Chapter 8

Vegetation Pattern and Process in Tree Islands of the Southern Everglades and Adjacent Areas

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Abstract: The tree islands of the Everglades area of southern Florida, including adjacent interior and coastal areas, are classified based on species composition and environmental factors controlling tree island distribution and structure. Tree islands occur on various substrates within surrounding habitats that may be freshwater or coastal wetlands, or rockland pine forest of the Atlantic Coastal Ridge. Eight tree island groupings within seven subregions are defined by cluster analysis of data from the literature and previously unpublished studies. Additional types are recognized based on distinguishing ecological features. Most of the types are dominated by native, tropical species found in the continental United States only in southern Florida. Hurricanes, drainage, excessive burning, spread of non-native species and logging have differentially affected all types and few undisturbed tree islands exist even within federally preserved lands. Collectively, the types occur along local and regional elevation gradients, with associated vulnerability to flooding and fires. Marked differences exist in the response of tree islands to protracted flooding that are consistent with their location in the landscape. Thus bayhead swamps, which occur as part of freshwater slough tree islands and are comprised mostly of temperate swamp forest species, have been inundated up to 10 months/yr in the past several decades, while tropical hardwood hammocks on the same tree islands were inundated for 0 to 23% of the year. Hammocks within rockland pine forests seldom if ever flood, but they are subject to periodic fires. A total of 164 woody species occur naturally in the area's forested islands, although many are rare or highly restricted in distribution. All 135 tropical species have distribution ranges centered in the West Indies where most occur in calcareous, dry sites, frequently as invaders of disturbed habitats.

1. INTRODUCTION

The southern tip of the Florida peninsula and adjacent coastal areas comprise the land areas of the continental United States closest to the Tropic of Cancer, thus approaching the Tropics in climate, as well as sharing common geological and coastal features with the Caribbean basin. The region we discuss (Figure 1) extends from the southern Big Cypress National Preserve (BCNP) east through Everglades National Park (ENP) to Biscayne Bay and south through the peninsula to the Florida Keys. North of the Keys, the area is commonly described as "subtropical", reflecting a climate with temperature regimes similar to the tropics, while experiencing below freezing temperatures frequent enough to be ecologically significant. The Keys are largely free of temperatures falling below 5° C thus they can be considered as having a tropical climate.

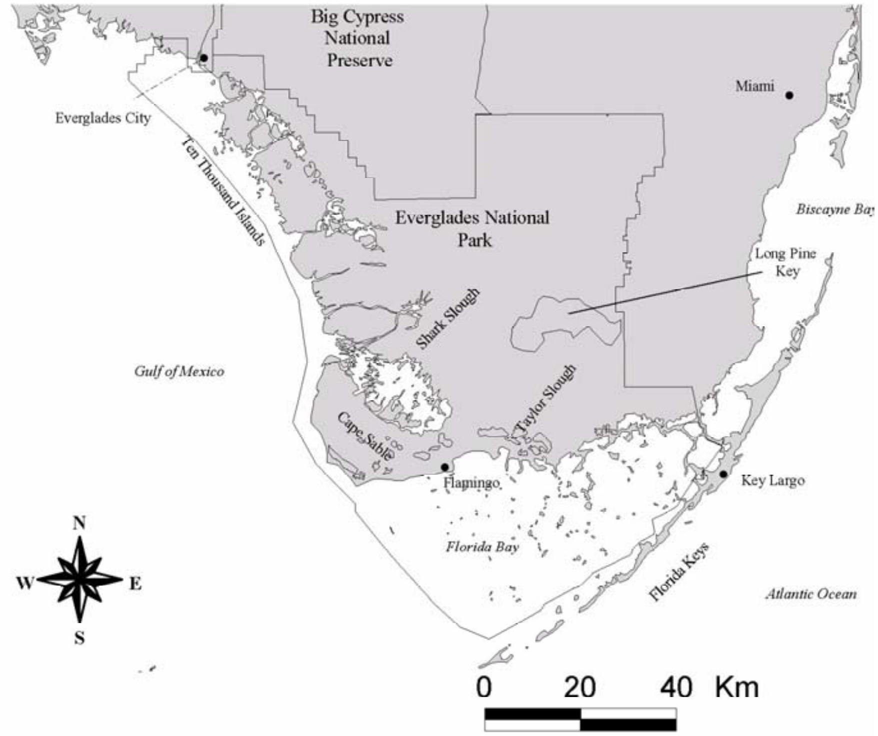

Figure 1. The southern Everglades area and its environs.

Although most remaining natural lands in south Florida consist of freshwater wetlands dominated by sedges and grasses of the North Temperate flora, significant areas are occupied by trees and shrubs of both temperate and West Indian floras. Our chapter is organized around a quantitative classification of tree island types and a review of the literature on the main factors known to influence tree island development.

As described below, the woody communities of the subject area fit into three categories based on species composition and substrate: tree islands on peat, marl or shell deposits on limestone outcrops; pine forests on limestone ridges; and several types of extensive swamp forests. Our chapter deals principally with the first category, as the other types have been well described elsewhere. Thus cypress (*Taxodium distichum* (L.) Rich.) forest, a freshwater swamp forest type that reaches its southernmost extent in ENP, but is best represented within our region in BCNP, is thoroughly covered by Duever et al. (1986) and Ewel and Odum (1984). Mangrove forests, which occupy nearly all of the tidally influenced coasts on both sides of the southern peninsula and the Florida Keys, are discussed by Odum and McIvor (1990), Craighead (1971), and Lugo and Snedaker (1974). The slash pine forests occupying the Miami Rock Ridge, the southernmost extent of the Atlantic Coastal Ridge, comparable areas in BCNP, and smaller outcroppings of Miami Limestone in the lower Florida Keys, are described in Snyder et al. (1990), Robertson (1953) and Olmsted et al. (1983).

"Tree island" is the term applied by most authors to small patches of woody vegetation embedded in a landscape of a contrasting vegetation type (Tomlinson 1980). The "matrix" within which tree islands occur in our area may be mangrove or freshwater swamp, freshwater or brackish marsh or rockland pine forest. The substrate on which tree islands are found often differs from that of the surrounding vegetation. Thus within the freshwater sawgrass marshes of Shark and Taylor Sloughs in ENP, tree islands can occur on woody peat or limestone outcrops in an area of freshwater calcitic mud (marl), or peat. Within the coastal zone, hardwood hammocks are found on marl, on sand ridges, or on midden deposits of anthropogenic origin within areas of mangrove peat or marine clay. Within slash pine forests on Long Pine Key within ENP and on Big Pine Key in the lower Florida Keys, hardwood hammocks are found on elevated limestone outcrops. In all of these cases, roots occupy a thin surficial layer of coarse, unsaturated organic material.

Two main tree island categories differentiate based on prevailing flora and principal controlling factors. *Tropical hardwood hammocks* are nearly always found on rock outcrops or well-drained soils and are composed of species with distribution ranges centered in the tropics. Tropical hammocks also occur as the dominant cover of the few remaining undeveloped upland areas of the Florida Keys. *Swamp forests* are stands comprised mainly of species with distributions centered in the temperate zone and adapted to poorly drained soils. Swamp forests may be aggregated into discrete, small stands or as components of larger tree islands which include hammocks on outcrops, but in either case they are regularly flooded, leading to formation of peat soils. Swamp forests also are found as extensive *Taxodium* or temperate hardwood stands that dominate landscapes or form savannahs with a graminoid understory in BCNP or ENP but these are not considered to be tree islands.

2. OVERVIEW OF GEOLOGICAL SETTING, SOILS, AND CLIMATE

2.1 Geology and Soils

The general geology of the area has been well described (Hoffmeister 1974) and remarks here are confined to aspects directly related to tree islands. Most of the substrate consists of Miami Limestone of Pleistocene origin, formed 100,000 to 25,000 years ago when the sea level was up to 10 meters (m) higher than at present. Other geologic formations include the Tamiami, formed during the Miocene six million years ago beneath the Big Cypress Basin and the Gulf Coast north of the Broad River, and the Fort Thompson Formation, formed during the Pleistocene and exposed from the central Everglades to Lake Okeechobee. The coralline Key Largo Limestone, comprising the land surface of the upper and middle Florida Keys, formed contemporaneously with the Miami Limestone.

In marine areas such as Florida Bay, the Miami Limestone is submerged beneath several meters of water and lime mud, only to reappear above the surface in the lower Florida Keys. The Miami Limestone occurs in two phases -- an oolitic phase in the east side of the peninsula with disjunct patches in the eastern Big Cypress and the lower Keys, and a bryozoan facies forming a broad band in the interior of the central and southern Everglades. In addition, oolitic limestone forms the Miami Rock Ridge, the southernmost extension of the Atlantic Coastal Ridge that parallels the east coast of Florida. It extends about 50 miles from Miami southwest through Long Pine Key in ENP, ending in disjunct outcrops near the mangrove zone at Mahogany Hammock. The Miami Rock Ridge decreases in elevation from around 6 m at the north to less than 1 m at its terminus. It comprises the most elevated land surface of this low-lying region. Over 90% of the Miami Rock Ridge outside ENP has been converted to agricultural and urban use, with Long Pine Key, an area of about 8000 ha within ENP, by far the largest natural remnant.

In most of the area under consideration, the limestone surface has long been mantled by deposits of marl or peat formed by wetland plant communities under, respectively, seasonal or nearly year-round inundation by fresh water. Within the range of tidal inundation, sediments reflect marine processes, comprising either lime muds high in aragonite or mangrove-derived peat which has accumulated in places to depths exceeding 4.5 m (Craighead 1971; Cohen and Spackman 1977).

Generally, limestone outcrops are local features a meter or less above the surrounding soil surface, the chief exception being the Miami Rock Ridge. The outcrops are important disproportionately to their small area because they comprise nearly all of the sites not subject to regular flooding by fresh or saline waters. In some cases the limestone beneath hammocks appears more dissected with larger solution holes than in the pinelands but it is unclear whether hammock formation followed or preceded the greater surface weathering

All the limestone types are relatively soft, permeable and prone to erosion and dissolution from exposure to ground water and precipitation. Exposure to the atmosphere has promoted a highly weathered microkarst topography with pits and solution holes of varying sizes that provide sites for soil accumulation and damp microhabitats for mesophytic plants. The action of roots and chemical byproducts of decomposition also contribute to limestone dissolution. However, limestone exposed to the atmosphere also undergoes induration or hardening of the immediate surface layer of the rock caused by reprecipitation of calcite that was dissolved by rain water, creating highly variable surface roughness.

The solution holes accumulate limestone fragments, sand grains, and organic debris that often serve as the principal rooting medium in hammocks (whether in sloughs or on the Atlantic Coastal Ridge) and in pinelands. Solution features within hammocks are more advanced than in the surrounding marshes, probably as a result of root organic acids and root penetration. In addition, a distinct pit and mound topography has formed from hammock trees uprooted in storms. Prior to the era of artificial drainage, the larger holes provided microhabitats for moisture-requiring ferns, orchids, *Peperomia* spp. and other herbaceous understory species. In the wet season, and sometimes year-round, the large holes held water that supported aquatic animal communities, and perhaps acted as a freshwater reservoir used by plants (Craighead 1971).

The limestone underlying the region, although rich in calcium, magnesium, iron and other minerals, releases very little phosphorus in forms available to plants, thus limiting plant growth, in conjunction with the nutrient limits associated with the shallow soils. Also the weakly acid pH which develops in soils developed from limestone minerals reduces solubility, and hence availability of certain mineral nutrients such as aluminum, silicon, manganese and phosphorus (Jenny 1980).

The shallow soils of hammocks, often well under 50 cm deep, restrict rooting depth, provide a limited moisture reservoir, and increase susceptibility to wind-throw, a tendency that has shaped tree islands perimeters and surfaces. In conjunction with the seasonally dry climate, these soil features help determine the structure and composition of the tree communities. The high leachability of limestone soils in rainy climates also is likely to affect plant growth.

2.2 Climate

The climate of south Florida is seasonal and subtropical, and potentially supports plant growth most of the year (Tomlinson 1980). Four seasons can be recognized but a wet, hot June-October and a cooler, drier November-May are most distinct. About 80% of the rain falls in the wet season. In the classification by Holdridge (1967), south Florida's climate, which often includes significant spring drought, can be considered to have a seasonally dry tropical climate.

Summer rains are usually cyclonic (thunderstorms) with heavy rainfall events from tropical storms occurring annually. Periodic hurricanes often bring damaging winds and heavy rainfall leading to flooding and tidal surges which can damage tree islands. The frequency of hurricanes has been about one every six to eight years somewhere in the region with severe ones occurring on average every 14 to 50 years since the advent of record-keeping in 1871 (Gentry 1984).

Key ecological factors relative to tree islands also include extreme events such as extended drought, excessively wet periods and winter low temperatures. There was a drought in nearly every decade in the 20th Century. In a severe drought, rainfall may be depressed 35% below average (Duever et al. 1986). A strong rainfall gradient within the region may influence species composition and growth on tree islands. Thus, annual rainfall totals around 60 inches (1400 mm) along the East Coast in Broward and eastern Miami-Dade counties, but is 15-20% lower within a mile of the coast and on nearby coastal barrier islands such as Miami Beach. Mean rainfall declines sharply south and west across the peninsula and down the Florida Keys. Thus period-of-record means range from 1544 mm at Homestead to 1280 mm in northwest ENP, 1140 mm near northeastern Florida Bay, and 965 mm at Key West.

The proximity of marine waters buffers coastal areas against the cold polar air masses that penetrate southern Florida in the winter. Even a short distance inland the chances of below-freezing temperatures may double (Chen and Gerber 1990). Freezing temperatures which on average have occurred every other year on the southern mainland during the period of record (until the 1990s when they became less common) occur rarely in the northern Florida Keys and not at all in the others. To a lesser extent the coastal mainland fringe also has a maritime climate. Thus low temperatures are essentially minimized there as a factor influencing species distributions. This pattern likely explains at least some of the differences in hammock composition between the Keys, coastal areas and the interior.

On the mainland, cold weather has periodically killed or damaged extensive areas of scrub mangrove (Craighead 1971). *Rhizophora mangle* L., *Laguncularia racemosa* (L.) C.F. Gaertn., *Conocarpus erectus* L. and *Chrysobalanus icaco* L. are the tropical species known to be sensitive to freezes (Olmsted et al. 1993), but probably all tropical species are vulnerable. Periodic freeze events, which can extend over large areas such as occurred in 1977, 1981 and 1989, may limit northward expansion of tropical species (Duever et al. 1986; Olmsted et al. 1993). In contrast, temperate species are essentially unaffected at temperatures experienced in southern Florida.

3. CLASSIFICATION OF TREE ISLAND TYPES

Review of the literature reveals an impressive variety of habitats and biological communities throughout the region but also a very uneven database. A multidimensional scaling ordination and cluster analysis was chosen to look for relationships among the various tree island communities based on data from the literature. Data from 84 study sites distributed throughout the southern Everglades area were used. A total of 61 native species, dead or alive, constituted the database. To be considered for inclusion, a species had to occur in more than three study sites. In order to incorporate data from all the sub-regions, however, only species presence data could be used, placing limits on the level of interpretation.

The cluster analysis (Euclidean distance, Ward's method, using PC-ORD v. 3.11) clearly differentiated grouping of coastal and interior communities (Figure 2). In addition, the cluster analysis produced eight groups at the 47% similarity level. Seven of these groups strongly correspond with geographic areas (or "sub-regions") of the southern Everglades (Table 1, Figure 2). One additional group, freshwater Indian midden, while having floristic affinities with other tree island types of the Big Cypress sub-region, was distinct enough to constitute its own "type".

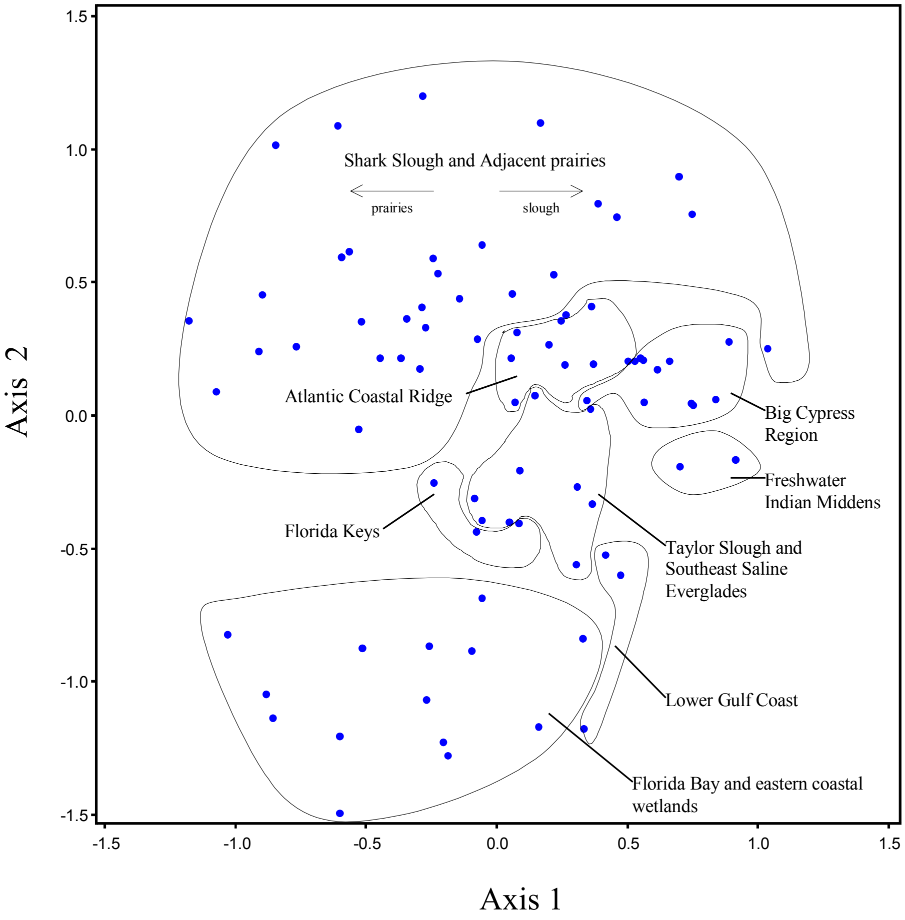

Figure 2. Results of multidimensional scaling ordination and cluster analysis of data from 84 tree island sites from the southern Everglades. Eight tree island cluster groups and seven geographical sub-regions are indicated. Data sources are given in Table 1.

Three tree island categories, i.e., tropical hardwood hammock, bayhead and bayhead-hammock forest, occur more than once because of floristic differences that make them distinctive within sub-regions (Table 1). Recognition of these types is generally supported by cluster analysis although at a lower similarity level than the sub-regional groups, and by other information as discussed under the type subheadings below. In addition, seven types were not represented in the cluster analysis but are separately recognized due to their distinctive botany and physiography (Table 1). *In toto*, then, 22 tree island communities are recognized reflecting the high diversity of habitats and growing conditions in the region.

