark grey (Gley1 3/N, Gley1 2.5/N), organic rich, more organics in lower half, large pebbles in lower half: ca. 18 cm (7 in)

(core bent on rock below)

GL-BH1 260m   Bayhead

Peat: ca. 4 cm (1.75 in)

Mucky Peat : black (10YR2/1), fines slick:, large woody root toward bottom, distinct bottom boundary: ca. 21 cm (8.25 in)

Appendix 5-1 (continued)

Mineral Sediment: Marl-like, ash?, mottled medium dark grey and medium yellow brown (10YR6/4, 10YR6/1), very firm and compacted, some root holes (with orangish-brown "halos" ca. 1 mm), no shell seen, some mixing at base with underlying muck: ca. 22 cm (8.5 in)

Muck to Peaty Muck: nearly black (10YR2/2), fines slick (black), grades into zone below: ca. 14 cm (5.5 in)

Mucky Peat: nearly black (10YR2/1), bottom ca. 4 cm (1.5 in) with tiny whitish shell fragments and at base one partial shell of a freshwater snail.: ca. 19 cm (7.5 in)

GL-BH 820m Bayhead

Peat: very dark brownish black (10YR2/2), with darker color (10YR2/1) and more fines (black but not sticky, peat fines) in lower half ca. 30 cm (12 in)

Peaty Muck: black (10YR2/1), fines black and stickier, somewhat shiny on slicked surface, woody roots at upper boundary, more fibrous in bottom ca. 5 in but indistinct boundaries, grades to zone below: ca. 57 cm (22.5 in)

Peat: dark brown (10YR2/2), relatively few fines: ca. 20 cm (7.75 in)

Marl: grey (Gley1 6/2, Gley1 8/1), upper half organic rich, sticky (clayey?), lower half fine gritty and with large limestone piece: ca. 7 cm (2.75 in)

GL BHS/M Bayhead/Marsh Interface

Peat: very dark brown, fines abundant and very dark brown, large root at top, many larger marsh plant-like fibers scattered throughout: ca. 60 cm (23 in)

Mucky Peat: very dark brownish-black, fines become slick and are black with depth (below ca. 20 cm (8 in) in this zone), woody (?) root at about same depth, large roots (not necessarily woody) near base: ca. 97 cm (38 in)

(bedrock found ca. 6 cm below)

Manatee Hammock

MH-BH NW Bayhead

Peat: very dark brown, fines common and dark brown: ca. 18 cm (7 in)

Mucky Peat: very dark brownish black, somewhat slick, fines slick and black: ca. 20 cm (8 in)

Appendix 5-1 (continued)

Peat: very dark brown, fines common, a woody root toward bottom: ca. 64 cm (25 in)

Marl: whitish, some shell fragments, broken off piece of limestone (yellowish): ca. 8 cm (3 in)

(bottom of core bent on rock)

Ficus Hammock

Bayhead

Peat: dark reddish brown (5YR3/2), considerable fines, a few wood roots: ca. 20 cm (8 in)

Peaty Muck: black (5YR2.5/1), transitional at top (ca. 4 cm [1.5 in]) then dense, shiny (on slicked surface): ca. 10 cm (4 in)

Mucky Peat: as above but less dominated by fines, gradational lower boundary: ca. 41 cm (16 in)

Peaty Muck: black (5YR2.5/1), much fine mineral matter (marl?) Including a small proportion of fine sand: ca. 20 cm (8 in)

Muck and Carbonate Sediment (segregated): granular carbonate with some limestone pebbles, muck: ca. 13 cm (5 in)

(Rock nicked by core and found at ca 4 cm below core, pinnacled?)

Transect 2

T2 800 m Marsh

Peat:
*Coarser: ca. 5 cm (2 in)

*Black (10YR2/1), firm, considerable fines (dark brown to near black): ca. 5 cm (2 in)

*With fines slicker and black, boundaries very transitional: ca. 30 cm (12 in)

*Less slick and less black (10YR2/2 in lighter parts), fines less dark, i.e., dark brown), thin (ca. □-1 cm) and some thicker darker zones (10YR2/1) with black fines (charcoal? sawgrass peat?), may be essentially the same as the zone below: ca. 25 cm (10 in)

*Very dark brown to near black (7.5YR2.5/1) with fines common to abundant, mostly brown, several zones (ca. 3-6 cm) merely dark brown (7.5YR2.5/2 [1.5], 7.5YR2.5/3 [2.5?]): ca. 76 cm (30 in)

Appendix 5-1 (concluded)

Peaty Marl (?) or Mud: very dark grey (Gley1 2.5/10Y, but with hint of brown), dense, only semislick (silt?), with freshwater snail shell near base: ca. 25 cm (10 in)

SRS Marsh

Wet-prairie

Peat: very dark brown (10YR2/2), fines common and brown and not very sticky (organic?), fines more common and darker nearer bottom: ca. 22 cm (8.5 in)

Marl

*Slightly brownish by organics (Gley1 6/1, Gley1 7/0), shelly by fragments of freshwater snails and one apple snail (?) fragment: ca. 11 cm (4.5 in)

*More greyish (Gley1 7/0) as in typical marsh marl, a freshwater snail shell: ca. 28 cm (7.5 in)

*Grey (Gley2 6/0, Gley2 5/0), stickier (clayey?), little shell material obvious, gritty toward bottom: ca. 17 cm (6.5 in)

Appendix 6-1

Species list for the three tree islands, including classification, species codes, life forms, and bibliographic sources. Reference codes: (1) Godfrey and Wooten 1979, 1981; (2) Long and Lakela 1976; (3) Lellinger 1985; (4) Wunderlin 1998; (5) Nelson 2000; (6) Correll and Correll 1982.

