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SEA-LEVEL RISE AND COASTAL FOREST RETREAT ON THE WEST COAST OF FLORIDA, USA

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Abstract. We investigated patterns, rates, and mechanisms of forest replacement by salt marsh in relation to sea-level rise on the west coast of Florida, USA. The geomorphology of this region typifies that of low-lying, limestone coastlines considered highly susceptible to sea-level rise (e.g., much of the eastern Gulf of Mexico, the Yucatan Peninsula, and low-lying limestone islands throughout the world). This coast is microtidal, shallowly sloping, and has a rate of relative sea-level rise similar to that of eustatic rise. To determine patterns of forest change in relation to sea-level rise, we examined patterns of tree species zonation, tree recruitment, and tree mortality in relation to site elevation and tidal-flooding frequency. To reconstruct histories of forest change in relation to sea-level rise, we estimated age distributions of *Sabal palmetto*, the most widely distributed tree species at our site, relating age structures of stands to reconstructed histories of tidal flooding in the stands. Finally, to assess the relative roles of flooding stress (hypoxia), salt exposure, and competition from encroaching salt-marsh vegetation in the decline of forest stands, we examined patterns of soil redox potential, groundwater salinity, and density of halophytic vegetation among stands in different stages of decline.

Zonation among tree species was related to tidal-flooding frequency. For most trees, seedlings were absent from the most frequently flooded stands in which the species occurred. Reconstructed flooding histories of stands and age estimates for *S. palmetto* suggest that many decades elapse between cessation of regeneration and local elimination of a tree species. Even during the relatively short duration of the study (4 yr), however, composition of some stands changed in the direction predicted from species zonation and sea-level rise. Forest understory replacement by halophytic vegetation appeared to follow, rather than cause, failure of tree regeneration. Tidal flooding rarely produced severe reducing conditions in soil, but groundwater salinity was correlated with tidal-flooding frequency. Forest retreat in this system, therefore, involves the development of relict (non-regenerating) stands of different tree species at different flooding frequencies. Exposure to salt appears to be the major cause of tree regeneration failure, with flooding stress and interference from marsh vegetation playing minor or negligible roles. These interactions differ somewhat from those on deltaic coasts or coasts with high freshwater outflows, where flooding stress may play a larger role in regeneration failure, and from sandy coasts, where erosion may play a larger role in forest retreat. Regardless of the cause of tree regeneration failure, the development of relict stands may be a general forest response to sea-level rise.

Key words: flooding stress; Florida, USA, west coast; forest retreat, coastal; global warming and sea-level rise; groundwater salinity; limestone coasts; relict stands; *Sabal palmetto*; sea-level rise; seedling survival; soil redox potential.

INTRODUCTION

Although sea level has risen and fallen many times in the past (e.g., Cooke 1939), extensive human settlement of coastal areas and conservation concerns have spurred increased interest in the effects of sea-

level rise on the retreat inland of terrestrial ecosystems (e.g., Mehta and Cushman 1989, Wanless 1989, Peshchik et al. 1990, Harris and Cropper 1992). Due in part to anthropogenic contributions to global warming, the rate of sea-level rise is expected to increase (Warrick and Oerlemans 1990, Edgerton 1991, Wigley and Raper 1992, Titus and Narayanan 1995, Warrick et al. 1996). In addition, other predicted environmental changes, including changing rainfall patterns, changing frequencies of violent storms, and decreasing groundwater supplies of freshwater, may interact with sea-level rise to affect the rate of change in terrestrial veg-

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etation along coastlines (summarized in Schneider [1993]).