Table 1. Tree islands of the southern Everglades, classified into types by region and subregion. Only sources of information used for the cluster analysis are given. The eight groups produced by cluster analysis are indicated in bold type. Tree island "types" followed by an asterisk (*) were not represented in the cluster analysis.

Region	Subregion	Type	Source
Interior	Atlantic Coastal Ridge	Tropical hardwood hammock	Olmsted et al. 1980; Horvitz et al. 1995
		Mahogany hammock	Olmsted et al. 1980
	Big Cypress Region	Tropical hardwood hammock	Gunderson and Loope 1982a
		Oak-*Sabal* hammock*	
		Freshwater Indian midden	Borel 1997
	Shark Slough and Adjacent Prairies	Tropical hardwood hammock	Oberbauer and Koptur, 1995; Loope and Urban 1980; Armentano, T.V. et al., unpublished raw data, 1995-97
		Bayhead swamp forest*	
		Bayhead*	
		Bayhead-hammock forest	Loope and Urban 1980
		Willowhead*	
	Taylor Slough and Southeast Saline Everglades	Tropical hardwood hammock	Ross et al. 1996
		Bayhead	Jones, D.T. et al., unpublished raw data, 1998
		Bayhead-hammock forest	
Coastal	Lower Gulf Coast	Tropical hardwood hammock*	
		Strand hardwood hammock*	
		Indian midden hammock	Borel 1997; Reimus,1997
	Florida Bay	Tropical hardwood hammock	Olmsted et al. 1981; Ross et al. 1996; Jones, D.T. et al., unpublished raw data, 1998
		Buttonwood hammock*	
		Thatch palm hammock	Jones, D.T. et al., unpublished raw data, 1998
		Florida Bay keys hammock	Jones, D.T. and Armentano, T.V., unpublished raw data, 1996
	Florida Keys	Upper Keys hammock	Ross et al. 1992
		Lower Keys hammock	

Available data indicate that the basal area of community types varies widely (Figure 3), reflecting the effects of differential factors such as the time since the last damaging hurricane or fire, but also probably differences in site quality. Thus the basal area of Shark Slough hammocks are much lower than those of the Atlantic Coastal Ridge sites despite both areas having suffered severe damage from Hurricane Andrew (Armentano et al. 1995). The largest basal areas (approaching 90 m^2 per ha) are seen in hammock sites within the Big Cypress and Atlantic Coastal Ridge sub-regions, followed by the coastal Coot Bay Hammock. Basal areas of the several hammocks in Shark Slough and the single Florida Bay thatch palm hammock were, on average, about one-third or less of the other sites.

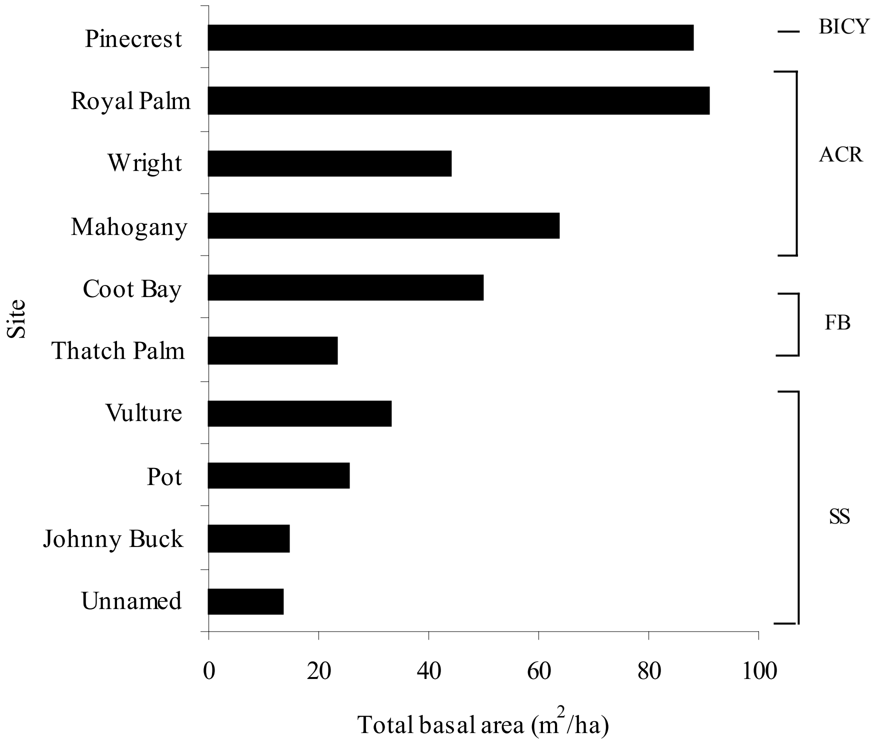

Figure 3. Comparison of total basal area of woody stems ≥ 2.5 cm dbh at select hammock sites representing four subregions: Atlantic Coastal Ridge (ACR); Big Cypress (BICY); Florida Bay (FB); Shark Slough and adjacent prairies (SS)

From a search of published literature (Leon and Alain 1946-53, 1957-63; Alain 1962; Correll and Correll 1982; Snyder et al. 1990; Olmsted and Armentano 1997) and the authors' field notes, 164 native, woody plant species and cacti, mostly tropical, are reported to occur in tree islands of the southern Everglades (Appendix I). The Florida Keys subregion has over twice the number of species as the Shark Slough and Taylor Slough-Southeast Saline Everglades subregions, and 40% more species than the Big Cypress, Florida Bay, and Lower Gulf Coast subregions. Thirty-six percent of the species are listed by the state as threatened (native species in rapid decline in number of plants within the state) or endangered (native species in imminent danger of extinction within the state -- see Appendix). Almost 80% of the threatened and endangered species occur in (but are not limited to) the Florida Keys, the highest of any subregion.

3.1 Tree Islands of the Atlantic Coastal Ridge

The southern terminus of the Atlantic Coastal Ridge ends in southern ENP, in Long Pine Key. This 8000 ha area of eroded, exposed limestone reaches elevations up to 5 m above mean sea level (Olmsted et al. 1983). Most of Long Pine Key is covered by fire-adapted pine rockland forests of *Pinus elliottii* Engelm. var. *densa* Little and Dorman. These forests once extended north to the Miami River, covering about 52,000 ha, but agriculture and urban expansion have replaced over 90% of the native plant cover (Snyder et al. 1990). Within the pine forests are numerous small “tree islands” of tropical hardwoods, or hammocks, ranging in area from 1 to 91 ha (although usually less than 10 ha) and having surface elevations between 1 and 4 m above mean sea level (Olmsted et al. 1980).

3.1.1 Tropical Hardwood Hammocks

The hammocks of Long Pine Key consist primarily of tropical hardwood species, dominated by *Lysiloma latisiliquum* (L.) Benth., *Quercus virginiana* Mill. var. *virginiana*, *Sideroxylon salicifolium* (L.) Lam., *Nectandra coriacea* (Sw.) Griseb., *Coccoloba diversifolia* Jacq., *Eugenia axillaris* (Sw.) Willd., *Bursera simaruba* (L.) Sarg., and *Metopium toxiferum* (L.) Krug and Urb. Olmsted et al. (1980) found that the numbers of trees and shrubs in four hammocks ranged from 21 to 25 species, and the number of non-woody taxa (e.g., vines, palms, orchids, bromeliads) varied from 21 to 32.

The distribution of species among Long Pine Key hammocks varies widely, with some species like *Q. virginiana* and *L. latisiliquum* found almost universally, and others, e.g., *Calyptranthes zuzygium* (L.) Sw., *Hypelate trifoliata* Sw., *Gymnanthes lucida* Sw., found in only a few sites. Few epiphytic orchid, bromeliad, and fern species occur in these hammocks except where light gaps have been created by canopy disturbance. Illegal collecting of epiphytes in the past is a possible factor limiting their present abundance (Olmsted et al. 1980).

Prior to Hurricane Andrew (August 1992), these stands formed closed canopies with tree heights of 5-12 m and occasional emergents to 15-17 m tall (Olmsted et al. 1980; 1983). Many of the hammock tree and shrub species also are found in surrounding pinelands where they form a shrub understory. In areas where they have long escaped the destructive effects of fire, the hardwood understories reach tree heights and may out-compete understory pines. Various investigators (Robertson 1953; Olmsted et al. 1983) have suggested that, in the absence of fire, these areas could begin developing hammock qualities in as little as 15 years. In fact, early writers, e.g., Egler (1952), have suggested that the pine rocklands of southern Florida supported extensive tropical hardwood forests “during pre-Indian times.” The consensus among scientists, however, is that wildfires occur frequently enough to confine tree-sized harwoods to hammocks within the pine forests..

Hammock soils are primarily organic, mostly of decomposing leaf litter and woody material, averaging 10-15 cm deep (Olmsted et al. 1980; 1983). Olmsted et al. (1983) found no relationship between elevation and hammock occurrence; they were found on sites with higher, lower, or similar elevations compared to pinelands. Craighead (1984) attributed the occurrence of hammocks on certain sites to differences in the hardness of the underlying limestone due to localized dissolution of the rock and reprecipitation of calcium. Like the surrounding pinelands, hammocks seldom flood because they are elevated as much as 2 m above the level of annual periodic flooding (Olmsted et al. 1980).

3.1.2 Mahogany Hammocks

A second tree island type of the Atlantic Coastal Ridge is the interior mahogany hammock, examples of which are located west of Long Pine Key adjacent to the red mangrove belt. These merit distinction because of differences in species, soils, and location. Proximity to the saline zone and to Shark Slough reduces exposure to fire and, during severe storms, increases exposure to saline water (Craighead 1964). The organic soils here, nearly twice as deep as the soils in hammocks of Long Pine Key, overlay marl instead of limestone (Olmsted et al. 1980). The relative absence of fires in these hammocks has probably contributed to these deeper soils.

West Indian mahogany (*Swietenia mahagoni* (L.) Jacq. dominates the upper canopy of mahogany hammocks in the later successional stages after disturbance by hurricanes (Olmsted et al. 1980). This species is generally absent in other interior hammocks, including Long Pine Key hammocks, where *Lysiloma,* like *Swietenia*, establishes by seed soon after disturbance, particularly after fires (Olmsted et al. 1980). Mahogany hammocks reveal their coastal affinities in the presence of such species as *Acoelorrhaphe wrightii* (Griseb. and H. Wendl.) Becc. (paurotis palm) and *Eugenia foetida* Pers. (Spanish stopper), both absent from the hammocks of Long Pine Key.

3.2 Tree Islands of the Big Cypress Subregion

3.2.1 Tropical Hardwood Hammocks

The tropical hardwood hammocks of Big Cypress are found within or near mixed hardwood swamp forests, cypress prairies and slash pine forests. They are dominated by *Quercus laurifolia* Michx., *Q. nigra* L., *Q. virginiana* or *Lysiloma* (Duever et al. 1986). The oaks, together with *Acer rubrum* L., are temperate species common in the northern Big Cypress region. Apparently responding to low winter temperatures, stand composition shifts from predominantly tropical to temperate northward within the region though understories have strong tropical representation throughout. The hammocks of the southern part of the region resemble tree islands of ENP in composition, including *Ficus aurea* Nutt., *C. diversifolia*, *B. simaruba, M. toxiferum,* and *Lysiloma.* The canopy species, which can attain heights of up to 20 m (Duever et al. 1986), are the first to become established during hammock recovery following disturbance by fire or hurricanes.

Hammock soils in BCNP consist of mixtures of sand and partially decomposed litter, with depths usually under 20 cm (Craighead 1971) although in some areas, hammock soil depths averaged 40 cm with a maximum of 80 cm (Gunderson and Loope 1982b; Gunderson et al. 1982a). Hammock elevations are the highest of any plant community in the Big Cypress region and thus are rarely flooded (Duever et al. 1986). In the Raccoon Point area, these stands occur at elevations up to 45 and 80 cm higher than the surrounding forests and prairies, respectively (Gunderson and Loope 1982b).

Tropical hardwood hammocks are the most diverse plant community of BCNP (Olmsted et al. 1980; Gunderson and Loope 1982a). In one hammock of the Pinecrest area, located in the southeastern part of the preserve**,** *Lysiloma* trees were the largest and tallest, supporting the observation that this species persists in hammocks only as mature individuals (Gunderson and Loope 1982a). On the other hand, *Nectandra* was more widespread and showed a high stem density due to its active regeneration. In hammocks destroyed by fires, typical successional species such as *Lysiloma, Q. virginiana, Sabal*, and *Myrica cerifera* often are found (Gunderson and Loope 1982a).

3.2.2 Oak-*Sabal* Hammocks

Oak-*Sabal* hammocks are small tree islands surrounded by swamp, cypress, or pine forests. Species diversity is generally lower than that of the hardwood hammocks. The dominant canopy species is *Q. laurifolia*, with *Q. virginiana* found on higher, drier sites. The oaks often form nearly closed canopies and can attain large sizes; trees in stands of the Deep Lake Strand area measured up to 18 m tall with diameters up to 65 cm (Gunderson and Loope 1982c).

Sabal palmetto is an important subcanopy species and occurs at varying densities. Other tree species, often occurring as scattered individuals, include *Myrcianthes, Myrsine floridana* A. DC., *Persea borbonia* (L.) Spreng., *F. aurea,* and *Acer.* Additional species include shrubs and a variety of ferns, epiphytic bromeliads and orchids.

Oak-*Sabal* hammocks occur on bedrock outcrops within the same range of elevations as the tropical hardwood hammocks. While some stands are rarely inundated, an oak-*Sabal* site within the Deep Lake Strand area, situated along the western border of the preserve, had a mean hydroperiod of 80 days with an annual range of 44 to 140 days in the 1973-1980 period (Gunderson and Loope 1982c). Oak-*Sabal* hammock soils, consisting of litter overlaying a muck-sand mixture, have depths ranging from 0.1 to 1 m deep.

3.2.3 Freshwater Middens

Freshwater Indian midden hammocks exist on mounds of shell and other debris deposited by humans. Some middens occur at sites that have been inhabited as early as the time of pre-Columbian Indians. The species composition of these anthropogenic sites resembles tropical hardwood hammocks, but middens also support species that were introduced and cultivated by native Americans and subsequently by white settlers.

Freshwater middens of the Turner River area of ENP and BCNP are composed of black soil on oyster shell elevated about 2 m above sea level (Borel 1997). The most characteristic species include *Bursera, Dalbergia brownii* (Jacq.) Shinz, *Erythrina herbacea* L. and *Annona glabra* L.. Other species found on these mounds, many of practical value, are *Morus rubra* L., *Yucca aloifolia* L., and *Cephalanthus occidentalis* L.

Middens found in the more interior areas of Big Cypress are characterized by temperate oak tree canopies and understories of tropical species (Snyder et al. 1990).

3.3 Tree Islands of Shark Slough and Adjacent Prairies

The Shark Slough drainage forms the southern portion of the greater Everglades system which, prior to development, began just below Lake Okeechobee and extended to the Gulf of Mexico. Shark Slough is a shallow, natural basin oriented northeast to southwest, with widths varying from 14 to 27 km. The Slough's hydraulic gradient (5-7.5 cm per 1.6 km) produces small velocity flow vectors characteristic of sheet flow (Olmsted and Armentano 1997). Shark Slough originally featured a "ridge and slough" topography with tall sawgrass and tree islands on the ridges and aquatic communities in the deeper water of the sloughs. Development, especially drainage and canal construction, has degraded the pattern and interrupted the directional flow of surface water that was channelled through the sloughs, leading to the Slough's depiction as a slow-moving, broad river.

The slough comprises a mosaic of marsh communities, dominated by *Cladium* and *Eleocharis cellulosa* Torr., tree islands, and ponds. Organic muck and marl are the major soil types of the slough, the former found in the main channel and the latter on the rockier, higher flanks of the slough. In some places, mixtures of these soils occur near the surface, suggesting that hydrological conditions have varied sufficiently to allow both soil types to form at different times (Olmsted and Armentano 1997).

The Shark Slough tree islands have developed on slightly elevated oolitic limestone outcrops and in adjacent, downstream bedrock depressions within the slough marshes. Four tree-dominated plant community types constitute tree island vegetation: tropical hardwood hammock, bayhead, bayhead swamp forest, and willow head. These forest types differ markedly in their vegetative structure and soils. Hammocks, bayheads, and willow heads have been described and discussed by many, e.g., Davis 1943; Egler 1952; Loveless 1959; Craighead 1971, and the bayhead swamp forest community type by Olmsted and Loope (1984) and Olmsted and Armentano (1997).

3.3.1 Tropical Hardwood Hammocks

Tropical hardwood hammocks form in the upstream portions of the largest tree islands in Shark Slough. These hammocks, seldom more than 500 m^2 in area, are found on limestone outcrops that rise up to 1 m above the surrounding marshes and are capped by soil up to 40 cm deep (Olmsted and Armentano 1997). Because the hammocks are the only dry places in the slough during the rainy (summer) season, they were inhabited by native Americans and, later, white settlers, prior to ENP's establishment in 1947. Human habitation of hammocks of Shark Slough is evidenced by the persistence of introduced species such as *Citrus sinensis* (L.) Osbeck (sweet orange), *C. aurantium* L. (sour orange), *Persea americana* Mill. (avocado), and *Psidium guajava* L (guava).

The major tree species of Shark Slough hammocks are *Celtis laevigata* Willd., *E. axillaris, F. aurea*, *Bursera*, and *Sideroxylon foetidissimum* Jacq. Large trees of the exotic, invasive *Schinus terebinthifolius* Raddi (Brazilian pepper) are present in some hammocks, while trees of the equally invasive *Melaleuca quinquenervia* (Cav.) S.T. Blake commonly fringe hammocks in northeastern Shark Slough.

Hammock understories are typically sparse and reproduction of overstory trees is low, at least partially due to herbivory by deer (Olmsted and Armentano 1997). Utilization of hammocks by deer and feral hogs during periods of prolonged flooding which limits animal movements, can result in severe damage to understory plants through browsing and trampling (Jones et al. 1997).