S. NO.	CLASS	FAMILY	SCIENTIFIC NAME	AUTHOR CITATION	SPCODE	LIFE FORM	REF	ALTERNATE NAME
1	PTERIDOPHYTE	PTERIDACEAE	*Acrostichum danaeifolium*	Langsd. & Fisch.	ACRDAN	Fern	3	
2	DICOT	FABACEAE	*Aeschynomene pratensis* var. *pratensis*	Small	AESPRA	Forb	2	4 *A. pratensis* Small
3	DICOT	VITACEAE	*Ampelopsis arborea*	(L.) Koehne	AMPARB	Vine	1	
4	MONOCOT	POACEAE	*Andropogon glomeratus* var. *glomeratus*	(Walt.) Britton et al.	ANDGLO	Graminoid	2	
5	DICOT	ANNONACEAE	*Annona glabra*	L.	ANNGLA	Tree	1	
6	DICOT	FABACEAE	*Apios americana*	Medic.	APIAME	Vine	1	
7	DICOT	ASTERACEAE	*Aster carolinianus*	Walt.	ASTCAR	Shrub	1	
8	DICOT	ASTERACEAE	*Aster dumosus*	L.	ASTDUM	Forb	1	
9	DICOT	ASTERACEAE	*Baccharis halimifolia*	L.	BACHAL	Shrub	1	
10	DICOT	SCROPHULARIACEAE	*Bacopa caroliniana*	(Walt.) Robins.	BACCAR	Forb	1	
11	DICOT	SCROPHULARIACEAE	*Bacopa monnieri*	(L.) Pennell	BACMON	Forb	1	
12	PTERIDOPHYTE	BLECHNACEAE	*Blechnum serrulatum*	L.C. Rich.	BLESER	Fern	3	
13	DICOT	URTICACEAE	*Boehmeria cylindrica*	(L.) Sw.	BOECYL	Forb	1	
14	DICOT	BURSERACEAE	*Bursera simaruba*	(L.) Sarg.	BURSIM	Tree	2	
15	DICOT	FABACEAE	*Caesalpinia bonduc*	(L.) Roxb.	CAEBON	Shrub	1	
16	DICOT	SCROPHULARIACEAE	*Capraria biflora*	L.	CAPBIF	Forb	1	
17	DICOT	CARICACEAE	*Carica papaya**	L.	CARPAP	Tree	2	
18	DICOT	FABACEAE	*Cassia ligustrina**	L.	CASLIG	Forb	2	
19	DICOT	ULMACEAE	*Celtis laevigata*	Willd.	CELLAE	Tree	1	
20	DICOT	RUBIACEAE	*Cephalanthus occidentalis*	L.	CEPOCC	Shrub	1	
21	DICOT	CHRYSOBALANACEAE	*Chrysobalanus icaco*	L.	CHRICA	Tree	1	
22	DICOT	SAPOTACEAE	*Chrysophyllum oliviforme*	L.	CHROLI	Tree	2	
23	DICOT	VITACEAE	*Cissus sicyoides*	L.	CISSIC	Vine	2	4 *Cissus verticillata* (L.) Nicholson & Jarvis

S. NO.	CLASS	FAMILY	SCIENTIFIC NAME	AUTHOR CITATION	SPCODE	LIFE FORM	REF	ALTERNATE NAME
24	MONOCOT	CYPERACEAE	*Cladium jamaicense*	Crantz	CLAJAM	Graminoid	1	
25	DICOT	POLYGONACEAE	*Coccoloba diversifolia*	Jacq.	COCDIV	Tree	2	
26	MONOCOT	POACEAE	*Coelorachis rugosa**	(Nutt.) Nash	COERUG	Graminoid	4	1,2 *Manisuris rugosa* (Nutt.) Kuntze
27	DICOT	ASTERACEAE	*Conoclinium coelestinum*	(L.) DC.	CONCOE	Forb	1	
28	MONOCOT	CYPERACEAE	*Cyperus distinctus**	Steud.	CYPDIS	Graminoid	1	
29	MONOCOT	CYPERACEAE	*Cyperus haspan*	L.	CYPHAS	Graminoid	1	
30	MONOCOT	CYPERACEAE	*Cyperus ligularis*	L.	CYPLIG	Graminoid	1	
31	MONOCOT	CYPERACEAE	*Cyperus odoratus*	L.	CYPODO	Graminoid	1	
32	DICOT	FABACEAE	*Dalbergia ecastophyllum*	(L.) Taub	DALECA	Vine	1	
33	MONOCOT	POACEAE	*Dicanthelium dichotomum*	(L.) Gould	DICDIC	Graminoid	4,6	1 *Panicum dichotomum* L.
34	DICOT	RUBIACEAE	*Diodia virginiana*	L.	DIOVIR	Forb	1	
35	MONOCOT	POACEAE	*Echinochloa crusgalli*	(L.) Beauv.	ECHCRU	Graminoid	1	
36	MONOCOT	CYPERACEAE	*Eleocharis caribaea*	(Rottb.) Blake	ELECAR	Graminoid	2	1 *E. geniculata* (L.) R. & S.
37	MONOCOT	CYPERACEAE	*Eleocharis cellulosa*	Torr.	ELECEL	Graminoid	1	
38	DICOT	ASTERACEAE	*Erechtites hieracifolia**	(L.) Raf.	EREHIE	Forb	1	
39	MONOCOT	POACEAE	*Erianthus giganteus**	(Walt.) Muhl.	ERIGIG	Graminoid	1	4 *Saccharum giganteum* (Walt.) Pers.
40	DICOT	MYRTACEAE	*Eugenia axillaris*	(Sw.) Willd.	EUGAXI	Tree	2	
41	DICOT	ASTERACEAE	*Eupatorium capillifolium*	(Lam.) Small	EUPCAP	Shrub	1	
42	DICOT	MORACEAE	*Ficus aurea*	Nutt.	FICAUR	Tree	1	
43	MONOCOT	CYPERACEAE	*Fuirena breviseta*	(Coville) Coville	FUIBRE	Graminoid	1	
44	DICOT	MALVACEAE	*Hibiscus grandiflorus*	Michx.	HIBGRA	Shrub	1	
45	DICOT	APIACEAE	*Hydrocotyle umbellata*	L.	HYDUMB	Forb	1	
46	DICOT	HYDROPHYLLACEAE	*Hydrolea corymbosa*	Macbr. ex Ell.	HYDCOR	Forb	1	
47	MONOCOT	AMARYLLIDACEAE	*Hymenocallis palmeri*	Wats.	HYMPAL	Forb	2	
48	DICOT	LAMIACEAE	*Hyptis alata*	(Raf.) Shinners	HYPALA	Forb	1	
49	DICOT	AQUIFOLIACEAE	*Ilex cassine*	L.	ILECAS	Tree	1	
50	DICOT	CONVOLVULACEAE	*Ipomoea alba*	L.	IPOALB	Vine	1	
51	DICOT	CONVOLVULACEAE	*Ipomoea sagittata*	Poir.	IPOSAG	Vine	1	