Much effort has been focused on responses of marsh vegetation to sea-level rise (e.g., Titus 1988, McKee and Mendelssohn 1989, Day et al. 1995), of mangrove forests to sea-level rise (e.g., Ellison and Stoddart 1991, Snedaker 1995), and of individual tree species to flooding and salinity, the major factors mediating forest response to sea-level rise (see Pezeshki et al. [1989, 1990], and references therein). A few studies have examined recent historical changes in coastal upland forest distribution in relation to sea-level rise (Clark 1986, Ross et al. 1994), linking patterns in stand decline to elevational gradients. Other studies have linked stand decline to elevated soil and groundwater salinity (Brinson et al. 1985, Ross et al. 1994), which are affected by drought, rainfall, and fresh groundwater flow as well as sea level. It has been postulated that soil flooding, resulting in low oxygen availability, reducing conditions, and perhaps H_2S formation, may contribute to the forest decline caused by sea-level rise (Salinas et al. 1986, Brinson et al. 1995). Competition from encroaching marsh vegetation may likewise contribute to the death of forests.

The mechanisms by which rising seas cause forest retreat may vary with geomorphological and hydrological characteristics of the coast. Although low-lying limestone coastlines and islands are considered susceptible to submergence by sea-level rise (Hendry 1993, Biljsma 1996), most research on the impacts of sea-level rise on coastal upland forest has been carried out on deltaic coastlines or sandy coastlines (see Williams et al. [1999] for review). On deltaic coasts with high freshwater outflows, such as the Mississippi Delta, rising seas may boost freshwater tables, eliminating tree regeneration through increased freshwater flooding (e.g., Baumann 1987, DeLaune et al. 1987, Conner and Day 1988). Zonation patterns in several coastal floodplain forests are consistent with gradients in flooding stress, with coastward stands being dominated by the most flood-tolerant tree species and abutting freshwater or brackish marsh, rather than salt marsh (White 1983, Doumlele et al. 1985, Pratt et al. 1989, Hackney and Yelverton 1990). Saltwater intrusion has been linked to stand decline in these forests (e.g., Penfound and Hathaway 1938, Platt and Brantley 1990, Allen 1992). However, this saltwater intrusion is often attributable to canal building, dredging, and other manipulations of water flows, making the role of sea-level rise difficult to discern (Penfound and Hathaway 1938, Hackney and Yelverton 1990). On sandy coasts, erosion and shifting sands, often caused by storms, are generally linked to forest retreat (e.g., Penfound and O'Neill 1934, Kurz 1942, Alexander and Crook 1974, Hayden et al. 1991).

The mechanisms by which rising seas affect forest retreat on stable coastlines with low freshwater outflows have not been well studied. On carbonate coastlines of the southeastern United States, forest zonation

correlates with both elevation and salinity of soil- and groundwater (Kurz and Wagner 1957, Ross et al. 1994). On such coasts, sea-level rise may affect forests primarily through increased salt exposure rather than through increased flooding stress or erosion, but conditions associated with initial stages of forest decline have not been described.

Regardless of the mechanism by which rising seas eliminate coastal forest, tree regeneration may be much more sensitive to rising seas than mature-tree survival. Increases in hydroperiod in the Mississippi Delta have eliminated tree regeneration in forest stands (DeLaune et al. 1987, Conner and Day 1988, Conner and Brody 1989). Failure of tree regeneration has also been linked to saltwater intrusion (e.g., Penfound and Hathaway 1938). On sandy coasts, catastrophic erosion may wash away entire forest stands. However, in the absence of catastrophic erosion, researchers have speculated that tree regeneration on sandy coasts is eliminated by seedling burial by shifting sands (Penfound and O'Neill 1934, Brown 1973). Because tolerance of flooding and salinity often increases with plant age (e.g., Briscoe 1957, Peterson and Bazzaz 1984, Conner and Askew 1992), and because shifting sands are known to impose restrictions on seedling recruitment (hence, the dominance of dunes by vegetatively reproducing species; e.g., Rainwell 1972, Van der Valk 1974), one would expect sea-level rise to eliminate forests primarily through impacts on seedling regeneration. Although failure of regeneration in coastal forest has frequently been noted (e.g., Brown 1973, Clark 1986, Conner and Day 1988), the generality and implications of this pattern have not been much explored. If coastal stands are relict (i.e., non-regenerating), then causes of canopy death at the coastal margin are relatively unimportant: these stands are effectively dead already. If canopy death lags regeneration failure, then aerial monitoring of coastal forest may fail to detect all but the very last stages of forest demise.