Between the Atlantic Coastal Ridge and Shark Slough is a region of low, highly dissected outcrops of Miami Limestone known as the Rocky Glades. The region is largely a seasonally flooded marl prairie, dominated by *Muhlenbergia filipes* M.A. Curtis, *Cladium*, and *Schizachyrium rhizomatum* (Swallen) Gould. The tree islands here range in size from 0.1 to 3 ha (Loope and Urban 1980) and number in the thousands. Tropical hardwood hammocks occur on raised limestone outcrops, and like the hammocks of Shark Slough, the dominant canopy species are *Bursera, Sideroxylon salicifolium* (L.) Lam.*, F. aurea, C. diversifolia,* and *Metopium.*

Rocky Glades hammocks, in early stages of recovery from fire, often are dominated by temperate species found on bayhead tree islands, including *Myrica, P. borbonia,* and *Ilex cassine* L. Bracken fern (*Pteridium aquilinum* (L.) Kuhn var. *caudatum* (L.) Sadeb.) and other herbaceous species often dominate hammock sites where a severe fire has killed the tropical hardwoods

Generally, species richness in these hammocks is low when compared to the larger hammocks of Long Pine Key. Conspicuously lacking in these hammocks are *Lysiloma* and *Q. virginiana*, two important species of Long Pine Key. An exception is Grossman Hammock, a large tree island situated about 3 km southeast of Shark Slough in the northern Rocky Glades. In this and adjacent hammocks, species diversity is high and resembles those of Long Pine Key. The exotic *Schinus* is found widely in Rocky Glades tree islands, dominating some, especially following disturbance such as fire. *Casuarina glauca* Spreng*.,* another widespread exotic, may form its own "tree islands" in the surrounding prairies, building up the elevation from the accumulation of leaf and stem litter.

Cross-sectional profiles of tropical hardwood hammocks (and adjacent communities) on three tree islands of Shark Slough are depicted in Figure 4. The profiles are based on topographic surveys along belt transects perpendicular to the long axis of each tree island. These tree islands were chosen because of their varying locations (and, hence, hydrologic regimes) within the slough, namely north-central (Gumbo Limbo), eastern (Black), and southern (West Twin).

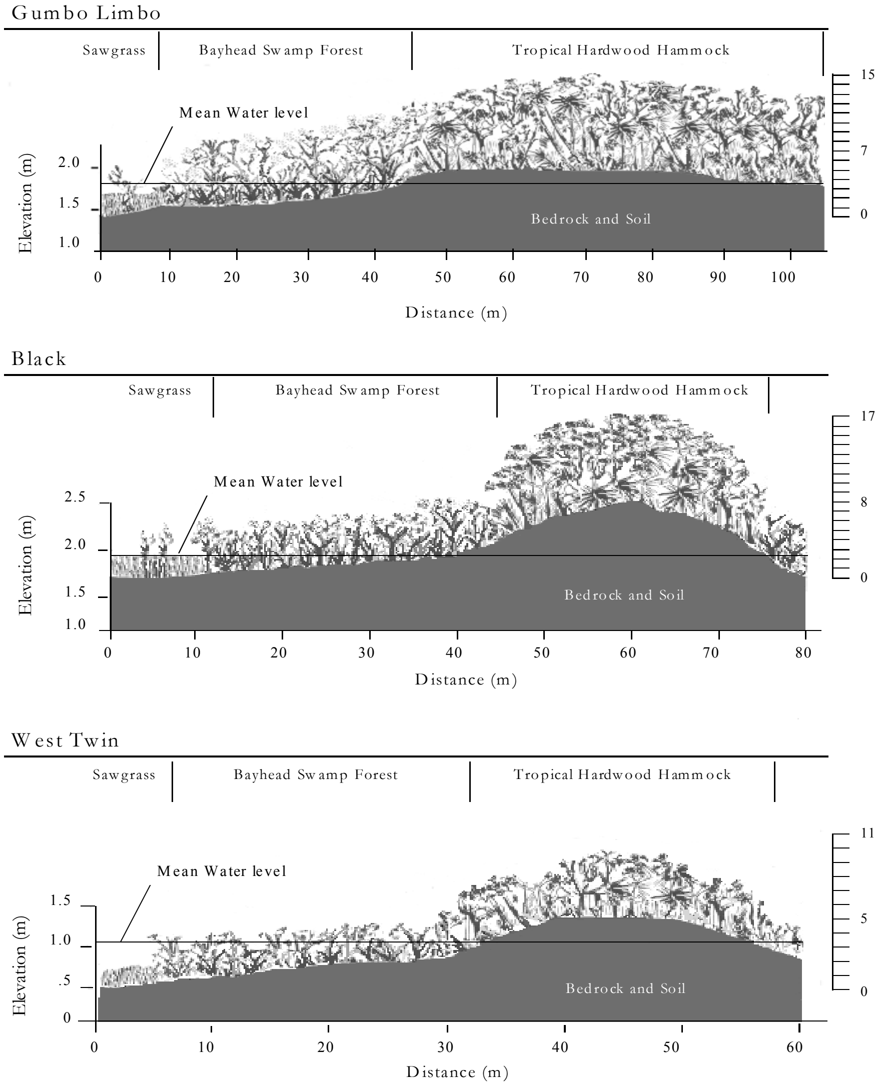

Figure 4. Profiles of three Shark Slough tree islands, derived from topographic surveys along belt transects. Mean water levels are calculated from over 25 years of data at adjacent hydrological monitoring stations. The elevation scales have been exaggerated. The vertical scale to the right of each profile is in 1 m increments for community height comparisons.

The canopies of the tropical hardwood forest portions of these sites average 9 m tall (West Twin averages 4.5 m) and are dominated by *Celtis, Bursera, Sideroxylon foetidissimum* Jacq., and *F. aurea.* Additional species are found in the subordinate layers such as *E. axillaris, Rivina humilis* L., *Myrica,* and *Myrsine.*

Considerable variation exists in ground elevation between the hammock portions of these tree islands, reflecting topographic differences in the slough. Gumbo Limbo Hammock, situated in the middle of the slough, has a mean elevation of 2.2 m, while Black Hammock, located at the edge of the slough and adjacent to the Rocky Glades to the east, has a mean elevation of 2.4 m. West Twin Hammock, located at the southern end of the slough, shows the lowest mean elevation of the three sites, approximately 1 m lower than Black hammock. Differences between the highest and lowest points within a hammock range from 25 cm (Gumbo Limbo) to 50 cm (West Twin). The relationship of elevation and hydrological conditions at these sites is discussed in a later section.

3.3.2 Bayhead Swamp Forests

These communities develop in depressions in limestone bedrock as part of tree islands which typically have a tropical hardwood hammock at their northern, upstream end; the "tails" of Shark Slough tree islands represent the bayhead swamp forest portion, often with tall *Cladium* along the periphery. The area of bayhead swamps within a tree island typically far exceeds that of bayheads and hammocks. In contrast to bayheads, the canopies of bayhead swamp forests are open. The difference in height between the hammock trees and the shorter trees of the adjacent swamp forest is quite obvious and can be as much as 3-5 m. At three tree island sites in Shark Slough (Figure 4), the tallest bayhead swamp forest trees (*Annona, Salix caroliniana* Michx., *Magnolia virginiana* L., and *Chrysobalanus*) ranged from 3.5 to 7 m high. Tree heights generally decrease toward downstream (Olmsted and Armentano 1997).

Because this community develops in bedrock depressions, hydroperiods are up to 10 months long, four to eight months longer than reported for bayheads (Olmsted and Armentano 1997). Mean elevations for bayhead swamp forests are 50-60 cm lower than the mean hammock elevations and have narrow ranges (20-30 cm) between their highest and lowest points. Soils are composed of organic muck with depths often exceeding 1 m (Olmsted and Armentano 1997). While similar in composition to bayheads, patches of *Cladium, Typha* spp., and aquatic plants such as *Sagittaria lancifolia* L., *Pontederia cordata* L., and *Bacopa caroliniana* (Walter) B.L. Rob. often occur, and *Cephalanthus* is frequent.

3.3.3 Bayheads

Bayheads are the most abundant tree island community type in Shark Slough. They form on limestone bedrock highs or on accumulated muck deposits and experience shorter hydroperiods than bayhead swamp forests, reportedly from two to six months (Olmsted and Loope 1984). Bayheads are typically circular in shape and often surrounded by tall sawgrass. Their soils are typically muck ranging from 15 to 100 cm deep in the middle of Shark Slough and 5 to 40 cm deep where bayheads are situated on higher bedrock along the slough's western and eastern flanks (Olmsted and Armentano 1997). Cohen and Spackman (1977) describe a *Myrica-Persea-Salix* peat in bayheads of Shark Slough. The presence of considerable charcoal, a high ratio of fine to coarse fragments, and the presence of fecal pellets and fungal material attest to the fact that some drying and aeration occur.

A mature bayhead is a closed canopy forest (heights reach an average of 8-10 m) consisting mainly of seven species: *P. borbonia*, *Magnolia*, *Ilex*, *Salix*, *Myrica*, *Chrysobalanus,* and *Annona* (Olmsted and Armentano 1997); only the last two species are tropical. The understory is sparse and comprises mostly the ferns *Blechnum serrulatum* Rich. and A*crostichum. danaeifolium*. Trees of *Taxodium* are often found on the edges of bayheads in southeastern Shark Slough. Similarly, bayheads are commonly fringed by scrub *Rhizophora* near the mangrove belt.

3.3.4 Bayhead-Hammock Forests

In the Rocky Glades, tropical hardwood species intermix with bayhead species. This type, referred to as a bayhead-hammock forest by Hofstetter and Hilsenbeck (1980), is common thoughout the area and reflects shorter hydroperiods than that experienced by typical bayheads. A bayhead-hammock forest typically includes *Chrysobalanus, P. borbonia*, *Myrsine, C. diversifolia, E. axillaris, Metopium*, and *S. salicifolium*, the latter four species being common in tropical hardwood hammocks; *Schinus* commonly invades disturbed sites. Structurally, these mixed bayheads resemble hammocks, with canopies averaging more than 10 m high. Where they occur on limestone outcrops, soils are thin, sometimes almost lacking. One reason for this may be that fires have consumed accumulated organic matter. Because of their small areas, and the increased frequency and intensity of fires in the Rocky Glades in the past 60-70 years, these stands have been vulnerable to severe damage or even to complete loss of woody vegetation. In some cases only the raised limestone outcrop remains (Hofstetter and Hilsenbeck 1980).

3.3.5 Willow Heads

Nearly monotypic stands of *Salix* are called willow heads; other marsh plants such as *Thalia geniculata* L., *Phragmites australis* (Cav.) Steud., and *Cephalanthus* commonly are associated with them. Willow heads form in the slough in areas of slightly lower elevation than the surrounding marshes; they are typically found on muck soils 1-2 m deep (Olmsted et al. 1983), mostly within tall sawgrass strands (Olmsted and Armentano 1997). Willow heads include ponds that may have originally been depressions in the soil later deepened by alligators (Craighead 1968). Willows often recruit by seed where fires consume surface muck, lowering the ground surface elevation. Willows are short-lived, intolerant of shade, and, therefore, successional or maintained by fire (Wade et al. 1980; Craighead 1971).

3.4 Taylor Slough and the Southeast Saline Everglades

Taylor Slough, the second largest natural drainage in ENP, encompasses an area of about 158 km^2 and stretches 40 km from its headwaters in the southern Rocky Glades to Florida Bay. Like Shark Slough, Taylor Slough occupies a depression in the oolitic limestone bedrock filled with peat and marl of variable depth. Taylor Slough lacks the variable topography that characterizes Shark Slough, and few outcrops occur. Tree islands typically do not develop the elongated tails as in Shark Slough and most are broadly rounded in shape.

Adjacent to Taylor Slough lies the “Southeast Saline Everglades” (SESE), a name coined by Egler (1952) to describe the broad coastal zone situated south of the Atlantic Coastal Ridge and east of Shark Slough. It is inundated periodically by storm tides associated with tropical storms. Hydrologic conditions reflect a dynamic balance between local rainfall, upstream water sources, and tidal influx from Florida Bay or Biscayne Bay. Craighead (1971) considered the wetlands interior to the Buttonwood Embankment, a modestly elevated strip of land bordering on the northern embayments of Florida Bay, to be fundamentally freshwater in character except in the wake of major storm surge events. After such storms, salts may be retained for several years in the heavy marl soils of the area.

3.4.1 Tropical Hardwood Hammocks

Well-defined hardwood hammocks developing on limestone outcrops occur to a limited extent on the east side of the central slough. In the Taylor Slough portion of the region, the hammocks are generally small (5-10 ha), with a layer of organic soil 5-15 cm deep, and are rarely inundated (Olmsted et al. 1980). Like the hammocks of Long Pine Key, *Q. virginiana*, *Lysiloma*, *Bursera*, *Nectandra*, *C. diversifolia*, and *E. axillaris* are common; epiphytic bromeliads and orchids are frequent. More description of these hammocks in the SESE are given below.

3.4.2 Bayheads

This is the commonest tree island type in the sub-region. The bayheads typically are better developed with respect to canopy closure, tree size, and species richness than those in Shark Slough (Schomer and Drew 1982). They are characterized by a spongy peat substrate that is elevated typically 10-60 cm higher than the adjacent marshes. Both the elevation and moisture-holding capacity of the soils buffer these stands from hydrologic fluctuations in the surrounding marsh and the associated temporal variation in salinity and water levels. Hydroperiods of these bayheads reportedly range from one to four months.

Hofstetter and Hilsenbeck (1980) found the principal species of a bayhead in central Taylor Slough to be *Chrysobalanus, F. aurea*, and *Taxodium*, the latter species often found along the bayhead fringe. Bayheads of the SESE are described below.

3.4.3 Bayhead-Hammock Forests

This tree island type occurs within the southern reaches of the subregion, in a band several kilometers wide, extending west to Mahogany Hammock, and forming a transition between the freshwater marshes to the north and the coastal communities to the south. Like the bayhead-hammock stands found in the Rocky Glades (Shark Slough subregion), these forests contain a mixture of bayhead and tropical hardwood species, but occur on marl in mid to long hydroperiod marshes. This tree island type may indicate a stage in succession towards a more mesic hammock forest.

The occurrence of *Swietenia*, *Metopium*, *Eugenia foetida* Pers., *Hippomane mancinella* L., *Sideroxylon celastrinum* (Kunth) T.D. Penn., *Conocarpus*, *Rhizophora*, and *Acoelorrhaphe wrightii*, among others, in the bayhead-hammock forest tree island type reflects marine affinities and further distinguishes them from those found in the Rocky Glades.

Ross et al. (1996) examined the species composition of 54 SESE tree islands by ranking tree species by canopy cover. The TWINSPAN classification procedure was applied to the set of relativized species abundances. The classification program identified four major tree island types in the SESE arrayed in the following roughly concentric, north to south, bands: bayheads, bayhead/hammock forests, tropical hardwood hammocks and coastal tropical hardwood hammocks (Table 2). The first three types grouped with the Taylor Slough tree islands in the cluster analysis and the coastal hammocks grouped with the Florida Bay sites discussed in the next section. Considerable overlap occurs between types partly due to the inclusion of border and interior trees. Bayhead and bayhead-hammocks share several freshwater swamp species, e.g., *Persea* and *Myrica*, with *Salix, Taxodium*, and *Annona* relatively abundant in the former. Bayhead-hammocks typically include species associated with mesic conditions*, e.g., Metopium* and *E. axillaris*, and may include halophytes such *as Rhizophora* or *Conocarpus* along their flanks. In tropical hardwood hammocks, nearly any SESE species may occur, especially mesic species, e.g., *C. diversifolia*, *Calyptranthes pallens* and *E. axillaris* and *E. foetida*. Finally, the coastal variant of the tropical hardwood hammock includes a more diverse mixture of woody halophytes than the other types. Besides *Conocarpus* and the three mangrove species, common associates are *Lycium carolinianum* Walter, *S. celastrinum*, and *Jacquinia keyensis* Mez. Other species, not restricted to coastal forests, are also well-represented, including *C. diversifolia*, *E. axillaris*, *Metopium, Pisonia aculeata*, *Swietenia*, and *Z. fagara*. *Swietenia* was more abundant in the past, but fires, logging, and hurricanes have reduced their numbers (Craighead 1971). These hammocks are flooded only during major storms.

The banding of tree islands of similar composition parallel to the coast is striking and the surrounding marsh communities are similarly arrayed. The zonation may be due to several factors that vary with distance from the coast. The coast-to-interior shift from salt-tolerant tropical species in the two tropical hammock types to freshwater temperate species in the two bayhead types suggests that periodic storm surges and freezing temperatures may be involved. However a number of other factors may be important, including precipitation amounts, surface water depth and fire frequency. Little is known about environmental variation in these remote wetlands.

Table 2. Mean relative abundance of common tree species (i.e., present in at least three sites) in a study of 54 tree islands in Taylor Slough and the Southeast Saline Everglades (SESE) by Ross et al. (1996).

Species	Tree island type			
	Bayhead	Bayhead-hammock forest	Tropical hardwood hammock	Tropical hardwood hammock (coastal)
Taxodium distichum	15.29 (7)			
Salix caroliniana	8.51 (4)	1.32 (2)	0.16 (1)	
Magnolia virginiana	4.91 (3)	1.87 (4)		
Ilex cassine	8.90 (6)	6.07 (12)	0.20 (2)	
Persea borbonia	11.81 (6)	7.37 (6)	0.63 (6)	
Annona glabra	7.00 (6)	2.49 (7)	0.97 (7)	
Chrysobalanus icaco	12.36 (6)	12.60 (16)	2.38 (10)	
Ficus spp.	2.74 (3)	2.17 (5)	1.49 (7)	
Sabal palmetto		1.51 (3)		
Myrsine floridana	6.29 (6)	6.93 (15)	4.22 (16)	
Myrica cerifera	15.16 (7)	13.06 (18)	7.72 (20)	2.27 (2)
Metopium toxiferum	3.12 (4)	10.09 (15)	10.38 (19)	0.98 (1)
Schinus terebinthifolius	0.41 (1)	2.32 (10)	4.88 (16)	
Calyptranthes pallens		1.22 (6)	5.18 (13)	
Eugenia axillaris		1.46 (3)	2.30 (10)	
Casuarina equisetifolia		0.84 (2)	2.39 (4)	
Coccoloba diversifolia		0.54 (2)	3.75 (11)	
Conocarpus erectus	2.02 (3)	13.99 (17)	15.17 (20)	19.48 (8)
Swietenia mahagoni		0.40 (1)	2.00 (15)	
Rhizophora mangle	1.48 (2)	11.16 (18)	13.45 (20)	19.48 (8)
Eugenia foetida		0.79 (1)	5.29 (15)	
Coccoloba uvifera		0.41 (3)	2.84 (12)	1.53 (2)
Randia aculeata		0.49 (3)	4.83 (15)	5.54 (4)
Pithecellobium keyense		0.08 (1)	0.26 (2)	0.98 (1)
Laguncularia racemosa		0.41 (3)	5.73 (15)	11.86 (7)
Sideroxylon celastrinum		0.39 (3)	3.23 (11)	12.96 (5)
Avicennia germinans			0.21 (2)	4.68 (3)
Lycium carolinianum			0.34 (1)	11.09 (6)
Jacquinia keyensis				9.16 (5)

3.5 Tree Islands of the Lower Gulf Coast

The Lower Gulf Coast subregion encompasses the west coast of ENP along the Gulf of Mexico, south to Cape Sable. This region differs considerably from the coastal area of Florida Bay in topography, geomorphology, and vegetation (Olmsted et al. 1981). Stands of tropical hardwoods occur on naturally-occurring coastal dunes and storm ridges that parallel the coast as well as on artificially-elevated Indian middens that have a distinctly human-influenced composition.