S. NO.	CLASS	FAMILY	SCIENTIFIC NAME	AUTHOR CITATION	SPCODE	LIFE FORM	REF	ALTERNATE NAME
52	DICOT	JUNCACEAE	*Juncus polycephalos**	Michx.	JUNPOL	Graminoid	1	
53	DICOT	ACANTHACEAE	*Justicia angusta*	(Chapm.) Small	JUSANG	Forb	4	1,2 *Justicia ovata* (Walt.) Lindau
54	DICOT	MALVACEAE	*Kosteletzkya virginica*	(L.) Presl.	KOSVIR	Shrub	1	
55	MONOCOT	POACEAE	*Leersia hexandra*	Sw.	LEEHEX	Graminoid	1	
56	DICOT	LEMNACEAE	*Lemna obscura*	(Austin) Daubs	LEMOBS	Forb	4	2 *L. minor* L.
57	DICOT	ONAGRACEAE	*Ludwigia alata*	Ell.	LUDALA	Forb	1	
58	DICOT	ONAGRACEAE	*Ludwigia curtissii*	Chapm.	LUDCUR	Forb	1	
59	DICOT	ONAGRACEAE	*Ludwigia repens*	Forst.	LUDREP	Forb	1	
60	DICOT	ONAGRACEAE	*Ludwigia sp.*	Forst.	LUDSPP	Forb	2	
61	MONOCOT	POACEAE	*Luziola fluitans**	(Michx.) Terrell & H. Rob.	LUZFLU	Graminoid	4	1,2 *Hydrochloa caroliniensis* P. Beauv.
62	DICOT	MAGNOLIACEAE	*Magnolia virginiana*	L.	MAGVIR	Tree	1	
63	DICOT	CUCURBITACEAE	*Melothria pendula*	L.	MELPEN	Vine	2	
64	DICOT	ASTERACEAE	*Mikania scandens*	(L.) Willd.	MIKSCA	Vine	1	*M. batatifolia* DC.
65	DICOT	LOGANIACEAE	*Mitreola petiolata*	(J.F. Gmel.) T. & G.	MITPET	Forb	1	2 *Cynoctonum mitreola* (L.) Britt.
66	DICOT	MYRICACEAE	*Myrica cerifera*	L.	MYRCER	Tree	1	
67	DICOT	MYRSINACEAE	*Myrsine floridana*	A. DC.	MYRFLO	Shrub	6	1,2 *M. guianensis* (Aubl.) Kuntze; 4 *Rapanea punctata* (Lam.) Lund.
68	PTERIDOPHYTE	DAVALLIACEAE	*Nephrolepis biserrata**	(Sw.) Schott	NEPBIS	Fern	3	
69	PTERIDOPHYTE	DAVALLIACEAE	*Nephrolepis exaltata*	(L.) Schott	NEPEXA	Fern	3	
70	DICOT	NYMPHAEACEAE	*Nymphaea odorata*	Ait.	NYMODO	Forb	1	
71	DICOT	MENYANTHACEAE	*Nymphoides aquatica*	(J.F. Gmel.) Kuntze	NYMAQU	Forb	1	
71	PTERIDOPHYTE	OSMUNDACEAE	*Osmunda regalis* var. *spectabilis*	L./(Willd.) A. Gray	OSMREG	Fern	3	
73	DICOT	APIACEAE	*Oxypolis filiformis*	(Walt.) Britt.	OXYFIL	Forb	1	
74	MONOCOT	POACEAE	*Panicum hemitomon*	Schult.	PANHEM	Graminoid	1	
75	MONOCOT	POACEAE	*Panicum rigidulum*	Nees	PANRIG	Graminoid	1	
76	MONOCOT	POACEAE	*Panicum virgatum*	L.	PANVIR	Graminoid	1	