In this study we investigated patterns and causes of coastal forest retreat on a stable carbonate coastline distant from the local influence of large freshwater outflows. The study area was on the Big Bend coast of north and central Florida along the Gulf of Mexico. The Big Bend coast, which extends >250 km, is relatively undeveloped, supporting extensive salt marshes that abut vast coastal forests. The coast has been described as a "low-energy" or "zero-energy" coast (Tanner 1960). Tide gauge records over the past century indicate that rates of relative sea-level rise in this area (1.5–2.4 mm/yr) are among the lowest on the Gulf of Mexico, similar to estimates of global sea-level rise (1.0–2.0 mm/yr) (Penland and Ramsey 1990, Maul and Hanson 1991, Davis and Mitrovica 1996, Stumpf and Haines 1998), and much lower than rates along the coasts of Louisiana and Texas (>11 mm/yr in many locations), where subsidence is occurring. Despite low rates of relative sea-level rise, the death of stands of

Sabal palmetto (cabbage palm) along this coast has been attributed to effects of sea-level rise since the 1930s (Cooke 1939). Because this coast is relatively undeveloped, changes in forest communities may be more easily attributed to natural forces such as sea-level rise, rather than to local alterations in hydrology that may affect both flooding and salt exposure. Furthermore, the low topographic relief of the region (Hine and Belknap 1986), typical of low carbonate coastlines, makes it ideal for studying effects of sea-level rise on forests: small changes in sea level affect large land areas.

The goals of this study were two-fold: to describe the pattern and process of forest retreat on a low-lying carbonate coastline and to identify the primary mechanism by which sea-level rise initiates forest retreat there (i.e., through increased flooding or salinity). To determine whether patterns of forest decline were consistent with effects of sea-level rise, we examined the correlation between indicators of forest decline and site elevation or exposure to sea water. To assess the extent and role of tree regeneration failure in coastal forest retreat, we examined the distribution of non-regenerating stands of different tree species across gradients of elevation and seawater exposure, examining current stand structures and monitoring tree population dynamics for 4 yr. To describe the development and persistence of relict stands in the face of sea-level rise, we estimated the age structures of non-regenerating *Sabal palmetto* stands, comparing estimated ages of the youngest plants in each stand to reconstructed histories of tidal flooding in those stands and current relationships between regeneration success and tidal flooding. To evaluate the relative roles of flooding and salt exposure in sea-level-induced forest retreat, we examined patterns of soil redox potential and shallow-groundwater salinity across stands in different stages of decline. We evaluated the possibility that sea-level rise causes forest decline indirectly through competition from invading marsh vegetation by comparing the dynamics of marsh-vegetation encroachment to the dynamics of stand decline. Due to the "low-energy" tidal activity and the proximity of erosion-resistant bedrock to the soil surface, we considered it unlikely that sea-level rise affected forest retreat through erosion on this type of coast.

METHODS

Study site

This study was carried out near Turtle Creek in the Waccasassa Bay State Preserve (29°7' N, 82°47' W). The site was 5 km from the low-volume Waccasassa River, which has an average annual flow of 4–9 m³/s (Wolfe 1990) and ~50 km from the high-volume Suwannee River. The forest adjacent to the marsh was coastal hydric hammock (a wetland hardwood forest type; Vince et al. 1989), and the salt marsh was dom-

inated by black-tipped needlerush (*Juncus roemerianus* Scheele). In this area a thin layer of sandy soil lies over a gradually sloping, highly karstic, limestone platform that extends throughout the region (Wolfe 1990). Within the salt marsh, forest stands occupy topographic highs in the limestone. The coastline is microtidal with a mean tide range of ~0.8 m (Hine and Belknap 1986, Wolfe 1990). Storm surges exceeding 0.6 m above mean higher high water (MHHW) occur most years.