3.5.1 Tropical Hardwood Hammocks

Inland of the beaches and coastal prairies that line portions of the Gulf Coast in ENP are hardwood hammocks on coastal dunes and storm ridges that parallel the coastline. Like the mainland hammocks fringing northern Florida Bay, these hammocks are found on elevated berms of marl, shell, and sand, at 1-1.5 m above mean sea level. Extensive mangrove forests form directly behind the hammock ridges. Degradation of the coastline is more severe here than along the shores of Florida Bay where wave action is less intense. In some areas of the Gulf Coast, hammock ridges front the ocean, as they do in Florida Bay.

3.5.2 Strand Hardwood Hammocks

The best examples of Gulf Coast strand hammocks are found on Cape Sable and Key McLaughlin on the inland side of Highland Beach, 25 km north of Cape Sable, an almost continuous strip of hardwoods about 16 km long and up to 100 m wide. Characteristic species include *Bursera, Piscidia, Coccoloba uvifera* (L.) L.*, Z. fagara, E. foetida, S. foetidissimum, Pithecellobium unguis-cati* (L.) Benth.*,* and *Sabal.* Succulent plants, such as the cacti *Acanthocereus tetragonus* (L.) Hummelinck and *Opuntia stricta* (Haw.) Haw.*, Yucca aloifolia,* and the exotic *Agave sisalana* Perrine are common; the exotics *Casuarina equisetifolia* L. and *Thespesia populnea* (L.) Correa are frequent. Fires and hurricanes have removed the rich, loamy soils, up to 25 cm thick or more, that developed within these forests. *Swietenia* and other large tropical hardwoods, once abundant on Cape Sable, have declined due to logging that began over 200 years ago and continued until establishment of the park (Craighead 1971).

Other strand hardwood stands are found on some of the sand keys that occur in the Ten Thousand Islands area. These forests are 6-9 m tall, resembling the mainland strand hammocks in species composition (Craig et al. 1971). The sandy soils are mainly siliceous (yet alkaline) rather than calcareous as found further south such as on Cape Sable. Pavilion Key, the largest of these offshore sand keys, is thought to be the northernmost currently known site for *Thrinax radiata* Schult. and Schult. f. (thatch palm). Substrate and/or microclimatic conditions may be responsible for the absence of *Swietenia* from the entire Ten Thousand Islands area.

3.5.3 Indian Midden Hammocks

These anthropogenic sites occur throughout the Lower Gulf Coast subregion being extensive in the Ten Thousand Islands area where they cover up to 40 ha in area and reach elevations of 12 m. They are distinguished by the presence of many plants introduced by early inhabitants, but also include most of the strand and sand key hammocks species. The rich shell and organic soil mixture of these hammocks creates a well-drained substrate that was farmed by white settlers in the late 19th century.

Dominant species, mainly tropical, include *Bursera, F. aurea, S. foetidissimum, Piscidia, Sabal, Exothea paniculata,* and *Krugiodendron ferreum* (Vahl) Urb. The rare royal palm, *Roystonea regia* (Kunth) O.F. Cook, is sometimes also found, probably introduced by early Indians (Small 1931). Coastal middens have fewer temperate species than the freshwater Indian midden hammocks of the Big Cypress region.

A 1997 inventory of plants on Johnson Mound, an Indian midden hammock located on Key McLaughlin, showed that mangroves increased since a 1957 survey, suggesting growing marine influence. Species present only in the recent inventory included halophytic species such as *Avicennia germinans* (L.) L., *Laguncularia racemosa, Batis maritima* L., and *Lycium*.

On the coastal Indian middens of the Turner River area, Borel (1997) showed that *Eugenia axillaris, E. foetida, P. nervosa, Ardisia, Bursera, C. diversifolia, Randia*, and *Chiococca alba* (L.) Hitchc, all of ethnobotanical use, were the most frequent species. Other useful plants, including *Piscidia, Citrus* spp., *Psidium guajava, Sapindus saponaria* L., *Carica papaya* L. and *Agave decipiens* Baker, attest to the importance of humans in the establishment of this tree island type.

3.6 Tree Islands of the Florida Bay Region

Florida Bay is a 1500 km^2 embayment bounded on the north by the Florida mainland, on the south and east by the Florida Keys, and on the southwest by slightly submerged mud banks that separate the Bay from the Gulf of Mexico. Although the Bay receives fresh water from the Everglades, its water budget is dominated by the balance of precipitation and evaporation and the influx of saline Gulf water. Based on species composition and abundance and soils, four tree island types can be delineated: tropical hardwood, buttonwood, thatch palm and Florida Bay keys.

These forests have been damaged by hurricanes in 1935, 1960, and 1965, but were unaffected by Hurricane Andrew in 1992. In addition, fires, largely associated with the charcoal industry of the early 20th century (Tebeau 1968), logging (Craighead 1971), and exotic plant introductions (Olmsted et al. 1981) are known human influences. A number of exotic species threaten the coastal and keys hammocks; these include *Schinus, Casuarina equisetifolia*, *Thespesia*, *Hibiscus tiliaceus* L., and *Colubrina asiatica* (L.) Brongn., all species that can form monotypic stands if left uncontrolled. The latter species, a scandent shrub native to Southeast Asia, is of particular concern (Jones 1997). Along Florida Bay, its areal extent doubled to 484 ha during the past decade.

3.6.1 Tropical Hardwood Hammocks

The tropical hardwood forests found along the northern shores of Florida Bay (from Flamingo west to Long Sound, a straight distance of about 45 km) are established on ridges up to 1 m high, which comprise old shorelines or marine sediments (marl, sand, coral) deposited after storms (Wanless et al., 1994). They are extensive and contain a large number of coastal species not typically found in interior forests, including *S. celastrinum, P. piscipula, Pithecellobium keyense* Britton and Rose, and cacti (*Opuntia stricta*, *Acanthocereus tetragonus*, *Harrisia simpsonii* Britton and Rose).

Coot Bay Hammock, a large hardwood hammock located between Florida Bay and Whitewater Bay, is a good example of a tree island in this region because of its strong floristic affinities with other Florida Bay tree islands. Surrounding the hammock are buttonwood, halophytic prairie, and mangrove communities (Figure 5).

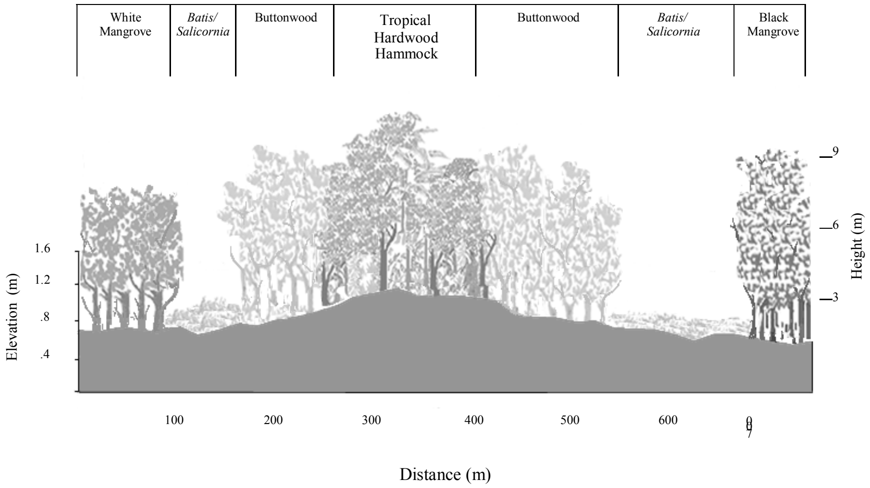

Figure 5. Profile of Coot Bay Hammock and adjacent communities, derived from a topographic survey along a transect baseline. The elevational scale is exaggerated. Heights are averaged for each community.

A thin organic soil layer overlays thick deposits of marine marl in the hammock. The stand was sampled in both 1980 (Olmsted and Loope 1980) and 1998 from the same 300 m^2 sample area. Total basal area increased from 47 to 58 m^2/ha over this period. Basal areas and stem densities of the 10 principal woody species in 1998, are given in Figure 6. Most stems are 4-8 m in height, with the tallest individuals at 9 m. The relatively high basal area of *S. foetidissimum, E. foetida,* and *C. diversifolia* arises from the large number of smaller stems, while *Piscidia piscipula* (L.) Sarg., *Swietenia*, *F. aurea*, and *Sabal*, occur as relatively few, large trees.

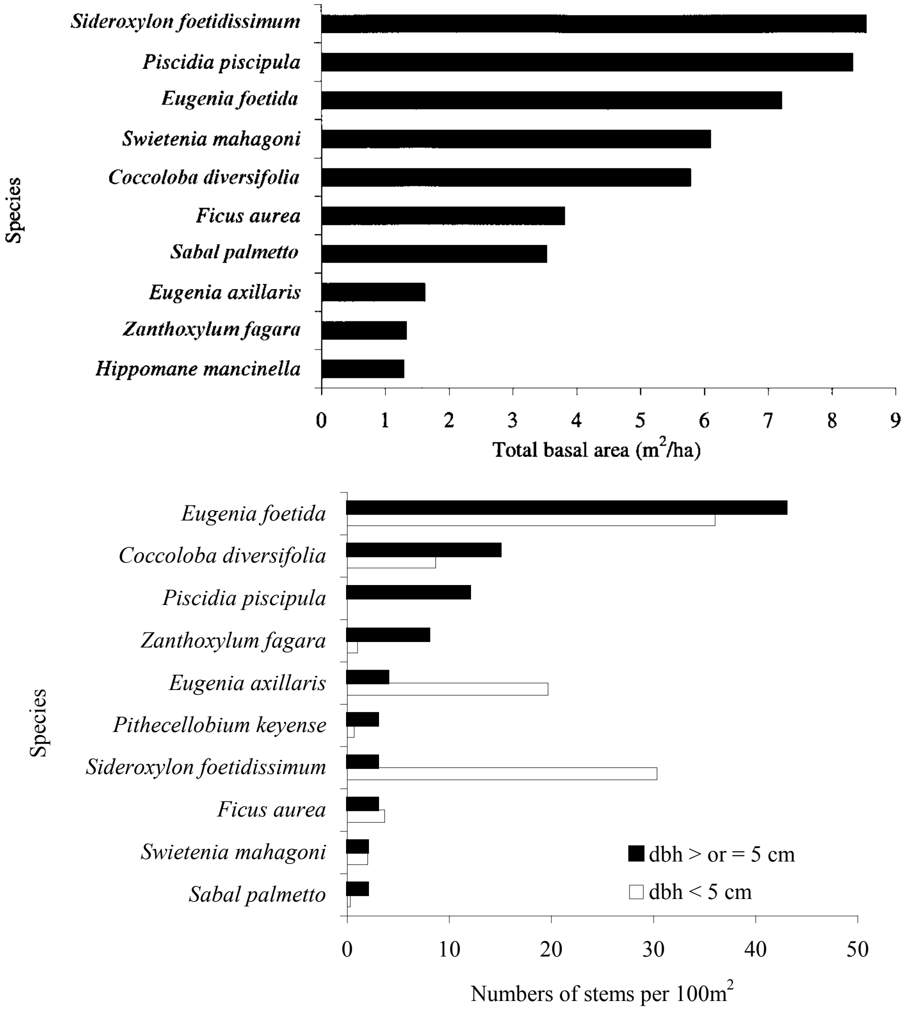

Figure 6. The ten highest (a) total basal areas for stems ≥ 2.5 cm (diameter at breast height--dbh), and (b) stem densities occurring in a 300 m^2 plot located in Coot Bay Hammock, as sampled in 1998.

In both years, *E. foetida, C. diversifolia, Piscidia*, and *S. foetidissimum* were highest in relative importance value (the sum of relative frequency, dominance, and density) among woody species with stem diameters of 5 cm or more (Figure 7).

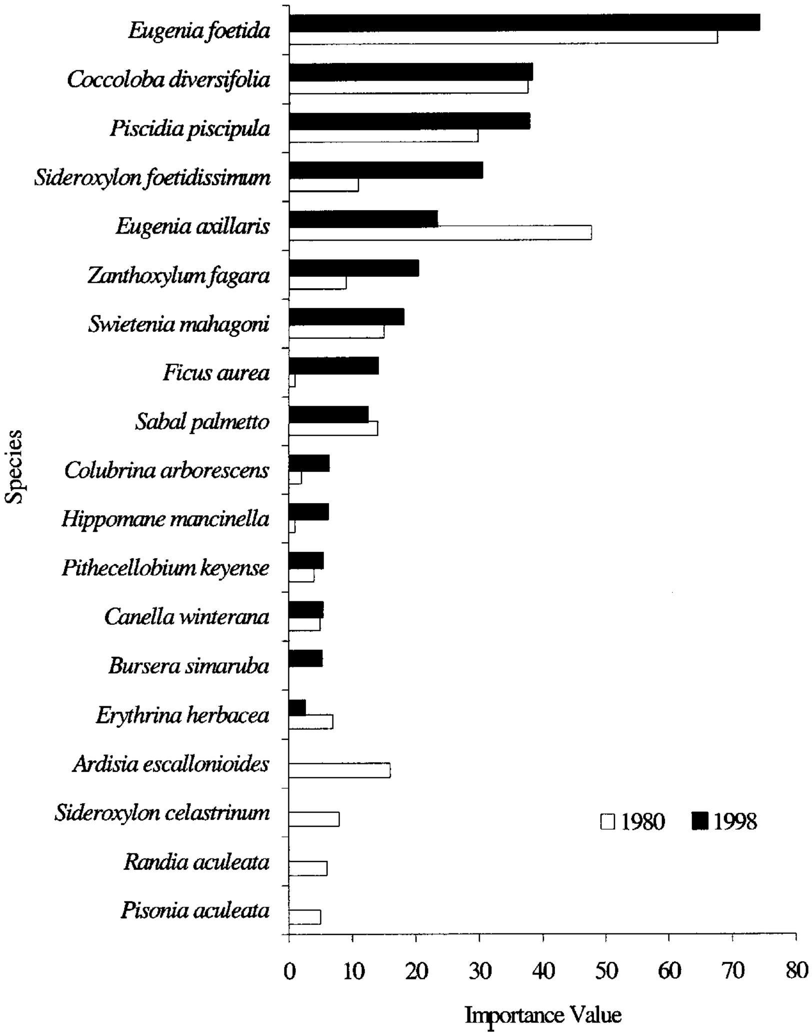

Figure 7. Importance values of all woody species (stems ≥ 5 cm dbh) occurring in a 300 m^2 plot located in Coot Bay Hammock: 1980 and 1998 compared.

Most species showed little change between 1980 and 1998; notable exceptions are decreases in *E. axillaris* and *Erythrina herbacea*, and increases in *F. aurea, S. foetidissimum, Z. fagara, Colubrina arborescens* (Mill.) Sarg., and *H. mancinella*. One new tree species was gained in 1998 (*Bursera*) and four were lost (*Ardisia, S. celastrinum, Randia,* and *Pisonia* *aculeata* L.); these latter four species were found, however, as smaller-stemmed individuals in 1998. The decline of *E. axillaris* and *Ardisia* is unexpected given that these species are regarded as shade-tolerant members of more mature hammocks (Olmsted and Loope 1984).

Comparison of the stand over the past two decades provides evidence that the stand is still maturing although the small changes in overall species composition and relative importance of the dominants in the canopy layer suggests an approach to structural stability. The absence of catastrophic hurricanes or fires over the period probably explains the relatively stable state and the observed scarcity of downed wood on the forest floor.

3.6.2 Buttonwood Hammocks

Buttonwood hammocks differ from the tropical hardwood type, since the former are dominated by *Conocarpus* and have lower species diversity. These hammocks occur at slightly lower elevations than the hardwood hammocks and are subject to more tidal flooding. In addition to *Conocarpus, Z. fagara*, *E. foetida*, *C. arborescens*, and *Piscidia* occur, among other species. The understory is composed of coastal shrubs and cacti.

Various other buttonwood forest types (e.g., "strands" and "scrub") occur in this region and often intergrade with buttonwood hammock. Halophytic plants (*Salicornia virginica* L., *Suaeda linearis* (Elliott) Moq., and *Batis maritima*) dominate the understory of these communities. *Hippomane* is often found in association with buttonwood, forming a narrow band of forest between buttonwood forest and tropical hardwood hammock. In several places in the coastal zone, former *Conocarpus* forests have yielded to halophytic prairie or mangrove, probably as a result of hurricane induced mortality of *Conocarpus* and subsequent alteration of the substrate. Much of the conversion occurred following the great 1935 hurricane (Craighead 1971; Olmsted and Loope 1980).

3.6.3 Thatch Palm Hammocks

Thatch palm hammocks derive their name from *Thrinax radiata.* These hammocks occur closest to Florida Bay and, hence, their soils consist of calcareous sand. Although similar in composition to tropical hardwood hammocks, thatch palm hammocks contain species that are sparsely represented in the former type, such as *Thrinax, Erithalis fruticosa* L., *Genipa clusiifolia* (Jacq.) Griseb., *Jacquinia keyensis*, and *Manilkara bahamensis* (Baker) H.J. Lam and B. Meeuse (Olmsted et al. 1981). Their canopies generally do not exceed 8 m in height. *Thrinax* is often the tallest species in the stand.

Trees of *Swietenia, Piscidia*, *Thrinax*, and *E. foetida* dominated the canopy of a thatch palm hammock on the north shore of Florida Bay, 30 km east of Flamingo in 1998. *Swietenia, Piscidia,* and *Conocarpus* had stem diameters greater than 16 cm, the largest (25 cm) recorded belonging to *Conocarpus*. Total basal area and stem density for all (16) woody species found in the study plot are shown in Figure 8. To our knowledge, this is the only such data that exists for this type of hammock. *Eugenia foetida* dominated the subcanopy layer as seen by its large total basal area (nearly five times that of the next highest species, *Conocarpus*) and high number of small stems. *Conocarpus, Piscidia, Thrinax,* and *Pithecellobium keyense* had the highest densities of stems with 5 cm or greater diamter t breast height (dbh).

3.6.4 Florida Bay Keys Hammocks

The 237 islands ("keys") that dot the bay constitute less than 2% of its total area (Enos 1989). The islands, built up from the floor of the bay by deposits of marine marl, mangrove peat, and sand, are up to 1 m higher than mean sea level. While most of the vegetation on these islands is comprised of algal flats, halophytic marshes and mangrove forests, the higher islands (constituting 9 and 20% of the total number and area of islands, respectively) found in the western and northern portions of the bay support plant communities dominated by mixtures of tropical hardwood species and *Conocarpus.* In addition, stands of these same species occur on a few islands that have elevated beach ridges, formed from the deposition of calcareous material and flotsam.