S. NO.	CLASS	FAMILY	SCIENTIFIC NAME	AUTHOR CITATION	SPCODE	LIFE FORM	REF	ALTERNATE NAME
77	DICOT	VITACEAE	*Parthenocissus quinquefolia*	(L.) Planch.	PARQUI	Vine	2	
78	MONOCOT	POACEAE	*Paspalidium geminatum* var. *geminatum*	(Forst.) Stapf	PASGEM	Graminoid	1	
79	DICOT	PASSIFLORACEAE	*Passiflora suberosa*	L.	PASSUB	Vine	2	
80	MONOCOT	ARACEAE	*Peltandra virginica*	(L.) Schott & Endl.	PELVIR	Forb	1	
81	DICOT	LAURACEAE	*Persea borbonia*	(L.) Spreng.	PERBOR	Tree	1	
82	DICOT	LORANTHACEAE	*Phoradendron rubrum**	(L.) Griseb.	PHORUB	Parasite	2	
83	DICOT	ASTERACEAE	*Pluchea odorata*	(L.) Cass.	PLUODO	Forb	1	
84	DICOT	ASTERACEAE	*Pluchea rosea*	Godfrey	PLUROS	Forb	1	
85	DICOT	POLYGONACEAE	*Polygonum hydropiperoides*	Michx.	POLHYD	Forb	1	
86	MONOCOT	PONTEDERIACEAE	*Pontederia cordata* var. *lanciifolia*	L./(Muhl.) Torr.	PONCOR	Forb	1	
87	DICOT	HALORAGACEAE	*Proserpinaca palustris*	L.	PROPAL	Forb	1	
88	DICOT	MYRTACEAE	*Psidium guajava*	L.	PSIGUA	Tree	2	
89	MONOCOT	CYPERACEAE	*Psilocarya nitens*	(Vahl) A.W. Wood	PSINIT	Graminoid	1	4 *Rhynchospora nitens* (Vahl) A Gray
90	PTERIDOPHYTE	PSILOTACEAE	*Psilotum nudum*	(L.) P. Beauv.	PSINUD	Fern	3	
91	PTERIDOPHYTE	DENNSTAEDTIACEAE	*Pteridium caudatum*	(L.) Maxon	PTECAU	Fern	3	2,5 *Pteridium aquilinum* (L.) Kuhn var. *caudatum* (L.) Sadebeck
92	MONOCOT	CYPERACEAE	*Rhynchospora inundata*	(Oakes) Fern.	RHYINU	Graminoid	1	
93	MONOCOT	CYPERACEAE	*Rhynchospora microcarpa*	Baldw. ex Gray	RHYMIC	Graminoid	1	
94	MONOCOT	CYPERACEAE	*Rhynchospora tracyi*	Britt.	RHYTRA	Graminoid	1	
95	DICOT	PHYTOLACCACEAE	*Rivina humilis*	L.	RIVHUM	Forb	2	
96	DICOT	BRASSICACEAE	*Rorippa floridana*	Al-Shehbaz & Rollins	RORFLO	Forb	4	1 *Nasturtium microphyllum* (Boenn.) Reichnb.
97	MONOCOT	ARECACEAE	*Sabal palmetto*	(Walt.) Lodd. ex Schult. & Schult.	SABPAL	Tree	1	
98	MONOCOT	POACEAE	*Sacciolepis striata*	(L.) Nash	SACSTR	Graminoid	1	

S. NO.	CLASS	FAMILY	SCIENTIFIC NAME	AUTHOR CITATION	SPCODE	LIFE FORM	REF	ALTERNATE NAME
99	MONOCOT	ALISMATACEAE	*Sagittaria lancifolia* var. *lancifolia*	L.	SAGLAN	Forb	1	
100	DICOT	SALICACEAE	*Salix caroliniana*	Michx.	SALCAR	Tree	1	
101	DICOT	CAPRIFOLIACEAE	*Sambucus canadensis*	L.	SAMCAN	Tree	1	
102	DICOT	PRIMULACEAE	*Samolus parviflorus*	Raf.	SAMPAR	Forb	1	4 *S. valerandi* L. var. *parviflorus* (Raf.) Hulten
103	DICOT	ASCLEPIADACEAE	*Sarcostemma clausum*	(Jacq.) Schult.	SARCLA	Vine	1	
104	DICOT	SAURURACEAE	*Saururus cernuus*	L.	SAUCER	Forb	1	
105	MONOCOT	POACEAE	*Setaria magna*	Griseb.	SETMAG	Graminoid	1	
106	DICOT	SAPOTACEAE	*Sideroxylon foetidissimum*	Jacq.	SIDFOE	Tree	4	2 *Mastichodendron foetidissimum* (Jacq.) Cronquist
107	DICOT	SIMAROUBACEAE	*Simarouba glauca*	DC.	SIMGLA	Tree	2	
108	MONOCOT	SMILACACEAE	*Smilax laurifolia*	L.	SMILAU	Vine	1	
109	DICOT	SOLANACEAE	*Solanum erianthum*	D. Don	SOLERI	Tree	2	
110	PTERIDOPHYTE	THELYPTERIDACEAE	*Thelypteris interrupta*	(Willd.) K. Iwatsuki	THEINT	Fern	5	2,3 *Thelypteris totta* (Thunb.) Schelpe
111	PTERIDOPHYTE	THELYPTERIDACEAE	*Thelypteris kunthii*	(Desv.) C.V. Morton	THEKUN	Fern	3	
112	PTERIDOPHYTE	THELYPTERIDACEAE	*Thelypteris palustris* var. *pubescens*	Schott/(Laws.) Fern.	THEPAL	Fern	3	
113	MONOCOT	BROMELIACEAE	*Tillandsia fasciculata var. densispica*	Sw./Mez	TILFAS	Epiphyte	2,4	
114	MONOCOT	BROMELIACEAE	*Tillandsia flexuosa*	Sw.	TILFLE	Epiphyte	2	
115	MONOCOT	BROMELIACEAE	*Tillandsia pauciflora*	Baker	TILPAU	Epiphyte	4	2 *T. circinnata* Schltdl.
116	MONOCOT	BROMELIACEAE	*Tillandsia recurvata*	(L.) L.	TILREC	Epiphyte	2	
117	MONOCOT	BROMELIACEAE	*Tillandsia usneoides*	(L.) L.	TILUSN	Epiphyte	2	
118	MONOCOT	BROMELIACEAE	*Tillandsia utriculata*	L.	TILUTR	Epiphyte	2	
119	DICOT	ANACARDIACEAE	*Toxicodendron radicans* var. *radicans*	(L.) Kuntze	TOXRAD	Vine	1	
120	DICOT	ULMACEAE	*Trema micranthum*	(L.) Blume	TREMIC	Tree	2	
121	MONOCOT	TYPHACEAE	*Typha domingensis*	Pers.	TYPDOM	Forb	1	