In the spring of 1992, one 400-m² plot was established on each of nine forested islands in the study area. Islands were selected based on extent of decline in their *Sabal palmetto* population. Three islands with apparently healthy palm populations (denoted "H" or "healthy") had high densities of large healthy palms and of small trunkless palms ("trunkless" here refers to palms in the establishment phase, during which the stem grows downward and increases in diameter for several years before emerging aboveground [Tomlinson 1990]). Three islands with palm stands denoted "I" or "intermediate" had large healthy palms but low densities of trunkless palms. Three islands with palm stands denoted "D" or "decadent" had high densities of standing dead palms and no trunkless palms. Stands that were reasonably accessible from a tidal creek, stratified with respect to distance from the Gulf of Mexico, were chosen. Three plots (H1, I1, and D1) were located farthest inland, and six plots (H2, H3, I2, I3, D2, and D3) were grouped closer to the Gulf (Fig. 1). Each plot was square (20 × 20 m), except D1 which, because of the shape of the island, was 40 × 10 m. In 1993, four additional plots were established farther inland: one (H0) on an island just inland from H1, and three (C1, C2, and C3) in coastal forest adjacent to the marsh/forest-island system. The plots in unbroken coastal forest, selected in a stratified random manner to be at least 100 m apart and at least 10 m from any access road, were ~180–400 m from the nearest salt-marsh boundary.

Elevation and tidal flooding of plots

Within each plot, elevation was determined with a laser transit (LB-2 Laser Beacon Model 3900, Laser Alignment, Inc., Grand Rapids, Michigan, USA) at 25 points in a 5 × 5 m grid. Elevations were related to two benchmarks: one 3 km inland from the study site, and one established by the U.S. Geological Survey near the edge of plot D3 (benchmark L270, Marth et al. 1995). Elevations were referenced to the North American Vertical Datum of 1988 (NAVD88; National Geodetic Survey 1996).

Tidal flooding of the plots established in 1992 was determined by measuring maximum weekly water depth at the edge of the salt marsh near each plot. Maximum water level was assessed from rings of floating powdered cork left on walls of perforated, transparent acrylic tubes. Readings were taken weekly (or every 2-wk, when poor weather prevented access) from