The elevated, well-drained areas supporting the growth of hammock vegetation flood only during high water events caused by storms. Increased elevation, favoring the formation of a freshwater lens and the concomitant reduction in pore-water salinity are necessary for hammock establishment and persistence. Enos (1989) has proposed that hardwoods represent the culmination of a sequential development of habitats (mangrove -> algal and halophytic marsh -> grass and shrub prairie -> hardwood hammock) through lateral and vertical sediment accumulation and overall island growth. However, as in the case of the other coastal tree island types discussed, hammock species may have, in at least some cases, become established on sediments accumulated in major storms.

The hammock portions of the "high keys" of Florida Bay can be quite extensive. Species composition is similar to the hammocks of the Florida Bay coast, with their mixtures of palms (*Sabal*, *Thrinax*), *Conocarpus,* and

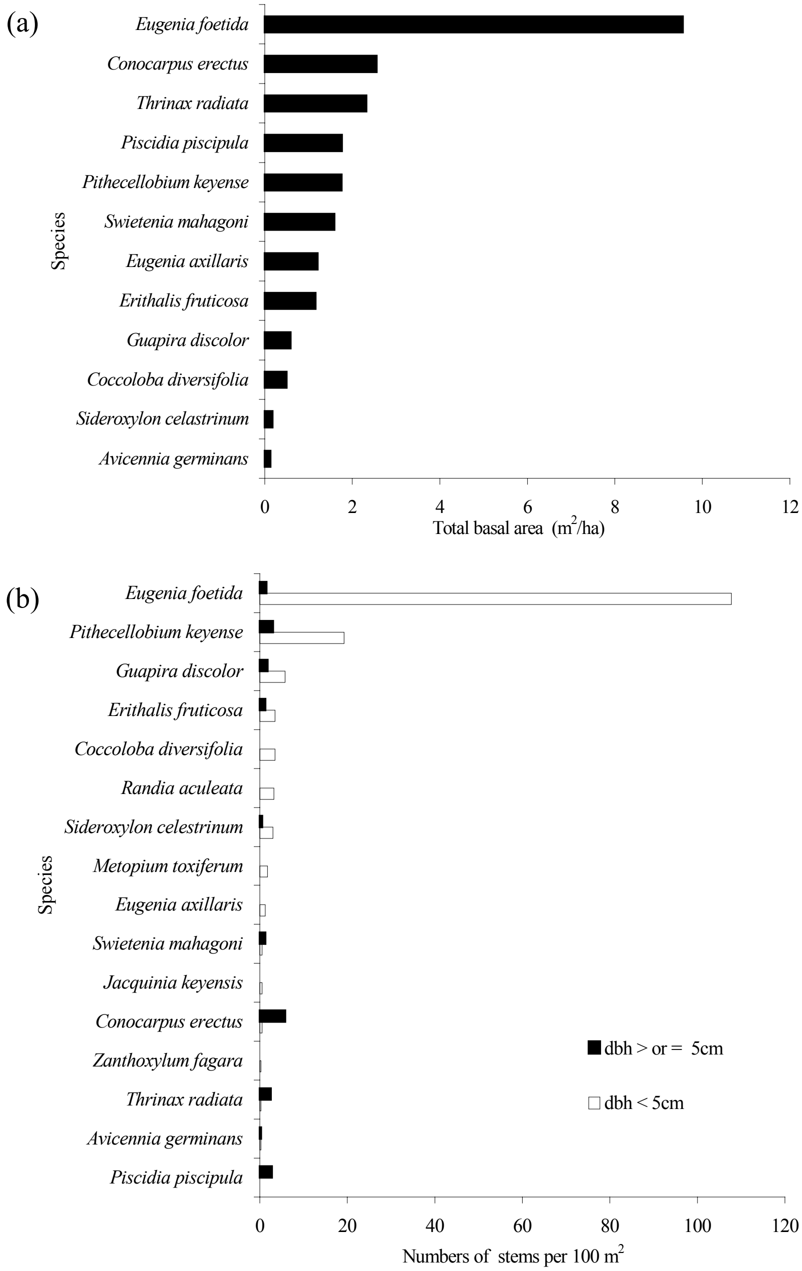

Figure 8. Total basal area of stems with ≥2.5 cm dbh (a) and stem densities (b) of all woody species occurring in a 400 m^2 plot located in a thatch palm hammock (Little Madeira Bay), as sampled in 1998.

tropical hardwoods including *Piscidia, E. foetida, Erithalis*, *Guapira*, *S. celastrinum*, and *P. keyense*. Like the hammocks fringing northern Florida Bay, the hammocks of the keys were depleted of *Conocarpus* and other valuable tropical hardwoods before about 1940 (Craighead 1971). However, the main factors influencing these and other coastal tree island types are severe hurricanes and progressive sea level rise (Craighead and Gilbert 1962; Wanless et al. 1994). In a recent survey of Florida Bay islands, we have observed decline or recent mortality of species such as *Thrinax*, *Conocarpus*, and *Sideroxylon celastrinum* in areas increasingly dominated by mangroves or open saline flats.

3.7 Florida Keys

Because they are not generally embedded within more extensive areas of pine forest, freshwater marsh, or mangrove swamp, the forests of the Florida Keys do not fit easily within the definition of "tree island" used in this chapter. However, as sea level continues to rise, forested uplands in the lower Keys are increasingly isolated within coastal wetland communities, and thus function more like tree islands (Ross et al. 1994).

The Florida Keys are a 210 km chain of limestone islands that begins in Biscayne National Park and arcs west-southwest to Key West. From northeast to southwest, the following physical changes may be of ecological importance: (1) a small but significant decrease in humidity, and an approximately twofold decrease in precipitation, (2) a more moderate temperature regime, with cooler summer highs and warmer winter lows, (3) a general decrease in the elevation of the islands at their highest points, and (4) an abrupt discontinuity in surface geology at Big Pine Key, where the coralline limestone gives way to an oolitic rock type. On Big Pine Key and beyond (Lower Keys), the less permeable oolitic limestone allows a permanent lens of fresh ground water to be maintained, which in turn favors the persistence of a suite of fresh water-dependent plants and animals.

Ross et al. (1992) divided the terrestrial habitats of the Florida Keys into thirteen ecological site units, most of which exhibited non-random geographic distributions within the islands. Vegetation composition of five units was comprised primarily of tropical upland tree species; these units are high, medium, and low productivity rockland hammock, coastal strand forest, and transitional thorn woodland. The first two are more common in the islands northeast of Lower Matecumbe Key (Upper Keys), the second two are characteristic of the Middle and Lower Keys, and the last one occurs throughout the islands. Apparent aboveground productivity of rockland sites generally decreases southwestward, reflecting the more stressful climatic conditions (Ross et al. 1992). Mean plant species richness in the five tropical hardwood forest units ranged from 23 to 28 species per 0.01 ha, with no evidence of spatial pattern in diversity within the region.

3.7.1 Upper Keys Hammocks

Mature rockland forests in the Upper Keys are characterized by a mean canopy height of 9 m, basal area of 32 m^2/ha, and fine litter production of 610 g/m^2/yr. Upper Keys forest assemblages, when compared to Lower Keys forests, more resemble the well-developed tropical hammock tree species, e.g., *Swietenia*, *Sideroxylon foetidissimum*, *Nectandra*, which are absent from Lower Keys forests.

3.7.2 Lower Keys Hammocks

In contrast to the Upper Keys hammocks, the mature rockland forests found in the Lower Keys have a mean canopy height of 6 m, basal area of 22 m^2/ha, and fine litter production of 470 g/m^2/yr. Despite similar species diversity to Upper Keys stands, Lower Keys hammocks contain a number of species not found in the former (e.g., *Psidium longipes* (O. Berg) McVaugh, *Savia bahamensis* Britton, and *Pisonia rotundata* Griseb.) (Little 1978).

4. HISTORY AND BIOGEOGRAPHIC RELATIONSHIPS OF TREE ISLAND FLORA

The modern vegetation of the southern Everglades region can be no more than about 5000 years old, based on dating of basal peats (Spackman et al. 1966; Cohen and Spackman 1977). Typically dates of basal deposits fall within the 4000-5000 year range. Reconstruction of Holocene climates and associated vegetation, and of sea levels (Delcourt and Delcourt 1981; Webb 1992) indicate that the Florida peninsula was drier before 5000 years ago than it is today, and was covered by savanna or oak-pine forests south through the peninsula. Such conditions were unlikely to have provided habitat for either the West Indian flora now dominating tree islands (Platt and Schwartz 1990) or the temperate species adapted to wet soils. This means that dispersal from tropical centers of distribution of the 819 native tropical species (Long 1984) and their spread across south Florida into suitable habitats must have principally occurred within the period of the last five millennia when a moderating climate with increased rainfall and high ground water levels provided conditions suitable for development of the Everglades.

The northern limits for many tropical species along both coasts occurs at Cape Canaveral and Tampa Bay, both lying about 390 km north along the peninsula and corresponding to the 54° January isotherm. Only within the southern Everglades do many tropical species reach the interior of the peninsula. In a pattern presumably related to low winter temperatures, species diversity declines in interior hammocks north of the southern Everglades as tropical species drop out faster than temperate species appear, while on the coasts, tropical species persist northward, maintaining higher species diversity (Platt and Schwartz 1990).

The distributions of the south Florida flora suggest that virtually all tropical tree species originated in the circum-Caribbean region (Tomlinson 1980). Indeed, as discussed below, all of the south Florida woody species are found commonly on the nearby Antillean islands of Cuba and the Bahamas. Because no land bridge existed between Florida and the Caribbean islands, colonization in Florida must have been preceded by dispersal of propagules across salt water, via birds, winds, and currents.

Information on species adaptations is generally quite sparse, but some inferences can be gained from knowledge of species' habitats near the center of their distribution where the species presumably have existed for time periods far longer than in south Florida. Of the 164 woody species found in the tree island and hammock forests of our region, 29 (17%) are predominantly temperate in distribution (Appendix I). All the temperate species are common on the southeastern coastal plain of North America. Species found mainly in bayhead, cypress or bayhead swamp types in our area are found further north in bottomland or other wetland habitats subjected to seasonal flooding. Species such as *Quercus laurifolia* and *Celtis laevigata*, that occur in tree islands in Big Cypress and Shark Slough, are found across a range of habitats that suggests broad adaptation to conditions that include wet soils. Even *Q. virginiana,* a dominant of hammocks on rock outcrops may occur in sites classifiable as wetlands (Godfrey and Wooten 1981), although such sites are usually not subject to protracted flooding. Overall, however, outside of slough hammocks, the temperate flora is scarce on limestone outcrop sites.

All 135 woody species of tropical origin known to occur in the tree island types of south Florida, occur widely in the circum-Caribbean region. In fact, all but four (*Ilex krugiana* Loes., *Drypetes diversifolia* Krug and Urb., *Thrinax morrissii* H. Wendl., and *Solanum donianum* Walp.) occur in Cuba, and 116, including *Ilex, Drypetes*, and *Thrinax*, may be found in the Bahamas Islands (Leon and Alain 1946-53, 1957-63; Alain 1962; Correll and Correll 1982).

Many of our most important species are also prominent in vegetation of the Caribbean region, and overwhelmingly the south Florida species are absent from aribbean closed forest unless these forests are on thin, rocky soils or subject to extended dry spells, in which case, deciduousness is characteristic (Beard 1944; Aspry and Robbins 1953; Dansereau 1966; Snook 1993). None are rare or highly restricted in distribution in the region.

Our species are especially common on limestone habitats that are widespread in Caribbean lands. For example, *Bursera simaruba* is abundant throughout the larger circum-Caribbean basin on limestone substrates and rocky soils extending into South America. It is a dominant species on these sites in Puerto Rico and Jamaica. *Coccoloba diversifolia* and *Ficus citrifolia* Mill. are common associates of *Bursera* in Puerto Rico, as they are in south Florida. *Gymnanthes lucida*, a hammock species of the upper Keys and Long Pine Key, forms monospecific thickets on plateaus in Puerto Rico, and *Colubrina arborescens* is the most conspicuous species in the xerophytic scrub of littoral woodlands along coasts of Puerto Rico (Dansereau 1966). *Roystonea regia* and *Cupania glabra* Sw. are characteristic of interior hillslope vegetation in the Habana-Matanzas region of Cuba, and *Roystonea* is common elsewhere (Leon and Alain 1946-53). *Quercus virginiana*, in its only extra-North American station, is found on sandy soils of the southwestern Cuban plains (Leon and Alain 1946-1953). Many other examples could be given to illustrate biogeographic similarities. Low coastal forests found along the limestone coast of Quintana Roo (southern Yucatan) have *Thrinax radiata* and *Piscidia piscipula*, both characteristic of our coastal areas, and *Metopium brownei* (Jacq.) Urban (closely related to *M. toxiferum*) among its five commonest species (Cano 1997). The most common interior forest is the low (5-10 m in height) semi-deciduous forest adjacent to the mangrove belt; *Bursera* and *Lysiloma* are among the dominants here. Interestingly, where the low forests are inundated in the rainy season, *Bursera* persists as a dominant, joined by *Piscidia.*

Similarities extend to tropical wetland communities. Besides strong similarities in mangrove forests between south Florida and the rest of the Neotropics, swampy woodlands found along estuaries in Puerto Rico feature *Conocarpus erectus* and *Chrysobalanus icaco*, and include *Annona glabra. Acoelorrhaphe wrightii* is the commonest palm on the shores of freshwater lakes in Cuba (Leon and Alain 1946-53) and occurs commonly in the Tabasco lowlands of southeastern Mexico as a dominant of “palm-heads” and pond borders (West et al. 1969).

5. SUCCESSIONAL PATTERNS

Plant succession is not well understood in south Florida; there is no clear basis for extending the well known relationships from temperate zones to our area, although broad patterns may be similar (e.g., in both temperate and tropical systems with adequate moisture, succession is projected to culminate in forests of long-lived, broad-leaved hardwoods) (Gomez-Pompa and Vasquez-Yanes 1981; Alexander and Crook 1984). In south Florida, convergence to a hammock climax is postulated to occur in wetland and upland sites, in the former case with increasing elevation resulting from accumulation of organic detritus or soil. An extended period free of severe fires is assumed to be essential for upland succession to proceed. Alexander (1967) has shown that a pineland protected from fire and located adjacent to two hammocks was replaced by tropical hardwoods within 25 years. Overall, however, fires are frequent on the ridge and tropical forest is restricted to small stands (hammocks) dispersed within a regional pine forest. The presence of a large number of endemic pineland understory species, which presumably required millennia for evolution, suggests a long history for the slash pine ecosystem type and, therefore, the fire regime (Robertson 1953). Thus, most likely, pinelands dominated the ridge during much or all of late Holocene or at least in the present climatic regime.

From work in Corkscrew Swamp, Duever et al. (1986) indicate that gradual accumulation of soil in wetlands can raise surface elevation sufficiently to reduce annual flooding to about 50 days, within the tolerances of hammock species. As proposed by Egler (1952), such a process could initiate with the recruitment of woody species into shallow drainage channels that provide some fire protection. In the natural Everglades system, fires and damaging storms, according to Egler (1952), would restrict the expansion of tree islands by burning partway into the stand or toppling perimeter trees, but not reverse the greater successional trend over the long-term. The interplay of developmental and destructive processes would lead to the present spatial pattern of small tree islands dispersed throughout a flooded landscape.

On smaller time scales, however, severe fires and storms can damage or destroy tree islands, and in especially dry conditions, fires can completely consume the organic soils, leading to permanent or long-term loss of tree islands. The occurrence of charcoal in soil cores supports an important role for fires in the natural system (Cohen and Spackman 1977), but no clear examples of tree island formation, other than relatively short-lived willow heads and thickets, has been reported. Although Egler’s qualitative model was formulated based on data collected a half-century ago, it seems to approximate our current understanding of tree island development in southern Everglades marshes.

Consistent with the succession model, bayheads sometimes form on sites underlain by sawgrass peat, which may lay upon a lower layer of peat formed from white water lily (*Nymphaea odorata* Sol.), signaling a temporal sequence of increasingly less flooded conditions recorded in the sediments (Davis 1946). In bayheads, peat sometimes accumulates above the water table to a level that might be suitable for hammock species. In some cases, bayhead species (particularly *Persea borbonia*) may occur intermixed with tropical species that appear to have some tolerance of wet soils, such as *Ficus aurea* and *Myrsine floridana*. However, there appears to be little evidence that in our region succession to hardwood hammocks has occurred on bayhead sites. For example, Olmsted and Loope (1984) report that none of the hammocks they inspected had bayhead soils at any level beneath the hammock vegetation. Although the lack of evidence may be attributable to a limited database, the sucessional sequence may not have had sufficient time to progress, and may require a climatic shift toward drier conditions.

In addition, damaging fires that have been severe and widespread in the 20th century have lowered the peat levels in many bayheads, thus truncating or reversing any successional sequence. Although the limited fire record does not allow us to determine to what extent modern fires have exceeded the natural regime, Taylor (1981) showed that in ENP during the 1948-1979 period, man-caused fires (exclusive of prescription burns) accounted for 77% of the total area burned. Possibly, modern fire frequencies mimic conditions during drier periods of the past. However, as Craighead (1971) described, widespread fires over the past century have reduced the peat that accumulated in the sloughs over past millennia, a destructive intervention into natural succession.

In addition to appropriating elevated sites spared long-term flooding, hammocks also appear to be levelling the outcrops through dissolution of the limestone by root acids. Although Everglades peat is markedly less acidic than typically found in northern climates, it is capable of accelerating the breakdown of limestone. In addition, the uprooting of trees in strong storms breaks up surface rock, increases surface roughness, and contributes to formation of deepened moats on the tree island perimeter (Duever et al. 1986). Thus, over some long time scale, tree island vegetation is accelerating bedrock weathering, thereby reducing the area of available for upland trees.

Secondary succession or species replacements are not well understood in our area. Most available information is from early stages of secondary succession in upland forests. Published analyses of longer-term dynamics are limited to a series of papers from a single Atlantic Coastal Ridge site in southern Miami-Dade County (Phillips 1940; Alexander 1967; Molnar 1990; Mack 1992). These studies document compositional change between 1940 and 1986, a period that included several hurricanes and the increasing isolation of the site from similar forested communities. Successional dynamics were spatially variable: some portions were relatively unchanged, while in others either the early-successional *Lysiloma* was replaced by native hardwoods, or sites were invaded by non-native species.

A detailed study of 23 hammocks in northern Key Largo, immediately adjacent to the southeastern tip of the Florida peninsula, provides insights into stand succession (M. Ross *et al*. in press). The stands encompassed a ca. 100-yr chronosequence since abandonment from disturbance, primarily low intensity agriculture. Time since disturbance was estimated from aerial photographs dating to 1928, and species were ordered along a succession gradient by a weighted-averaging procedure (Table 3).