S. NO.	CLASS	FAMILY	SCIENTIFIC NAME	AUTHOR CITATION	SPCODE	LIFE FORM	REF	ALTERNATE NAME
122	DICOT	MALVACEAE	*Urena lobata**	L.	URELOB	Forb	1	
123	DICOT	LENTIBULARIACEAE	*Utricularia foliosa*	L.	UTRFOL	Forb	1	
124	DICOT	LENTIBULARIACEAE	*Utricularia purpurea*	Walt.	UTRPUR	Forb	1	
125	MONOCOT	HYDROCHARITACEAE	*Vallisneria americana*	Michx.	VALAME	Forb	1	
126	DICOT	VERBENACEAE	*Verbena scabra*	Vahl	VERSCA	Forb	1	
127	DICOT	VITACEAE	*Vitis aestivalis*	Michx.	VITAES	Vine	1	
128	DICOT	VITACEAE	*Vitis shuttleworthii**	House	VITSHU	Vine	1	

* Species were found outside the sampling plots.

Appendix 6-2

List of species present in hardwood hammock (HH), bayhead (BH) and bayhead swamp (BS) forest communities of three Shark Slough tree islands.

Species	Black Hammock			Gumbo Limbo			Satinleaf		
	HH	BH	BS	HH	BH	BS	HH	BH	BS
Trees									
Annona glabra		x	x	x	x	x		x	x
Bursera simaruba	x			x	x		x	x	
Celtis laevigata	x			x			x		
Chrysobalanus icaco	x	x	x	x	x		x	x	
Chrysophyllum oliviforme							x		
Coccoloba diversifolia							x		
Eugenia axillaris	x			x			x		
Ficus aurea	x	x	x		x		x	x	
Ilex cassine		x	x		x			x	x
Magnolia virginiana			x		x			x	x
Myrica cerifera		x	x		x	x		x	x
Persea borbonia		x			x	x	x	x	x
Salix caroliniana		x	x		x	x		x	
Sambucus canadensis		x		x	x	x			
Sideroxylon foetidissimum	x			x					
Solanum erianthum				x					
Trema micranthum							x		
Shrubs									
Aster carolinianus			x			x			
Caesalpinia bonduc				x					
Cephalanthus occidentalis		x	x			x		x	x
Myrsine floridana				x			x		
Graminoids									
Cladium jamaicense			x			x			x
Cyperus haspan			x			x		x	
Dicanthelium dichotomum									x
Echinochloa crusgalli						x			
Fuirena breviseta			x			x			x
Panicum hemitomon			x						
Panicum virgatum									x

Species	Black Hammock			Gumbo Limbo			Satinleaf		
	HH	BH	BS	HH	BH	BS	HH	BH	BS
Psilocarya nitens									
Rhynchospora inundata									x
Rhynchospora microcarpa									
Sacciolepis striata						x			
Forbs									
Aeschynomene pratensis									
Bacopa caroliniana		x	x					x	x
Boehmeria cylindrica		x	x		x	x		x	x
Capraria biflora				x					
Diodia virginiana		x	x			x		x	x
Hyptis alata									x
Ludwigia alata						x		x	x
Ludwigia repens			x						x
Ludwigia sp.									
Mitreola petiolata									x
Nymphoides aquatica						x			
Peltandra virginica		x	x						
Pluchea odorata					x				
Pluchea rosea									x
Polygonum hydropiperoides			x		x	x		x	x
Pontederia cordata			x			x		x	x
Proserpinaca palustris			x						x
Rivina humilis	x			x					
Sagittaria lancifolia			x						
Saururus cernuus		x	x		x			x	x
Typha domingensis			x						
Utricularia foliosa			x			x			
Utricularia purpurea									
Vallisneria americana									
Vines									
Ampelopsis arborea					x		x		
Apios americana					x				
Cissus sicyoides		x		x			x		
Dalbergia ecastophyllum							x	x	
Ipomoea sagittata			x						x
Mikania scandens		x	x		x	x		x	x
Parthenocissus quinquefolia	x	x	x	x			x	x	

Species	Black Hammock			Gumbo Limbo			Satinleaf		
	HH	BH	BS	HH	BH	BS	HH	BH	BS
Sarcostemma clausum	x	x	x		x	x		x	
Toxicodendron radicans		x							
Vitis aestivalis		x					x		
Ferns									
Acrostichum danaeifolium		x	x	x	x	x			
Blechnum serrulatum		x	x					x	x
Nephrolepis exaltata	x	x		x					
Psilotum nudum		x	x						
Pteridium caudatum							x		
Thelypteris interrupta		x	x		x			x	
Thelypteris kunthii				x					
Epiphytes									
Tillandsia recurvata		x							
Tillandsia usneoides	x	x			x				

Appendix 6-3

Species elevation, hydroperiod and mean water level optima (Opt) and tolerances (Tol) obtained from weighted averaging inference models with inverse de-shrinking and tolerance weighting.