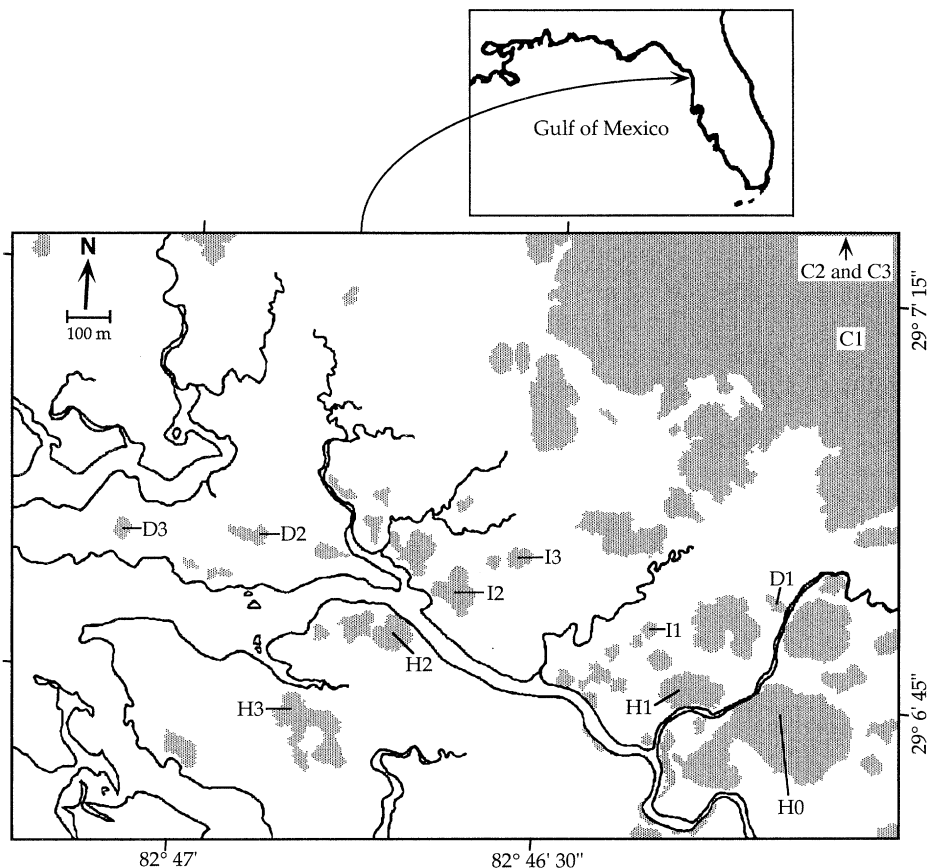


FIG. 1. Location of study plots on the west coast of Florida, USA, showing tidal creeks, marsh, and forest (stippled). Plots were established on forested islands in the salt marsh (healthy stands, H0–H3; intermediate stands, I1–I3; and decadent stands, D1–D3), and in unbroken coastal forest (C1–C3).

May 1992 through January 1993. Thirty-four readings were obtained at each plot during the 37-wk period. The number of census periods during which a plot flooded was determined from the depth of flooding at the edge of the salt marsh and the elevation difference between the acrylic tube location and the plot. Because of variation in elevation across a plot, a plot was considered flooded when more than half of the 25 measured elevations in the plot were under water.

Forest decline with tidal flooding: tree zonation, mortality, and recruitment

Stand structure, recruitment, and mortality were determined by tagging trees in each plot and censusing the plot annually for 3–4 yr. In the nine plots established in 1992 (censused four times) all trees and tree seedlings were tagged and censused. In the plots established in 1993 (censused three times) all large trees (palms with aboveground trunks and other trees >2 m tall) were censused. Smaller individuals were censused in 25 1-m² subplots, except in plot C3, where they were censused in a combination of 1 × 1-m plots and 5 × 5-m plots because of their low density.

Histories of Sabal palmetto recruitment and sea level

To determine if rates of forest decline were consistent with effects of sea-level rise, we compared histories of recruitment in *Sabal palmetto* to reconstructed histories of tidal flooding in the six most frequently flooded plots. Recruitment histories were estimated from age structures of the stands (see below). Attempts to analyze the recruitment history of *Juniperus virginiana* var. *silicicola* were abandoned due to the absence of distinct annual growth rings in the trunk. We expected most recruitment to have occurred when the flooding frequency was as low or lower than that in currently healthy stands, little recruitment to have occurred when the flooding frequency was similar to that in currently intermediate stands, and no recruitment to have occurred during periods with more frequent tidal flooding.

Histories of tidal flooding were reconstructed from data on tidal flooding in 1992 and changes in relative sea level over the past several decades. A tide gauge maintained by the U.S. National Oceanic and Atmospheric Administration at Cedar Key, Florida, ~23 km from the study site, provided records of sea level since 1939 and annual mean higher high water (MHHW, the

higher of the two high tides each day). The sea-level record was extended back to 1924 based on data from a tide gauge at Pensacola, Florida, and the relationship between recorded sea-level at the two sites.

To model tidal flooding, we used a model that described the number of weeks that a plot was flooded (May 1992–January 1993) as a function of median plot elevation and distance from the Gulf of Mexico. Distance along tidal creeks from the Gulf of Mexico was incorporated into the model, because elevation alone proved a poor predictor of tidal flooding, and because resistance to movement of tidal water from the Gulf inland should be, in part, related to the distance that the water must travel along tidal creeks. The distance along tidal creeks was estimated from aerial photographs. To recreate histories of tidal flooding in each plot, effective plot elevation (elevation above sea level) was modified for the years 1924–1994 based on the difference between MHHW in each year and MHHW in 1992. This approach assumes that the distance between each plot and the open Gulf has not changed over this period, an assumption supported by studies showing limited movement of the coastal boundary of salt marsh in this region over the past half century (Hine and Belknap 1986).