Table 3. Successional age optima of 35 tree species from 23 hammock sites in northern Key Largo. Successional age optima are calculated by weighted averaging regression and calibration technique (Birks et al. 1992), and are based on the relationship between relative species abundances and stand age in the 23 Key Largo hammocks (Ross et al. in press). Leaf phenology categories: D, deciduous; E, evergreen.

Age (years)	Leaf phenology	Species
<50	D	*Bourreria ovata, Guettarda elliptica, G. scabra, Lysiloma latisiliquum, Solanum bahamense*
	E	
50-75	D	*Bursera simaruba, Ficus* sp., *Metopium toxiferum, Piscidia piscipula, Swietenia mahagoni*
	E	*Ardisia escallonioides, Canella winterana, Coccoloba diversifolia, Eugenia axillaris, E. foetida, Exostema caribaeum, Guapira discolor, Pithecellobium keyense, P. unguis-cati, Reynosia septentrionalis, Sideroxylon salicifolium, Ximenia americana, Zanthoxylum fagara*
>75	D	
	E	*Amyris elemifera, Calyptranthes pallens, Colubrina elliptica, Drypetes diversifolia, D. lateriflora, Eugenia confusa, Exothea paniculata, Gymnanthes lucida, Krugiodendron ferreum, Nectandra coriacea, Sideroxylon foetidissimum, Simarouba glauca*

Early-successional species were primarily deciduous trees with relatively wide tolerances (i.e., they establish rapidly after disturbance, but remain important components of the stand for several decades or more). Several (e.g., *Metopium*, *Swietenia*) may persist as scattered dominants in the upper canopy of very old stands. Late-successional species were all evergreen trees, apparently unable to become established in the open conditions of young stands. Soil development may also play a role, as the organic rockland soils increase in depth and change in character during the first few decades of stand development. These results are relevant to the tropical hardwood hammock portions of Everglades tree islands, but are probably of little relevance to bayhead or other wet tree island types.

6. ENVIRONMENTAL FACTORS CONTROLLING TREE ISLAND PERSISTENCE AND DEVELOPMENT

6.1 Inundation

The tree island types in our area differ markedly in their exposure to inundation by marsh waters. As a generalization, the tropical species, with a few exceptions such as *Chrysobalanus* and the mangroves, are confined to sites protected from long-term flooding. In contrast, sites supporting trees exposed to regular flooding are, outside of mangrove forests, predominantly temperate in origin. Although the literature suggests ranges for the annual flooding duration experienced by tree islands, they vary considerably. Thus, bayheads are reported to be inundated 2 to 6 months annually by Gunderson and Loftus (1993) and 1 to 4 months annually by Olmsted et al. (1980). Olmsted and Armentano (1997) report that average inundations in bayheads are 2 to 3 months in southeastern Shark Slough and 2 to 6 months in middle and northern Shark Slough. However, none of these papers presents field data to support the estimates. Tropical hardwood hammocks are reported to be restricted to sites that are seldom flooded (Gunderson and Loftus 1993) but Duever et al. (1986) report that they flood up to several months annually. Few observations are available for coastal hammocks. These may experience flooding only in conjunction with intense storms, when saline waters force inland (Craighead 1971).

The range of inundation estimates is attributable to several factors, including species-specific differences in tolerances, annual variability of flooding levels, and the limited data base. Wallace et al. (1996), for example, found *Persea palustris*, closely related or perhaps identical to *P. borbonia* (Godfrey and Wooten 1981; Duncan and Duncan 1988), to be the least flood tolerant of nine wetland tree species. *Persea* is the dominant tree in many bayhead forests (Egler 1952), but also may be infrequent or absent in some communities of the same type. Presumably this difference involves plasticity in adaptation to hydrological conditions, although other factors may be important. In contrast, seedlings of the tropical hardwood *Ficus aurea* were found to tolerate flooding nearly to the degree of *Chrysobalanus, Myrica,* and *Ilex cassine*, three typical bayhead species (Gunderson et al. 1988). Thus overlapping distributions and variations in tolerances of tree islands types are to be expected.

Differences in flooding tendencies in Shark Slough tree islands are better understood when elevation gradients can be tied to long-term records of water level. Unfortunately, such data are available from few sites. Below we present an integrated data set from three Shark Slough tree islands described earlier: Gumbo Limbo, Black, and West Twin.

Water levels from the nearest water level recorder superimposed on each transect are illustrated in Figure 9. Average monthly water levels for the periods of record (as early as 1952) were calculated for each site using station and tree island elevation data. Results show that the three tree islands differ markedly in the extent of inundation (Table 4).

In all cases, the bayhead swamp forest, because of its lower elevation, was inundated much longer than the hammocks. On the least flooded island (Black), the bayhead swamp was flooded from 25 to 61% of the time during the 47 year period of record, while the hammock portion, even at its minimum elevation, was essentially above water for the entire period. In contrast, at West Twin, the bayhead swamp was flooded over more than 96% of the 31 year record and the hammock was flooded from 18 to 23% of the time. Figures for Gumbo Limbo were intermediate, with the bayhead swamp inundated well over half the time and the hammock flooded nearly 13% of the time. In terms of annual hydroperiods, the range of flooding for the two forest types, based on mean elevations, would be 0-2.5 and 4.9-11.5 months for the hammock and bayhead swamp forests, respectively. The elevation extremes in each type would, of course, widen the range.

The same data were used to examine the response of individual species to flooding. Based on mean annual water level and species cover within 10 m segments, we calculated an optimum and tolerance based on abundance-weighted means and standard deviations, respectively. Spearman's rank correlation showed that the ranking of species optima was similar among stands (Gumbo Limbo-Black, $r = 0.48$, $p = 0.02$; Gumbo Limbo-West Twin, $r = 0.50$, $p = 0.04$; Black-West Twin, $r = 0.58$, $p = 0.009$). Average optimum and tolerance ranges were calculated for 13 woody species present along the three transects (Figure 10), following the procedures of (Line et al. 1990).

Nine species had optimal water depths below the soil surface, while *Annona*, *Cephalanthus*, *Myrica*, and *Salix* were most abundant in flooded conditions. *Myrsine* had the widest average tolerance along the three transects, but the tolerances of the upland species (except *F. aurea*) were consistently narrow. However, the assumption of a flat water table in the analyses could overestimate depth to water when water level falls below the surface (Duever et al. 1986). More tree islands must be examined in a similar fashion and tied to long-term water records before the realized hydrologic niche of tree island species can be definitively described.

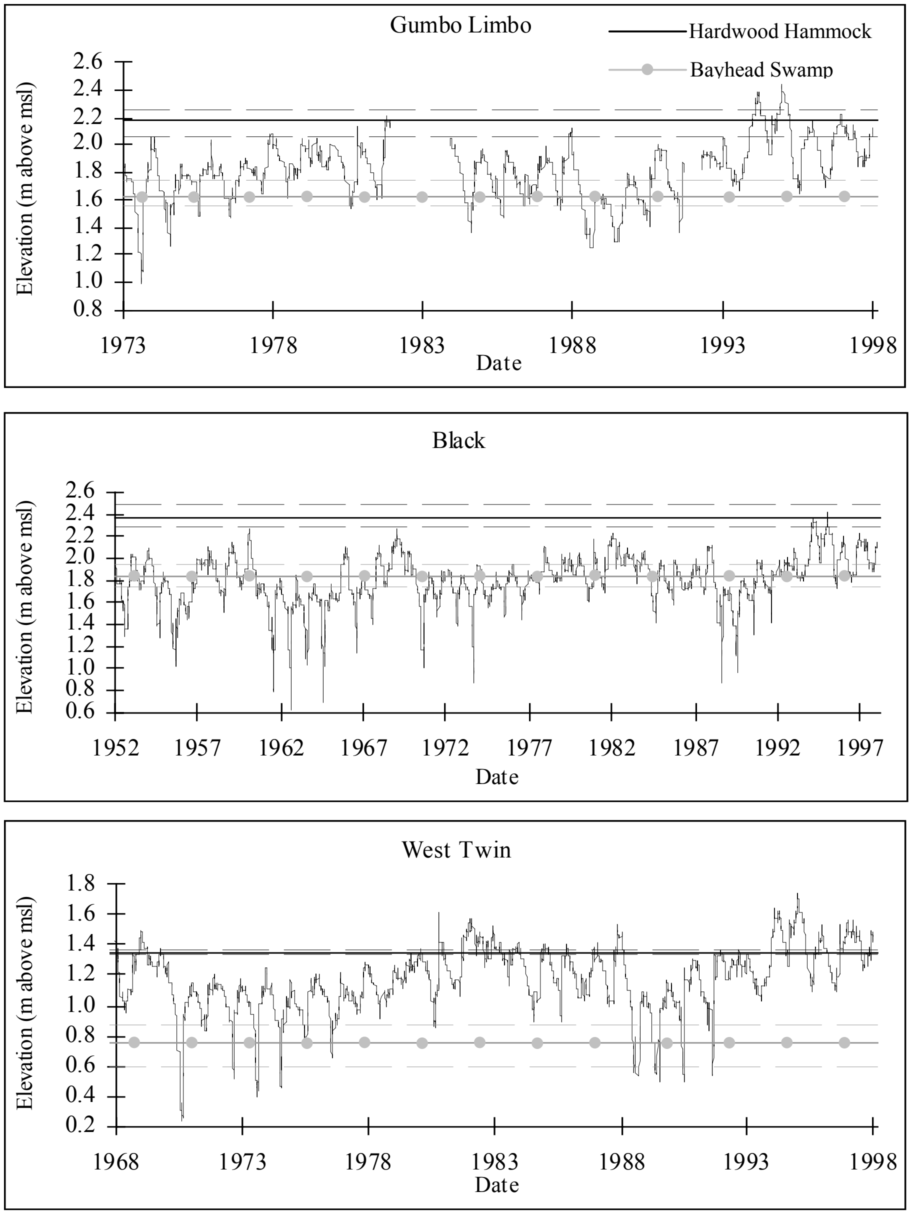

Figure 9. Average monthly water levels, for the available periods of record, at three Shark Slough tree islands. Mean (solid horizontal lines) and maximum/minimum (dashed horizontal lines) elevations of the tropical hardwood hammock (black lines) and bayhead swamp forest (gray dots) are indicated for each tree island.

Table 4. Percent of time water exceeds the maximum, mean, and minimum elevations within the bayhead swamp forests and tropical hardwood hammocks communities, at three tree island sites within Shark Slough. Periods of record (POR) and specific water gages used for each tree island are given.

Site	POR	Gage	Bayhead swamp forest			Tropical hardwood hammock		
			max	mean	min	max	mean	min
Black	1952-99	P33	25.3	40.7	61.1	0	0	0.6
Gumbo Limbo	1973-99	NP203	66.8	84.0	92.1	2.3	3.8	12.7
West Twin	1968-99	P36	96.1	97.8	99.5	18.3	20.6	23.5

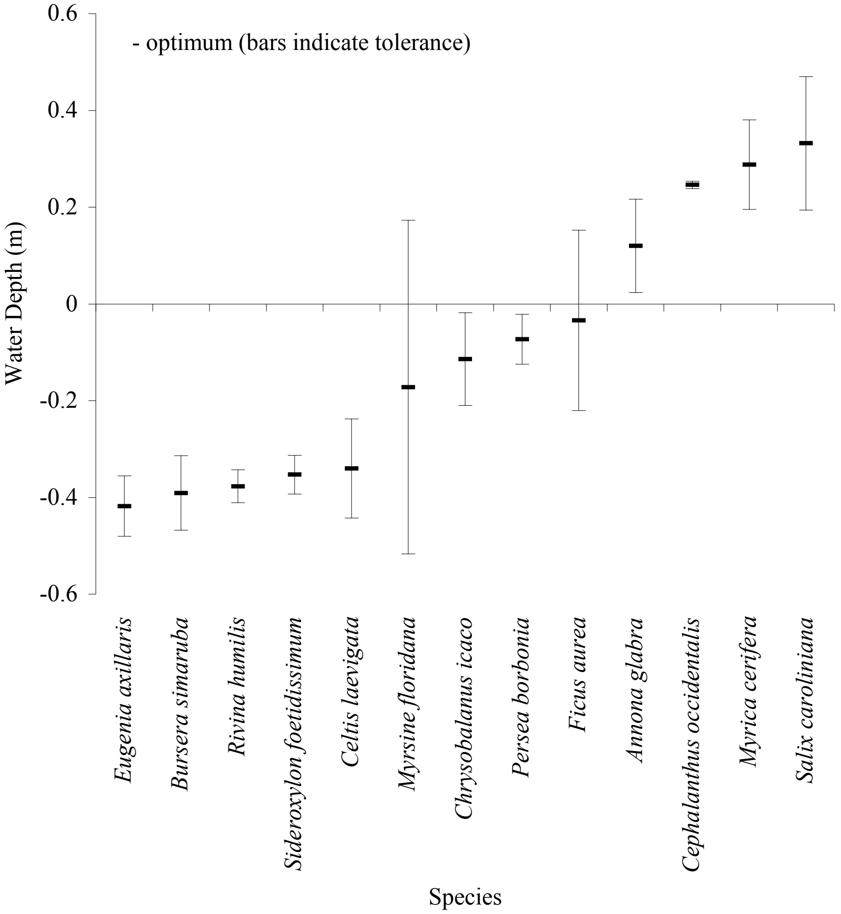

Figure 10. Average water level optimum and tolerance for woody species occurring along transects at three Shark Slough tree island sites

6.2 Fire Effects

As suggested above, fire is a primary agent in the development of tree islands. Historically, it is likely that the tree islands of the limestone ridges, most of which are embedded in pyrogenic pine forests, burned more frequently than coastal and slough tree islands. The slough tree islands receive protection from their location within a flooded wetland landscape, except during severe droughts. Most commonly, fires stop short of entering slough tree islands. In the uplands, fires often enter tree islands and damage some vegetation without destroying the soils, although, in most years, fires fail to penetrate beyond the hammock perimeter (Robertson 1953; Olmsted et al. 1983); the moisture of the vegetation and soils seems to retard penetration of fire into the hammocks. Craighead (1971) has suggested that fires can burn into hammocks when the water table drops more than 0.7 m below ground surface or soil moisture falls below 35%, a condition that occurs in droughts. Olmsted et al. (1980) report that fires had not penetrated Wright Hammock in Long Pine Key for 60 years, and Deer Hammock in Long Pine Key and the Pinecrest hammocks in southern Big Cypress for 40 years, prior to their report. However, Royal Palm Hammock experienced severe fire in 90% of its 91 ha in 1945, and Craighead (unpublished raw data) described numerous Long Pine Key hammocks that were burned through in the 1950s. Loope and Urban (1980) found that 31 out of 100 tropical hardwood tree islands in the Rocky Glades showed no evidence of fire damage during the period 1940-1976. Twenty-seven of these appeared mature in 1940 photographs, suggesting several additional decades without destructive fires. Ten tree islands, however, were severely damaged by fire in the 36-year period. In such fires, many trees, including canopy individuals, may be lost and replaced for decades by thickets of bracken fern, vines, and shrubs (Craighead 1971; Wade et al. 1980).

Natural fires in the coastal areas are relatively rare. Lightning strikes, however, are common judging from the frequent occurrence of circular “holes” in the canopies of the extensive Gulf Coast mangrove forest, but these have not been seen to spread beyond the local scale. Mahogany Hammock, one of the largest tree islands on the interior edge of the mangrove forest, had no evidence of fire damage for 50 years according to Olmsted et al. (1980), and none since, contributing to a fire-free period of nearly 70 years. The most likely situation for fire penetrating coastal tree islands, outside of man-caused fires, which were common in the Flamingo area (Craighead 1971), develops during a drought after a hurricane kills trees, producing a large volume of combustible material. Such a scenario unfolded the year after Hurricane Donna hit extreme southern Florida in 1960 (Craighead and Gilbert 1962).

Not all fire effects are damaging. Combustion of surface detritus and opening of the canopy improves conditions for recruitment from the seed bank or from root sprouts. Harold Slater (Louisiana State University, personal communication) has shown experimentally that seeds of *Lysiloma*, a dominant species in hammocks of the Atlantic Coastal Ridge, respond favorably to high temperatures such as are generated by ground fires in hammocks. Rapidly growing, short-lived "pioneer" species such as *Carica papaya* and *Trema* spp., and numerous vines (e.g. *Smilax* spp., *Ipomoea* spp.), germinate quickly from the seed bank. Bracken fern (*Pteridium aquilinum*) also rapidly appropriates burned upland sites. *Trema micranthum* (L.) Blume, a pioneer species filling a similar niche in Mexico and south Florida, has been shown to have photoblastic seed dormancy, a condition that can be broken by increased light (Gomez-Pompa and Vasquez-Yanes 1981). Many of the species common to upland hammocks in the interior and coastal tree islands, such as *Bursera*, sprout readily following fires, conferring an advantage in all but severe fires over species dependent on seedling recruitment.

Generally, oaks (*Quercus virginiana, Q. laurifolia, Q. nigra*) and *Lysiloma* act as long-lived pioneers quickly reaching the canopy in post-fire tree islands, yet allowing shade-tolerant species to recruit as seedlings. Most tree island species in south Florida, with the notable exception of the wind-dispersed *Lysiloma*, reach the seed bank by zoochory, involving birds.

6.3 Hurricanes

Like fires, hurricanes vary in intensity and, therefore, in how they affect tree islands. The interval between severe hurricanes determines to a great extent the status of the vegetation (Armentano et al. 1995). Although south Florida, lies in a hurricane belt, with strong hurricanes striking Florida, on average, every 6-8 years (Chen and Gerber 1990), a given location may not experience severe storm damage for decades. In addition, hurricane frequencies fluctuate with periods of relatively high and low return intervals (Gentry 1984). Forests along Biscayne Bay were damaged by major hurricanes in 1926, 1947, and 1965, whereas the southwestern Gulf area was hit hard in 1910, 1935, 1960, and 1965.