Species	Spp Code	Elevation (m)						Hydroperiod (days)						Mean Water level	
		Black Hammock		Gumbo Limbo		Satinleaf		Black Hammock		Gumbo Limbo		Satinleaf			
		Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol
Acrostichum danaeifolium	ACRDAN	1.520	0.084	1.373	0.134	1.538	0.112	224	53	281	62	238	68	0.141	0.126
Aeschynomene pratensis	AESPRA			1.173	0.045	1.754	0.288			359	4	112	136	-0.073	0.317
Ampelopsis arborea	AMPARB	1.532	0.162	1.360	0.105			213	111	288	55			0.180	0.107
Andropogon glomeratus	ANDGLO	1.431	0.014			1.531	0.057	280	7			245	36	0.114	0.055
Annona glabra	ANNGLA	1.456	0.094	1.321	0.077	1.509	0.095	263	59	306	31	267	54	0.163	0.098
Apios americana	APIAME			1.451	0.065					240	36			0.090	0.065
Aster carolinianus	ASTCAR			1.340	0.054					300	26			0.201	0.054
Aster dumosus	ASTDUM	1.521	0.041					222	26					0.055	0.041
Bacopa caroliniana	BACCAR	1.402	0.061	1.262	0.079	1.465	0.092	295	32	331	25	281	52	0.195	0.083
Bacopa monnieri	BACMON	1.469	0.126			1.485	0.007	258	79			270	3	0.146	0.065
Blechnum serrulatum	BLESER	1.505	0.085	1.336	0.083	1.567	0.111	234	67	300	39	242	60	0.158	0.110
Boehmeria cylindrica	BOECYL	1.492	0.102	1.357	0.117	1.726	0.308	247	70	287	54	170	111	0.144	0.152
Bursera simaruba	BURSIM	2.297	0.235	1.992	0.115	2.265	0.058	26	60	15	34	12	21	-0.507	0.209
Caesalpinia bonduc	CAEBON			1.932	0.091					3	37			-0.391	0.111
Celtis laevigata	CELLAE	2.279	0.262	2.025	0.081	2.190	0.057	3	19	6	22	0	51	-0.487	0.100
Cephalanthus occidentalis	CEPOCC	1.531	0.088			1.478	0.163	217	51			325	43	0.162	0.160
Chrysobalanus icaco	CHRICA	1.598	0.088	1.445	0.195	1.970	0.226	155	73	237	109	34	48	-0.067	0.217
Chrysophyllum oliviforme	CHROLI					2.121	0.063					6	13	-0.478	0.064
Cissus sicyoides	CISSIC	1.599	0.101	1.504	0.168	2.055	0.180	122	104	211	88	24	42	-0.225	0.280
Cladium jamaicense	CLAJAM	1.337	0.059	1.164	0.070	1.409	0.091	333	28	355	15	324	39	0.284	0.100
Coccoloba diversifolia	COCDIV					2.289	0.118					0	51	-0.646	0.118
Conoclinium coelestinum	CONCOE			1.543	0.091					195	37			-0.001	0.111
Cyperus haspan	CYPHAS	1.337	0.053	1.249	0.071			336	30	335	23			0.258	0.065
Cyperus ligularis	CYPLIG					1.458	0.083					292	54	0.185	0.083
Cyperus odoratus	CYPODO	1.341	0.054					335	29					0.235	0.054
Dalbergia ecastophyllum	DALECA					1.836	0.293					106	122	-0.192	0.293
Dicanthelium dichotomum	DICDIC					1.409	0.115					326	51	0.234	0.111