Conservative (minimum) age estimates were obtained for all palms from the number of leaf scars on aboveground trunks and leaf production rates, combined with an estimate of the duration of the trunkless phase for rapidly growing plants. Leaf scars were counted on the trunks of 29 trees distributed among five plots (H0, H1, I2, D2, and D3) and ranging in height from 0.2 to 4.9 m. Relationships between trunk height and leaf-scar number were used to estimate leaf-scar number on all other trees. The relationship for trees in H0 and H1 differed from that for trees in other plots, because small plants in H0 and H1 had longer internodes ($P < 0.001$, 1 SE of estimates 30 leaf scars for all regressions). Therefore, the equation used to estimate annual growth depended on the estimate of flooding frequency for that year. Leaf production rates were determined by painting the back of the midrib of the youngest leaf (at least half expanded) on each censused palm. Some palms just outside the plots were included to increase sample sizes. Leaves were marked in 1993, 1994, and 1995, and the number of leaves produced during the subsequent year was determined. For each plant, we averaged leaf production over 2–3 yr, using only data for plants that survived until 1996. Mean and maximum leaf production rates were calculated for plants in five height classes and different stages of stand decline. Minimum age of the aboveground trunk was calculated from the maximum leaf production rates encountered in each size/health class and a simulation model that allowed leaf production to vary as a function of plant size and plot flooding, incorporating historical changes in plot flooding.

Sabal palmetto has an establishment phase during

which the stem apex grows downward before turning back toward the soil surface. The belowground portion of the stem is difficult to age; older parts disintegrate and adventitious roots obliterate leaf scars. Estimates for the duration of this phase were based on a matrix model that predicted length of the establishment phase from rates of increase in leaf size of small plants near plots C1, C2, and C3 (McPherson and Williams 1996). Similar data from more frequently flooded plots (H2 and H3) were used to confirm model parameters. The median duration of the establishment phase for the most rapidly growing 1% of the population was estimated as 32 yr.

Changes in understory composition in relation to forest decline

Changes in understory vegetation that were associated with forest decline were determined by identifying all vascular plant species in all plots. Species in the 10 island plots were identified during four censuses in different seasons of 1992. In the three plots in unbroken coastal forest (C1, C2, and C3), a cursory survey was conducted in 1992, before monitoring of tree populations began, and a complete survey was conducted in April 1996. For the purposes of this study, *Myrica cerifera*, *Ilex vomitoria*, and shrubs of lesser stature were considered shrubs and part of the understory, rather than trees.

To describe how the relative abundances of different understory species varied among plots, 25 1-m² subplots were established in each plot in 1994. The number of subplots in which each species occurred was recorded.

Soil redox potential in relation to forest decline

To determine the relationship between forest decline and reducing conditions in the top 10 cm of soil, where tree seedlings are most likely to be affected, soil redox potential was measured on the nine islands with plots established in 1992. We examined whether soil redox potential was lower in declining stands than in healthy stands and whether it was higher in centers of forest stands than at the marshward limit of trees on an island. Measurements were taken over a 14-mo period (June 1992 to August 1993).

Redox potential was measured with platinum electrodes constructed by welding 1.5 cm of 1-mm-diameter platinum wire to insulated, solid copper wire and sealing it with epoxy resin so that only bare platinum wire was in contact with soil (DeLaune et al. 1983). The reference electrode was a calomel electrode. The potential across the electrodes was read with an Orion model 250A pH/ISE meter (Orion, Boston, Massachusetts, USA) and corrected for temperature. No correction was made for pH due to the uniformity in pH among sites (range: 7.2–7.9).