Prior to 1935, portions of the mangrove belt of extreme southern Florida appear not to have experienced severe storms for many decades judging from the large stature of the Gulf Coast mangrove forests. Craighead and Gilbert (1962) report that trees here reached diameters and heights of over 0.6 m and 24 m, respectively. Presumably, such large trees represented growth of "centuries". The great Labor Day hurricane of 1935, a Category 5 storm on the Simpson-Saffer scale, destroyed most of these forests, while many of the survivors were felled by Hurricane Donna in 1960. A 1965 hurricane further damaged coastal forests, and coastal hammocks were damaged by Hurricane Donna, but less so than mangroves. *Sabal* and *Conocarpus*, important species where soil salinity is relatively low, are wind resistant and suffered relatively little direct mortality. Mortality in these species, instead, was often caused by accumulated silt and marl driven inland by the storm (Craighead and Gilbert 1962). Hurricane Donna also damaged hammocks further inland, destroying the canopy of Mahogany and Royal Palm Hammocks, reducing the numbers of royal palms in both locations and uprooting many trees, especially large canopy emergents

In 1992, Hurricane Andrew, a Category 4 storm, crossed the south peninsula at the latitude of central Shark Slough. This storm damaged virtually all tree islands in the northernmost Keys (especially in Biscayne National Park), in southern Miami-Dade County and in the interior of the southern Everglades, including those of Shark Slough and Long Pine Key (Armentano et al. 1995; Horvitz et al. 1995). Coastal tree islands and hammocks of the southern coastal areas, including those north of Florida Bay and on Cape Sable, largely escaped serious damage. Throughout the area of major damage, defoliation was nearly universal (Armentano et al. 1995), consistent with earlier major storms (Craighead 1971).

In a survey of Shark Slough tree island hammocks four years after Hurricane Andrew, Jones et al. (1997) found that most canopy trees suffered damage, often loss of crowns, but that mortality rate was very low. Surveys were not made of the large bayhead swamp forests downstream of the hammocks, but it was noted that *Sabal palmetto* of the bayhead swamp forest periphery was little damaged. Four years after the storm, the seedling layer of four Shark Slough tree island hammocks had few early successional recruits and, in several hammocks, was dominated by *Eugenia axillaris*, a persistent and shade-tolerant understory tree (Jones et al. 1996).

Patterns in Long Pine Key were similar (Slater et al. 1995). Over 85% of the hammock trees were damaged, 45% snapped, 9% were blown down, but only 1.5% of stems were dead four months after the storm. The authors suggest that there is selection for species capable of rapid resprouting and abundant dormant buds. Koptur et al. (1995) found that Hurricane Andrew killed over 30% of hammock tree species in sample stands of Long Pine Key and 51% of bayhead trees. These values exceed mortality rates observed in five other hurricane studies. The high losses in bayheads may have resulted because windthrows in wet soils are more likely than in well-drained soils (Weaver 1989). In contrast, rooting in rock, a common condition in our area, frequently results in breaking of the boles, a response that is fatal to slash pine, but not necessarily to hardwoods.

Snook (1993) summarized patterns in the Yucatan Peninsula, Mexico, that appear to apply to south Florida tree islands. At any one time, in a disturbance-prone area, stand composition is comprised of several components: survivors of past disturbances, either as regrowing crowns or basal sprouts; advanced regeneration of small stems that survived the storm and responded to the opened canopy; and as recruits that arrived since disturbance, either from the seed bank or from seed rain. Variations in the relative importance of these demographic responses to disturbance helps explain how a heterogeneous pattern can develop across a population of stands or tree islands, particularly given that catastrophic events may occur repeatedly over the life span of a canopy tree. Snook (1993) reports a similar response occurring with fires, although severe fires are often more damaging than storms because the subordinate forest layers, including sometimes the seedbed, are destroyed. Again, this appears to parallel the situation in south Florida, where severe fires completely consumed many of the smaller tree islands.

The long-term effect of hurricanes appears to favor a cyclic steady-state in which hurricane-resistant species have a greater chance of maintaining or increasing their importance in a stand (Crow 1980). Furthermore, hurricanes increase the flux of organic matter and nutrients to the forest floor (Frangi and Lugo 1991), a process that may be important in the oligotrophic Everglades. Thus, frequent disturbances free up nutrients and break up surface rock, stimulating soil development and setting the stage for recovery. How far recovery proceeds would depend on the time until the next severe hurricane and the probability of interceding droughts and attendant fires. In the present day Everglades, artificial drainage has reinforced the drought and fire cycle, likely leading to lower overall structural development of the vegetation.

6.4 The Role of Sea Level Rise

In coastal areas and ultimately the entire peninsula, sea level is a primary factor affecting long-term succession. In a scenario of a slow mean sea level rise rate, which has been the general pattern over the last 3200 years (except in the last 60 years when the sea level rise rate has accelerated -- Wanless et al. 1994), vertical peat accretion and marine transgression have maintained an extensive mangrove forest along the Gulf of Mexico and Florida Bay. Conceptually, accretion could raise the soil surface sufficiently to ultimately support hardwood species adapted to low-salinity and well-drained soils. However, hardwood tree islands in the mangrove zone are principally present either as hammocks on Indian middens raised above the surrounding mangrove forest by human action or on ridges of sand or marl deposited by storms. There is little basis for assuming that these sites could maintain their position in the midst of rising sea levels. The absence of mangrove peat beneath any coastal hardwood hammocks examined by the authors or reported in the literature (e.g., Cohen and Spackman 1977; Gleason et al. 1984), suggests that the replacement of mangrove forest by communities of hardwoods and palms with relatively little salt tolerance was rare in the past and would be even less likely to occur in the present era of accelerated sea level rise.

At the sea level rise rate occurring before about 3200 years ago and apparently in the present period, peat accretion rates have been insufficient to maintain elevations relative to tidewater. Consequently marine transgression has prevailed, which, if continued long enough, favors flooding of coastlines, retreat or loss of coastal vegetation, including, presumably, hardwood stands established on storm deposits, and submergence of mangrove peat (Wanless et al. 1994, Ross et al. 2000). The potential for establishment of new communities on storm ridges displaced into the interior is unclear. However, although there is considerable uncertainty on the matter, the elimination of coastal upland habitat, may be expected to proceed as it has in the Florida Keys, where salt water intrusion eliminated pine habitat in this century (Ross et al. 1994).

7. CONCLUSION

In this chapter we have shown that despite occupying only a small fraction of the remaining natural areas, the forested areas of the southern Everglades region harbor a rich variety of plant communities and species. Tree islands are especially significant as reservoirs of West Indian species diversity and of specialized plant guilds such as epiphytic orchids, bromeliads and ferns. Probably none of the tree island types has escaped the harmful effects of man’s actions. These can be especially damaging when superimposed on a natural regime of multiple environmental stresses.

As described in this chapter, discrete, relatively small plant communties dominated by trees can be found in a variety of landscapes. In freshwater wetlands, hydrological regime is instrumental in determining community type while fires appear secondary. Tree communities embedded in upland landscapes, or in seasonal wetlands such as in the East Everglades and Rocky Glades, are heavily influenced by fires that are regular features of the landscape. Near the coast, flooding by saline waters associated with major storms is an important influence although protection from low temperatures and other unspecified aspects of proximity to the coast may be important. The assumed persistence of tree islands for at least several millennia attests to their durability in the face of hurricanes, fires, droughts, freezes and flooding. However, it seems evident that coastal hammocks, particularly along the north coast of Florida Bay and near the Gulf of Mexico are especially vulnerable to rising sea level and storm damage, while invasive non-native species threaten most tree island types.

Although tree island communities differ widely in tolerance of flooding, all wetland species, even those confined to hammocks in slough tree islands, are adapted to survive some level of flooding. Elevation above the surrounding habitat is important in determining tree island composition, but other aspects, including soils properties, fires and damaging storms, and history of human use also influence community responses. However, because of limiting data, we are unable in a quantitative sense to fully understand how tree islands respond to varying intensities of stresses such as hydrological regime (duration, frequency and depth of surface flooding and soil saturation) or to stress interactions such as fire-flood or flood-storm effects. Similarly, the influence of soil physical and nutrient properties, and of soil depth on plant responses to hydrological extremes, needs study. In sloughs, although it appears obvious from aerial photographs that directional flow patterns were instrumental in shaping tree island development, the implications of the recent disturbance of historic sheet flow is poorly understood. All of the research needs are pertinent at several levels: 1) in affecting individual plant growth and survival rates; 2) in determining species composition and dominance within tree community types; 3) in possibly controlling conversion of one type to another, and, 4) particularly in the modern era of artificial manipulation of water levels, in damaging or causing potentially long-term obliteration of one or more types.

Progress has been made in recognizing the importance of the natural landscape including the embedded tree islands. Modification of the present water management protocols and control of non-native invasive plants are two regional efforts having the potential to improve future prospects for remaining natural communities, although neither of these efforts can reverse the effects of sea level rise. However, a restored natural hydrology is perhaps the only mechanism for promoting a vigorous rate of soil accretion that can offset for a time the inexorable effects of the sea level rise and for approximating the environmental regime that fostered the development of these unique botanical treasures.

8. REFERENCES

Alain, H. 1962. *Flora de Cuba, Part 5.* Rio Piedras, Puerto Rico, University of Puerto Rico Press,

Alexander, T.R. 1967. A tropical hammock on the Miami (Florida) Limestone - a twenty-five year study. Ecology, 48: 863-867.

Alexander, T.R. and Crook, A.G. 1984. Recent vegetational changes in southern Florida. In: Gleason, P.J. ed. *Environments of South Florida: Present and Past II.* Coral Gables, FL, Miami Geological Society, pp. 199-210.

Armentano, T.V., Doren, R.F., Platt, W.J., and Mullins, T. 1995. Effects of Hurricane Andrew on coastal and interior forests of southern Florida: overview and synthesis. Journal of Coastal Research, 21:111-144.

Aspry, G.F. and Robbins, R.G. 1953. The vegetation of Jamaica. Ecological Monographs, 23:359-412.

Beard, J.S. 1944. Climax vegetation in tropical America. Ecology, 25:127-158.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C., and ter Braak, C.J.F. 1992. Diatoms and pH reconstruction. Philosophic Transactions of the Royal Society of London, B327:263-278.

Borel, J.S. 1997. *Coevolution of landscape and culture: the vegetation of Indian shell mounds in Florida's Ten Thousand Islands.* Master's Thesis. University of Florida, Gainesville, FL 274 p.

Cano, E.F.C. 1997. La vegetacion en la zona de Xcalak. Amigos de Sian Ka'an, 17:24- 31.

Chen, E. and Gerber, J.F.. 1990. Climate. In: Myers, R.L. and Ewel, J.J. eds. *Ecosystems of Florida.* Orlando, University of Central Florida Press, pp. 11-34.

Cohen, A.D. and Spackman, W. 1977. Phytogenic organic sediments and sedimentary environments in the Everglades-Mangrove complex, Part 2. Paleontographica, 162:71-114.

Coile, N. C. 1998. Notes on Florida's endangered and threatened plants. Gainesville, FL, Florida Department of Agriculture and Consumer Affairs,

Correll, D.S. and Correll, H.B. 1982. *Flora of the Bahama Archipelago.* Vaduz, Lichtenstein: J. Cramer.

Craig, A.K., McJunkin, D.M., and Stone, P.A. 1971. Phytogeography of Pavilion Key. Department of Geography, Florida Atlantic University, Boca Raton.

Craighead, F.C. 1964. Land, mangroves and hurricanes. Fairchild Tropical Garden Bulletin, 19:1-28.

Craighead, F.C. 1968. The role of the alligator in shaping plant communities and maintaining wildlife in the southern Everglades. The Florida Naturalist, 41:2-7, 69-74, 94.

Craighead, F.C. 1971. *The Trees of South Florida, Volume I: The Natural Environments and their Succession.* Coral Gables, FL University of Miami Press.

Craighead, F.C. 1984. Hammocks of south Florida. In: Gleason, P.J. ed. *Environments of South Florida: Present and Past II.* Coral Gables, FL, Miami Geological Society, pp. 191-198.

Craighead, F.C. and Gilbert, T. 1962. The effects of Hurricane Donna on the vegetation of southern Florida. Quarterly Journal of the Florida Academy of Sciences, 25:1-28.

Crow, T.R. 1980. A rainforest chronicle: a 30 year record of change in structure and composition at El Verde, Puerto Rico. Biotropica, 12: 42-55.

Dansereau, P. 1966. *Studies on the Vegetation of Puerto Rico.* Special Publication No. 1. University of Puerto Rico, Mayaguez.

Davis, J.H. 1943. The natural features of south Florida, especially the vegetation and the Everglades. Florida Geological Survey Bulletin, 25:1-311.

Davis, J.H., 1946. *The Peat Deposits of Florida: Their Occurrence, Development and Uses.* Geological Bulletin No. 30. Tallahassee, FL State of Florida.

Delcourt, P.A. and Delcourt, H.R. 1981. Vegetation maps for eastern North America: 40,000 yr b.p. to the present. In: Romans, R.C. ed. *Geobotany II.* New York, Plenum Press, pp. 123-165.

Duever, M.J., Carlson, J.E., Meeder, J.F., Duever, L.C., Gunderson, L.H., Riopelle, L.A., Alexander, T.R., Myers, R.L., and D.P. Spangler. 1986. *The Big Cypress National Preserve.* Research Report No. 8. New York. National Audubon Society,

Duncan, W.H. and Duncan, M.B. 1988 *Trees of the Southeastern United States.* Athens, GA, The University of Georgia Press.

Egler, F.E. 1952. Southeast saline Everglades vegetation, Florida, and its management. Vegetation Acta Geobotanica, 3: 213-265.

Enos, P. 1989. Islands in the bay – a key habitat of Florida Bay. Bulletin of Marine Science, 44:365-386.

Ewel, K.C. and Odum, H.T. eds. 1984. *Cypress Swamps.* Gainesville, FL University of Florida Press.

Frangi, J.L. and Lugo, A.E. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. Biotropica, 23: 324-335.

Gentry, R.C. 1984. Hurricanes in south Florida. In: Gleason, P.J. ed. *Environments of South Florida: Present and Past II.* Coral Gables, FL, Miami Geological Society, pp. 510-519.

Gleason, P.J., Cohen, A.D., Smith, W.G., Brooks, H.K., Stone, P.A., Goodrick, R.L. and Spackman, W. 1984. The environmental significance of Holocene sediments from the Everglades and saline tidal plain. In: Gleason, P.J. ed. *Environments of South Florida: Present and Past II.* Coral Gables, FL, Miami Geological Society, pp. 297-351.

Godfrey, R.K. and Wooten, J.W. 1981. *Aquatic and Wetland Plants of Southeastern United States: Dicotyledons.* Athens, GA, The University of Georgia Press.

Gomez-Pompa, A. and Vasquez-Yanes, C. 1981. Successional studies of a rain forest in Mexico. In: West, D.C., Shugart, H.H., and Botkin. D.B. eds. *Forest Succession Concepts and Application.* New York, Springer-Verlag, pp. 246-266.

Gunderson, L.H. and Loftus, W. 1993. The Everglades. In: Martin, W.H., Boyce, S.G., and Echternacht, A.C. eds. *Biodiversity of the Southeastern United States.* New York, John Wiley and Sons, pp. 199-255.

Gunderson, L.H. and Loope, L.L. 1982a. *A survey and inventory of the plant communities in the Pinecrest Area, Big Cypress National Preserve.* South Florida Research Center Report T-655. Homestead, FL, Everglades National Park, 43 p.

Gunderson, L. H. and Loope, L.L. 1982b. *A survey and inventory of the plant communities of the Raccoon Point Area, Big Cypress National Preserve.* South Florida Research Center Report T-665. Homestead, FL, Everglades National Park, 36 p.

Gunderson, L.H. and Loope, L.L. 1982c. *An inventory of the plant communities within the Deep Lake Strand Area, Big Cypress National Preserve.* South Florida Research Center Report T-666. Homestead, FL, Everglades National Park, 39 p.

Gunderson, L.H., Loope, L.L. and Maynard, W.R. 1982. *A survey and inventory of the plant communities of the Turner River Area, Big Cypress National Preserve.* South Florida Research Center Report T-648. Homestead, FL, Everglades National Park, 53 p.

Gunderson, L.H., Stenberg, J.H. and Herndon, A.K. 1988. Tolerance of five hardwood species to flooding regimes. In: Wilcox, D.A. ed.. *Interdisciplinary Approaches to Freshwater Wetland Research.* East Lansing, MI, Michigan State University Press, pp. 119-132.

Hoffmeister, J.E. 1974. *Land from the Sea: the Geologic Story of South Florida.* Coral Gables, FL, University of Miami Press.

Hofstetter, R.H. and Hilsenbeck, C.E. 1980. Vegetational studies of the East Everglades. Miami, FL, Metropolitan Dade County Planning Department.

Holdridge, L.R. 1967. *Life Zone Ecology.* San Jose, Costa Rica, Tropical Science Center.

Horvitz, C.C., McMann, S. and Freedman, A. 1995. Exotics and hurricane damage in three hardwood hammocks in Dade County parks. Florida Journal of Coastal Research, 21:145-158.

Jenny, H. 1980. *The Soil Resource: Origin and Behavior.* Ecological Studies 37. New York: Springer-Verlag.

Jones, D.T. 1997. Ecological consequences of latherleaf (*Colubrina asiatica*) in southern Florida. Wildland Weeds (Winter):11-12.

Jones, D.T., Armentano, T.V., Snow, S. and Bass, S. 1996**.** Evidence for flooding effects on vegetation and wildlife in Everglades National Park, 1994-95. In: Armentano, T.V. ed. *Ecological Assessment of the 1994-1995 High Water Conditions in the Southern Everglades*. Miami, FL: South Florida Management and Coordination Working Group, pp. 31-46.

Koptur, S., Oberbauer, S. and Whelan, K.R.T. 1995. *A comparison of damage and short-term recovery from Hurricane Andrew in four upland forest types of the Everglades*. Report to Everglades National Park, Homestead, FL: National Park Service 34p.

Leon, H. and Alain, H. 1946-53. *Flora de Cuba, Parts 1 and 2. Habana.* Koenigstein. Reprinted by Otto Koeltz Science Publishers, 1974.

Leon, H and Alain, H. 1957-63. *Flora de Cuba, Parts 3 and 4. Habana and Rio Piedras.* Koenigstein. Reprinted by Otto Koeltz Science Publishers, 1974.

Line, J.M., ter Braak, C.J.F. and H.J.B. Birks. WACALIB version 3.3 - a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging and to derive sample-specific errors of prediction. Journal of Paleolimnology, 10:147-152.

Little, E. L. 1976. *Rare Tropical Trees of South Florida.* Conservation Research Report No. 20. Washington DC: U.S. Department of Agriculture, U.S. Forest Service,

Little, E.L. 1978. *Atlas of United States Trees, Vol. 5: Florida.* Miscellaneous Publication No. 1361. Washington, DC: U.S. Department of Agriculture, 22 p.

Long, R. 1984. Origin of the vascular flora of south Florida. In: Gleason, P. J. (ed), *Environments of South Florida: Present and Past II.* Coral Gables, FL: Miami Geological Society, pp. 118-126.

Loope, L.L. and Urban, N.H. 1980. *A Survey of Fire History and Impact in Tropical Hardwood Hammocks in the East Everglades and Adjacent Portions of Everglades National Park.* South Florida Research Center Report T-592. Homestead, FL: National Park Service, 48 p.

Loveless, C.M. 1959. A study of the vegetation in the Florida Everglades. Ecology, 40:1-9.