Species	Spp Code	Elevation (m)						Hydroperiod (days)						Mean Water level	
		Black Hammock		Gumbo Limbo		Satinleaf		Black Hammock		Gumbo Limbo		Satinleaf			
		Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol
Diodia virginiana	DIOVIR	1.449	0.117	1.296	0.049	1.577	0.085	270	74	319	19	222	56	0.134	0.113
Echinochloa crusgalli	ECHCRU	1.300	0.046	1.252	0.024			351	16	337	9			0.284	0.031
Eleocharis caribaea	ELECAR					1.388	0.115					338	51	0.255	0.111
Eleocharis cellulosa	ELECEL	1.319	0.071	1.149	0.059	1.340	0.050	339	33	359	6	350	12	0.357	0.071
Eugenia axillaris	EUGAXI	2.361	0.114	2.042	0.070	2.224	0.102	0	51	3	15	1	1	-0.584	0.144
Ficus aurea	FICAUR			1.707	0.286	2.293	0.045			83	80	0	51	-0.407	0.298
Fuirena breviseta	FUIBRE			1.244	0.095	1.469	0.061			333	27	284	40	0.250	0.102
Hydrolea corymbosa	HYDCOR									341	37			0.297	0.111
Hydrocotyle umbellata	HYDUMB	1.353	0.065					327	28					0.223	0.065
Hymenocallis palmeri	HYMPAL			1.068	0.091					364	37			0.473	0.111
Hyptis alata	HYPALA			1.245	0.091	1.711	0.115					140	51	-0.068	0.111
Ilex cassine	ILECAS	1.474	0.074	1.325	0.074			255	46	306	35			0.211	0.077
Ipomoea alba	IPOALB			1.309	0.003					317	2			0.232	0.003
Ipomoea sagittata	IPOSAG	1.414	0.042	1.317	0.060	1.526	0.109	292	27	311	23	251	66	0.196	0.083
Justicia angusta	JUSANG	1.346	0.088	1.171	0.054	1.369	0.055	335	51	357	11	346	10	0.299	0.070
Leersia hexandra	LEEHEX	1.388	0.046	1.268	0.039	1.493	0.123	306	22	330	12	270	79	0.205	0.057
Lemna obscura	LEMOBS	1.508	0.088					227	51					0.068	0.111
Ludwigia alata	LUDALA	1.447	0.147	1.253	0.072	1.453	0.024	271	92	333	20	293	20	0.249	0.097
Ludwigia curtissii	LUDCUR					1.586	0.008					212	5	0.057	0.008
Ludwigia repens	LUDREP	1.403	0.066	1.306	0.065	1.461	0.060	305	45	315	25	292	35	0.210	0.081
Magnolia virginiana	MAGVIR	1.454	0.037	1.390	0.080	1.586	0.131	286	47	274	42	259	60	0.119	0.107
Melothria pendula	MELPEN			1.305	0.085					313	40			0.236	0.085
Mikania scandens	MIKSCA	1.381	0.062	1.321	0.086	1.452	0.046	312	39	306	40	295	29	0.204	0.070
Mitreola petiolata	MITPET	1.305	0.088	1.215	0.091	1.516	0.069	354	51	352	37	253	46	0.170	0.109
Myrica cerifera	MYRCER	1.448	0.097	1.360	0.120	1.549	0.125	270	61	286	61	259	59	0.133	0.121
Myrsine floridana	MYRFLO			1.940	0.049	2.096	0.194			5	7	5	42	-0.436	0.090
Nephrolepis exaltata	NEPEXA			1.932	0.091					3	37			-0.391	0.111
Osmunda regalis	OSMREG			1.307	0.091					318	37			0.235	0.111
Oxypolis filiformis	OXYFIL					1.319	0.115					355	51	0.324	0.111
Panicum hemitomon	PANHEM	1.385	0.168	1.232	0.061	1.302	0.127	295	95	341	17	354	58	0.303	0.104
Panicum rigidulum	PANRIG	1.413	0.083	1.270	0.091	1.549	0.103	290	47	330	37	238	62	0.184	0.097
Panicum virgatum	PANVIR					1.582	0.103					230	33	0.061	0.103

Species	Spp Code	Elevation (m)						Hydroperiod (days)						Mean Water level	
		Black Hammock		Gumbo Limbo		Satinleaf		Black Hammock		Gumbo Limbo		Satinleaf			
		Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol
Parthenocissus quinquefolia	PARQUI	1.583	0.360	1.497	0.291	2.091	0.256	220	126	228	134	0	1	-0.156	0.372
Paspalidium geminatum	PASGEM	1.268	0.088	1.148	0.101	1.331	0.052	362	51	360	26	352	15	0.373	0.068
Passiflora suberosa	PASSUB	1.667	0.029					110	26					-0.091	0.029
Peltandra virginica	PELVIR	1.378	0.067	1.213	0.063	1.540	0.128	311	37	346	18	271	41	0.206	0.076
Persea borbonia	PERBOR	1.456	0.069	1.375	0.132	1.996	0.227	265	44	275	66	18	67	0.106	0.124
Pluchea odorata	PLUODO			1.530	0.187					201	93			0.011	0.187
Pluchea rosea	PLUROS	1.414	0.052	1.267	0.071	1.454	0.071	292	33	333	26	295	46	0.191	0.071
Polygonum hydropiperoides	POLHYD	1.358	0.041	1.251	0.065	1.411	0.066	331	25	335	27	320	40	0.269	0.066
Pontederia cordata	PONCOR	1.344	0.062	1.247	0.057	1.461	0.079	331	32	337	19	291	48	0.234	0.083
Proserpinaca palustris	PROPAL	1.439	0.058	1.257	0.066	1.459	0.073	275	36	335	27	288	48	0.191	0.094
Psilotum nudum	PSINUD	1.463	0.087					259	55					0.113	0.087
Pteridium caudatum	PTECAU					2.263	0.057					0	51	-0.620	0.057
Rhynchospora inundata	RHYINU			1.187	0.068					352	15			0.354	0.068
Rhynchospora microcarpa	RHYMIC			1.333	0.091					308	37			0.209	0.111
Rhynchospora tracyi	RHYTRA	1.339	0.077	1.231	0.034	1.331	0.052	333	45	345	14	352	15	0.251	0.074
Rivina humilis	RIVHUM			2.029	0.075					1	2			-0.488	0.075
Rorippa floridana	RORFLO			1.543	0.091					195	37			-0.001	0.111
Sabal palmetto	SABPAL	1.648	0.080			2.093	0.115					2	51		
Sacciolepis striata	SACSTR	1.396	0.072	1.248	0.038			303	45	338	14			0.212	0.084
Sagittaria lancifolia	SAGLAN	1.409	0.062	1.159	0.091	1.532	0.115	291	35	353	20	242	51	0.180	0.115
Salix caroliniana	SALCAR	1.556	0.078	1.339	0.079	1.519	0.099	200	53	300	38	270	40	0.140	0.113
Sambucus canadensis	SAMCAN			1.525	0.153					204	84			-0.173	0.220
Samolus parviflorus	SAMPAR			1.565	0.054					179	38			-0.057	0.124
Sarcostemma clausum	SARCLA	1.510	0.084	1.311	0.096	1.664	0.146	239	61	309	42	164	94	0.162	0.146
Saururus cernuus	SAUCER	1.397	0.084	1.330	0.111	1.529	0.107	301	50	301	58	255	61	0.180	0.105
Setaria magna	SETMAG			1.208	0.091					355	37			0.334	0.111
Sideroxylon foetidissimum	SIDFOE	2.408	0.061	2.106	0.042			0	51	0	37			-0.698	0.148
Simarouba glauca	SIMGLA					2.110	0.115					2	51	-0.467	0.111
Smilax laurifolia	SMILAU	1.525	0.100	1.375	0.078	1.682	0.074	224	61	283	41	191	51	0.141	0.098
Solanum erianthum	SOLERI			2.018	0.088					2	4			-0.477	0.088
Thelypteris interrupta	THEINT	1.527	0.071	1.362	0.090	1.652	0.154	219	47	288	43	178	83	0.140	0.115
Thelypteris kunthii	THEKUN			1.965	0.251					7	93			-0.424	0.251

Species	Spp Code	Elevation (m)						Hydroperiod (days)						Mean Water level	
		Black Hammock		Gumbo Limbo		Satinleaf		Black Hammock		Gumbo Limbo		Satinleaf			
		Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol
Thelypteris palustris	THEPAL			1.192	0.096					351	28			0.349	0.096
Tillandsia fasciculata	TILFAS	1.399	0.120	1.364	0.220			298	73	292	101			0.162	0.192
Tillandsia flexuosa	TILFLE			1.311	0.145					307	47			0.231	0.145
Tillandsia pauciflora	TILPAU			1.329	0.066					308	26			0.212	0.066
Tillandsia recurvata	TILREC	1.466	0.088	1.229	0.095			260	51	339	29			0.306	0.098
Tillandsia usneoides	TILUSN	1.575	0.063	1.436	0.118			191	37	249	74			0.085	0.105
Tillandsia utriculata	TILUTR			1.245	0.091					341	37			0.297	0.111
Typha domingensis	TYPDOM	1.376	0.056			1.440	0.115	320	36			305	51	0.220	0.079
Utricularia foliosa	UTRFOL	1.322	0.069	1.239	0.052	1.232	0.115	339	34	340	15	360	51	0.296	0.056
Utricularia purpurea	UTRPUR	1.244	0.088	1.162	0.070	1.396	0.173	363	51	358	5	303	61	0.319	0.124
Vallisneria americana	VALAME			1.251	0.019					338	8			0.291	0.019
Verbena scabra	VERSCA			1.543	0.091					195	37			-0.001	0.111
Vitis aestivalis	VITAES	1.947	0.359	1.512	0.101			57	129	204	65			-0.145	0.283
Seedlings															
Annona glabra	ANNGLA	1.402	0.064	1.300	0.087	1.514	0.113	297	38	315	38	267	66	0.201	0.089
Aster carolinianus	ASTCAR	1.480	0.063	1.326	0.066			247	42	306	31			0.198	0.078
Baccharis halimifolia	BACHAL			1.300	0.091					320	37			0.241	0.111
Bursera simaruba	BURSIM	1.626	0.009	1.987	0.091	2.092	0.010	106	92	0	37	3	0	-0.334	0.206
Celtis laevigata	CELLAE	2.377	0.071	2.028	0.092			0	51	8	23			-0.526	0.132
Cephalanthus occidentalis	CEPOCC	1.384	0.080	1.243	0.073	1.476	0.084	314	48	336	21	290	45	0.235	0.101
Chrysobalanus icaco	CHRICA	1.524	0.131	1.388	0.182	2.007	0.259	218	87	275	96	49	87	0.065	0.223
Chrysophyllum oliviforme	CHROLI					2.177	0.113					2	4	-0.508	0.169
Coccoloba diversifolia	COCDIV					2.159	0.115					0	51	-0.516	0.111
Eugenia axillaris	EUGAXI	2.394	0.067	2.050	0.075	2.216	0.095	0	51	6	22	1	2	-0.569	0.136
Eupatorium capillifolium	EUPCAP			1.580	0.052					171	34			-0.038	0.052
Ficus aurea	FICAUR			1.191	0.191	1.411	0.115			341	66	323	51	0.156	0.085
Hibiscus grandiflorus	HIBGRA					1.551	0.103					240	68	0.092	0.103
Ilex cassine	ILECAS	1.453	0.015	1.316	0.039			267	9	312	18			0.221	0.051
Kosteletzkya virginica	KOSVIR			1.287	0.063					322	29			0.254	0.063
Magnolia virginiana	MAGVIR	1.469	0.048	1.333	0.059	1.467	0.176	258	30	304	29	319	61	0.201	0.073
Myrica cerifera	MYRCER	1.467	0.053	1.368	0.086	1.737	0.210	258	34	286	43	115	133	0.156	0.102

Species	Spp Code	Elevation (m)						Hydroperiod (days)						Mean Water level	
		Black Hammock		Gumbo Limbo		Satinleaf		Black Hammock		Gumbo Limbo		Satinleaf			
		Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol
Myrsine floridana	MYRFLO			1.945	0.059	2.110	0.115			5	7	2	51	-0.408	0.059
Persea borbonia	PERBOR	1.530	0.122	1.387	0.105	1.712	0.228	214	81	277	52	168	219	0.132	0.128
Psidium guajava	PSIGUA			1.932	0.091					3	37			-0.391	0.111
Sabal palmetto	SABPAL							130	75					-0.086	0.062
Salix caroliniana	SALCAR	1.426	0.083	1.296	0.088			285	51	317	41			0.245	0.088
Sambucus canadensis	SAMCAN			1.617	0.091					147	37			-0.075	0.111
Sideroxylon foetidissimum	SIDFOE	2.458	0.041	2.109	0.091			0	51	0	37			-0.641	0.187
Solanum erianthum	SOLERI			2.021	0.091					0	37			-0.480	0.111