Lugo, A.E. and Snedaker, S.C. 1974. The ecology of mangroves. Annual Review of Ecology and Systematics, 5: 39-64.

Mack, A.L. 1992. Vegetation analysis of a hardwood hammock in Dade County, Florida: changes since 1940. Florida Scientist, 55(4):258-263.

Molnar, G. 1990. *Successional Dynamics of a Tropical Hardwood Hammock on the Miami Rockridge.* Master's Thesis, Florida International University, Miami, FL 197 pp.

Oberbauer, S.F. and Koptur, S. 1995. *Short and Long Term Responses of Non-tidal Forest Communities in Everglades National Park to Hurricane Andrew.* Report to Everglades National Park. Homestead, FL: National Park Service, 34 pp.

Odum, W.E. and McIvor, C.C. 1990. Mangroves. In: Myers, R.L . and Ewel, J.J. eds. *Ecosystems of Florida.* Orlando FL: University of Central Florida Press, pp. 517-548.

Olmsted, I.C. and Armentano, T.V. 1997. *Vegetation of Shark Slough, Everglades National Park.* South Florida Research Center Report 97-001. Homestead, FLNational Park Service, 41 p.

Olmsted, I.C. and L.L. Loope. 1980. *Vegetation along a microtopographic gradient in the estuarine region of Everglades National Park, Florida.* Unpublished report. Homestead, FL: National Park Service, 42 p.

Olmsted, I.C. and L.L. Loope 1984. Plant communitiies of Everglades National Park. In: Gleason, P. J. ed. *Environments of South Florida: Present and Past II.* Coral Gables, FL: Miami Geological Society, pp. 167-184.

Olmsted, I.C., Loope, L.L. and Hilsenbeck, C.E. 1980. *Tropical hardwood hammocks of the interior of Everglades National Park.* South Florida Research Center Report T-604. Homestead, FL: National Park Service. 58 p.

Olmsted, I.C., Loope, L.L. and Russell, R.P. 1981. *Vegetation of the southern coastal region of Everglades National Park between Flamingo and Joe Bay.* South Florida Research Center Report T-620. Homestead, FL: National Park Service. 18 p.

Olmsted, I.C., Dunevitz, H. and Platt, W.J. 1993. Effects of freezes on tropical trees in Everglades National Park Florida, USA. Tropical Ecology, 34:17-34.

Olmsted, I.C, Robertson, W.B., Johnson, J. and Bass, O.L. 1983. *The Vegetation of Long Pine Key, Everglades National Park.* South Florida Research Center Report 83/05. Homestead, FL: National Park Service.

Phillips, W.S. 1940. A tropical hammock on the Miami (Florida) limestone. Ecology, 21:166-174.

Platt, W.J. and Schwartz, M.W. 1990. Temperate hardwood forests. In: Myers, R.L. and J.J. Ewel eds. *Ecosystems of Florida*. Orlando, FL: University of Central Florida Press, pp. 194-229.

Reimus, R. 1997. *A List of Species Observed at Johnson Mound-- an Indian Midden near the Gulf Coast* . Report to Everglades National Park. Homestead, FL: National Park Service, 5 pp.

Robertson, W.B. 1953. *A Survey of the Effects of Fire in Everglades National Park.* National Park Service Report. Homestead, FL: National Park Service. 159 p.

Ross, M.S., O'Brien, J.J. and Flynn, L.J. 1992. Ecological site characterization of Florida Keys terrestrial habitats. Biotropica, 24:488-502.

Ross, M.S., O'Brien, J.J. and Sternberg, L S.L. 1994. Sea-level rise and the reduction in pine forests in the Florida Keys. Ecological Applications, 4:144-156.

Ross, M.S., Meeder, J.F., Sah, J.P., Ruiz, P.L. and Telesnicki, G. 1996. *The Southeast Saline EvergladesRrevisited: a Half-Century of Coastal Vegetation Change*. Final Report for Contract C-4244. Miami, FL: Florida International University.

Ross, M.S., Meeder, J.F. Sah, J.P. Ruiz, P.L. and Telesnicki, G.J. 2000. The Southeast Saline Everglades revisited: 50 years of coastal vegetation change. Journal of Vegetation Science, 11:101-112.

Ross, M.S., Carrington, M., Flynn, L.J. and Ruiz, P.L. (In Press). Forest succession in tropical hardwood hammocks of the Florida Keys: effects of direct mortality from Hurricane Andrew. Biotropica.

Schomer, N.S. and Drew, R.D. 1982. *An Ecological Characterization of the Lower Everglades, Florida Bay and the Florida Keys.* Report for Cooperative Agreement 14-16-009-80-999. Tallahassee, FL: Florida State Department of Environmental Regulation.

Slater, H., Platt, W.J., Baker, D.B. and Johnson, D.B. 1995. Effects of Hurricane Andrew on damage and mortality of trees in subtropical hardwood hammocks of Long Pine Key, Everglades National Park. Journal of Coastal Research, 21:197-207.

Small, J.K. 1931. Botanical crossroads, historic and prehistoric. Journal of the New York Botanical Garden, 32:92-94.

Snook, L.K. 1993. *Stand Dynamics of Mahogany (Swietenia macrophylla King) and Associated Species after Fire and Hurricane in the Tropical Forests of the Yucatan Peninsula, Mexico.* Ph.D. Dissertation, Yale University, New Haven CT.

Snyder, J.R., Herndon, A. and Robertson, W.B. 1990. South Florida rockland. In : Myers, R.L. and Ewel, J.J. eds. *Ecosystems of Florida.* Orlando, FL: University of Central Florida Press, pp. 230-280.

Spackman, W., Dolsen, C.P. and Riegel, W. 1966. Phytogenic organic sediments and sedimentary environments in the Everglades-Mangrove complex, Part 1. Phytogeographica, 117B:135-152.

Taylor, D. 1981. *Fire History and Fire Records for Everglades National Park, 1948-1979.* South Florida Research Center Report T-619. Homestead, FL: National Park Service. 121 p.

Tebeau, C.W. 1968. *Man in the Everglades*. Coral Gables, FL: University of Miami Press.

Tomlinson, P.B. 1980. *The Biology of Trees Native to Tropical Florida.* Allston, MA: Harvard University Printing Office.

Wade, D., Ewel, J. and Hofstetter, R. 1980. *Fire in South Florida Ecosystems.* Forest Service General Technical Report SE-17. Asheville, NC: Southeastern Forest Experiment Station.

Wallace, P.M., Kent, D.M. and Rich, D.R. 1996. Responses of wetland tree species to hydrology and soils. Restoration Ecology, 4: 33-41.

Wanless, H.R., Parkinson, R.W. and Tedesco, L.P. 1994. Sea level control on stability of Everglades wetlands. In: Davis, S.M. and Ogden, J.C. eds. *Everglades: the Ecosystem and its Restoration.* Delray Beach, FL: St. Lucie Press, pp. 199-223.

Ward, D.B. ed. 1978. *Rare and Endangered Biota of Florida, Vol. 5: Plants*. Gainesville, FL: University Presses of Florida.

Weaver, P.L. 1989. Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. Interciencia, 14:181-192.

Webb, S.D. 1992. Historical biogeography. In: Myers, R.L. and Ewel, J.J. eds. *Ecosystems of Florida*. Orlando, FL: University of Central Florida Press, pp. 70-102.

West, R.C., Psuty, N.P. and Thom, B.G. 1969. *The Tabasco lowlands of southeastern Mexico.* Coastal Studies Series No. 27. Baton Rouge, LA: Louisiana State University Press.

Wunderlin, R.P. 1998. *Guide to the Vascular Plants of Florida*. Gainesville, FL: University Presses of Florida.

Appendix 1. Distribution and status of native, southern Florida woody species occurring in tree islands, by region and subregion. Subregions: Atlantic Coastal Ridge (CR); Big Cypress (BC); Florida Bay (FB); Florida Keys (FK); Lower Gulf Coast (LG); Shark Slough and adjacent prairies (SS); Taylor Slough/Southeast Saline Everglades (TS). Notes: C, cactus; P, palm; Temp, temperate; V, vine; * Little (1976); ** Ward (1978); *** Little (1978). Status: E, endangered; T, threatened (see Coile 1998). Plant nomenclature follows Wunderlin (1998).

Species	Notes	Interior				Coastal			Status
		CR	BC	SS	TS	FB	LG	FK	
Acacia choriophylla Benth.	*							●	E
A. farnesiana (L.) Willd.		●				●	●	●	
A. macracantha Willd.	*							●	
A. pinetorum F.J. Herm.		●							
Acanthocereus tetragonus (L.) Hummelinck	C					●	●		T
Acer rubrum L.	Temp		●						
Acoelorrhaphe wrightii (Griseb. and H. Wendl.) Becc.	P		●	●	●	●	●		T
Alvaradoa amorphoides Liebm.		●							E
Ampelopsis arborea (L.) Koehne	Temp V	●	●	●	●				
Amyris balsamifera L.	***							●	
A. elemifera L.		●	●			●	●	●	
Annona glabra L.		●	●	●	●		●	●	
Ardisia escallonioides Schldl. and Cham.		●	●	●	●	●	●	●	
Avicennia germinans (L.) L.						●	●	●	
Baccharis angustifolia Michx.		●							
B. glomeruliflora Pers.	Temp		●			●	●	●	
B. halimifolia L.	Temp	●	●	●	●	●	●	●	
Berchemia scandens (Hill) K. Koch	Temp V		●						
Bourreria cassinifolia (A. Rich.) Griseb.		●							E
B. ovata Miers		●						●	
B. succulenta Jacq.								●	E
Bursera simaruba (L.) Sarg.		●	●	●	●	●	●	●	
Byrsonima lucida (Mill.) DC.		●						●	T
Caesalpinia bonduc (L.) Roxb.	V			●		●	●	●	
C. crista L.	V							●	
Callicarpa americana L.	Temp	●						●	
Calyptranthes pallens Griseb.		●	●		●	●	●	●	T
C. zuzygium (L.) Sw.		●						●	E
Canella winterana (L.) Gaertn.						●	●	●	E
Capparis cynophallophora L.						●	●	●	
C. flexuosa L.						●	●	●	
Celtis laevigata Willd.	Temp	●	●	●					
Cephalanthus occidentalis L.	Temp	●	●	●	●				
Chiococca alba (L.) Hitchc.		●	●	●		●	●	●	
Chrysobalanus icaco L.			●	●	●	●	●	●	
Chrysophyllum oliviforme L.		●	●			●	●	●	T
Cissus verticillata (L.) Nicolson and C.E. Jarvis	V	●	●	●	●	●	●	●	
Citharexylum fruticosum L.		●	●					●	

Appendix I Distribution and status of species in tree islands, (Cont.)

Species	Notes	Interior				Coastal			Status
		CR	BC	SS	TS	FB	LG	FK	
Clusia rosea Jacq.								•	
Coccoloba diversifolia Jacq.		•	•	•	•	•	•	•	
C. uvifera (L.) L.					•	•	•	•	
Coccothrinax argentata (Jacq.) L.H. Bailey	P	•						•	T
Colubrina arborescens (Mill.) Sarg.			•			•	•		E
C. cubensis (Jacq.) Brongn.		•							E
C. elliptica (Sw.) Brizicky and W.L. Stern								•	E
Conocarpus erectus L.					•	•	•	•	
Cordia globosa (Jacq.) Kunth			•			•	•	•	E
C. sebestena L.						•	•	•	
Cornus foemina Mill.	Temp		•						
Crossopetalum rhacoma Crantz		•						•	E
Cupania glabra Sw.								•	E
Dalbergia brownii (Jacq.) Schinz	V			•	•	•	•	•	E
D. ecastaphyllum (L.) Taub.	V	•	•			•	•	•	
Diospyros virginiana L.	Temp	•	•						
Dodonaea viscosa (L.) Jacq.		•						•	
Drypetes diversifolia Krug and Urb.								•	E
D. lateriflora (Sw.) Krug and Urb.		•				•	•	•	T
Echites umbellata Jacq.	V	•						•	
Erithalis fruticosa L.						•	•	•	T
Erythrina herbacea L.	Temp	•	•			•	•		
Eugenia axillaris (Sw.) Willd.		•	•	•	•	•	•	•	
E. confusa DC.		•	•					•	E
E. foetida Pers.		•		•	•	•	•	•	
E. rhombea Urb								•	E
Exostema caribaeum (Jacq.) Schult.								•	E
Exothea paniculata (Juss.) T. Durand		•	•	•				•	
Ficus aurea Nutt.		•	•	•	•	•	•	•	
F. citrifolia Mill.		•	•	•	•		•	•	
Forestiera segregata (Jacq.) Krug and Urb.		•				•	•		
Genipa clusiifolia (Jacq.) Griseb.						•	•	•	
Gouania lupuloides (L.) Urb.	V	•						•	
Guaiacum sanctum L.								•	E
Guapira discolor (Spreng.) Little		•		•	•	•	•	•	
Guettarda elliptica Sw.		•						•	
G. scabra (L.) Vent.		•						•	
Gyminda latifolia (Sw.) Urb.								•	E
Gymnanthes lucida Sw.		•						•	
Hamelia patens Jacq.		•	•	•				•	
Harrisia simpsonii Britton and Rose	C					•	•	•	E
Hippocratea volubilis L.	V	•				•	•	•	
Hippomane mancinella L.					•	•	•	•	E
Hypelate trifoliata Sw.		•						•	E

Appendix I Distribution and status of species in tree islands, (Cont.)

Species	Notes	Interior				Coastal			Status
		CR	BC	SS	TS	FB	LG	FK	
Ilex cassine L.	Temp	•	•	•	•				
I. krugiana Loes.		•							E
Jacquinia keyensis Mez					•	•	•	•	T
Krugiodendron ferreum (Vahl) Urb.		•	•				•	•	
Laguncularia racemosa (L.) C.F. Gaertn.					•	•	•	•	
Lantana involucrata L.		•				•	•	•	
Licaria triandra (Sw.) Kosterm.[1]									E
Lycium carolinianum Walter					•	•	•	•	
Lysiloma latisiliquum (L.) Benth.		•	•	•	•			•	
Magnolia virginiana L.	Temp		•	•	•				
Manilkara bahamensis (Baker) H.J. Lam and B. Meeuse						•	•	•	T
Maytenus phyllanthoides Benth.						•	•	•	T
Metopium toxiferum (L.) Krug and Urb.		•	•	•	•	•	•	•	
Morinda royoc L.		•	•	•			•		
Morus rubra L.	Temp	•	•						
Myrcianthes fragrans (Sw.) McVaugh		•	•					•	T
Myrica cerifera L.	Temp	•	•	•	•		•	•	
Myrsine floridana A. DC.		•	•	•	•	•	•	•	
Nectandra coriacea (Sw.) Griseb.		•	•	•	•	•	•	•	
Opuntia stricta (Haw.) Haw.	C					•	•	•	T
Parthenocissus quinquefolia (L.) Planch.	Temp V	•	•	•	•				
Persea borbonia (L.) Spreng.	Temp	•	•	•	•				
P. palustris (Raf.) Sarg.	Temp		•						
Picramnia pentandra Sw.	*	•							E
Pilosocereus robinii (Lem.) Byles and G.D. Rowley	** C							•	E
Pinus elliottii Engelm.	Temp	•						•	
Piscidia piscipula (L.) Sarg.				•	•	•	•	•	
Pisonia aculeata L.	V					•	•	•	
P. rotundata Griseb.								•	E
Pithecellobium keyense Britton and Rose					•	•	•	•	T
P. unguis-cati (L.) Benth.						•	•	•	
Prunus myrtifolia (L.) Urb.		•							T
Pseudophoenix sargentii Sarg.	P							•	E
Psidium longipes (O. Berg) McVaugh		•						•	T
Psychotria ligustrifolia (Northr.) Millsp.								•	E
P. nervosa Sw.		•	•	•	•	•	•	•	
P. sulzneri Small		•	•	•					
Quercus laurifolia Michx.	Temp		•	•					
Q. nigra L.	Temp		•						
Q. virginiana Mill.	Temp	•	•	•	•			•	
Randia aculeata L.		•	•	•	•	•	•	•	
Reynosia septentrionalis Urb.								•	T

Appendix I Distribution and status of species in tree islands, (Cont.)

Species	Notes	Interior				Coastal			Status
		CR	BC	SS	TS	FB	LG	FK	
Rhabdadenia biflora (Jacq.) Mull. Arg.	V					●	●	●	
Rhizophora mangle L.					●	●	●	●	
Rhus copallina L.		●							
Roystonea regia (Kunth) O.F. Cook	P	●	●				●		E
Sabal palmetto (Walter) Schult. and Schult. f.	Temp P	●	●	●	●	●	●	●	
Salix caroliniana Michx.	Temp	●	●	●	●				
Sambucus canadensis L.	Temp		●	●	●				
Sapindus saponaria L.		●	●	●		●	●	●	
Savia bahamensis Britton		●							E
Schaefferia frutescens Jacq.								●	E
Schoepfia chrysophylloides (A. Rich.) Planch.		●	●					●	
Senna ligustrina (L.) H.S. Irwin and Barneby		●		●				●	
S. mexicana (Jacq.) H.S. Irwin and Barneby		●						●	
Sideroxylon celastrinum (Kunth) T.D. Penn.					●	●	●	●	
S. foetidissimum Jacq.		●	●	●	●	●	●	●	
S. reclinatum Michx.		●	●						
S. salicifolium (L.) Lam.		●	●	●	●	●	●	●	
Simarouba glauca DC.		●	●	●				●	
Smilax spp.	V	●	●	●	●	●	●	●	
Solanum bahamense L.								●	
S. donianum Walp.						●	●	●	T
S. erianthum D. Don		●	●	●				●	
Swietenia mahagoni (L.) Jacq.		●			●	●	●	●	E
Taxodium distichum (L.) Rich.	Temp		●	●	●				
Tetrazygia bicolor (Mill.) Cogn.		●						●	T
Thrinax morrissii H. Wendl.	P					●		●	E
T. radiata Schult. and Schult. f.	P					●	●	●	E
Tournefortia hirsutissima L.	V	●	●						
T. volubilis L.	V		●			●	●	●	
Toxicodendron radicans (L.) Kuntze	Temp V	●	●	●	●	●	●	●	
Trema lamarkianum (Schult.) Blume		●							E
T. micranthum (L.) Blume		●		●				●	
Turbina corymbosa (L.) Raf.	V			●					
Vallesia antillana Woodson						●	●	●	E
Viburnum obovatum Walter	Temp		●						
Vitis rotundifolia Michx.	Temp V	●	●	●	●	●	●	●	
Ximenia americana L.		●		●	●	●	●	●	E
Zanthoxylum coriaceum A. Rich.	*							●	E
Z. fagara (L.) Sarg.		●	●	●		●	●	●	
Z. flavum Vahl	**							●	E

[1] found only in coastal hammocks along Biscayne Bay