Soil redox potential was measured at two sites on each island: the center of the island and at the edge,

just beyond the outermost rim of trees. Because of substantial variability among microsites at each location, 15 platinum electrodes were randomly placed at each site. Electrodes were inserted in the soil to a depth of 10.0 cm (or less where soil was shallower than 10 cm) and left in place for ~2 h before they were read. These measurements were made on several islands each month, but, because of the difficulty in getting from island to island, complete censuses with measurements from all nine islands were made only six times. Both center and edge were measured at the same time on each island. To analyze the variation in soil redox potential with stand health and position (center vs. edge), data from the six complete censuses were used. Means of the 15 probe measurements taken at each site on each date were subjected to a repeated-measures ANOVA. Additionally, at each census, the significance of a difference in soil redox potential between the center and edge of a stand was determined by subjecting individual probe readings (15 at each site) to a Student's *t* test.

Because transit time between islands necessitated measuring redox on different islands at different times of day (involving different soil temperatures, different tidal stages, etc.), we investigated short-term changes in redox potential over time. During several censuses, redox potential was measured twice at a site during a 24–48 h period. To determine if there was change, the two sets of probe readings taken at a site during such a census were compared with a Student's *t* test.

Groundwater salinity in relation to stand decline

Groundwater salinity was monitored in wells in paired healthy (H1) and decadent (D1) stands and in the tidal creek between them. The well at D1 was 1 m deep; soil surface elevation was 0.54 m NAVD. The well at H1 was 1.4 m deep; surface elevation was 1.01 m NAVD. Wells consisted of polyvinyl-chloride casing with 0.254-mm slotted screen. The void outside the casing was filled with sand to 0.3 m below ground level and the remainder with bentonite clay to slope away from the well base.

Water level in wells was measured using a Druck Model PDCR 950 strain-gauge pressure transducer (Druck, Inc., New Fairfield, Connecticut, USA), and temperature and conductivity were determined using a YSI series 400 thermistor (YSI, Inc., Yellow Springs, Ohio, USA) and a USGS Minimonitor type 4 electrode sensor (Ficken and Scott 1988), respectively. Specific conductance (in millisiemens per centimeter [mS/cm]) was calculated from temperature and conductivity and recorded at 15-min intervals by a data logger (model CR10, Campbell Scientific, Logan, Utah, USA). The pressure transducer was mounted immediately above the temperature and conductivity sensors, ~0.23 m above the bottoms of the wells. Rainfall, salinity in the tidal creek, and water level in the tidal creek were monitored with a tipping-bucket rain gauge (Texas

Electronics, Dallas, Texas, USA), conductivity sensors, as described above, and a Metritape depth sensor (Metritape, Inc., Littleton, Massachusetts, USA), respectively, connected to a data logger (21X, Campbell Scientific, Utah, USA).

To examine the correlation between groundwater salinity and gradients in forest decline and tidal flooding frequency, groundwater was sampled from shallow wells in or adjacent to each of the nine original island plots (H1, H2, H3, I1, I2, I3, D1, D2, and D3) in September 1997. Water from the top 10 cm of the water table was sampled and filtered through fast filter paper. Specific conductance of the water was measured with an HI 8733 conductivity meter (Hanna Instruments, Woonsocket, Rhode Island, USA).

RESULTS

Elevation and flooding of plots

The range of elevations measured in the study plots was <1 m (0.384–1.339 m NAVD88); median plot elevations ranged from 0.522 m to 1.100 m NAVD88. Estimates of elevation made from two different benchmarks fell within 4 mm of each other. The lower elevations measured were below the level of MHHW (mean higher high water—the higher of the two tides each day) recorded at Cedar Key, Florida, during the study (MHHW > 0.48 m NAVD88). In general, plots at lower elevation flooded more frequently than plots at higher elevation. However, inland plots (I1 and D1) flooded less frequently than plots at similar or higher elevations that were closer to the Gulf of Mexico (Table 1).

Forest decline with tidal flooding: tree zonation, mortality, and recruitment

Frequency of tidal flooding in the nine original island plots correlated well with both the number of standing dead palms in a plot ($r = 0.91$, $df = 7$, $P < 0.01$) and the number of trunkless palms per plot ($r = -0.89$, $df = 7$, $P < 0.01$; data for trunkless palms log-transformed ($\log_{10}(x + 1)$). The density of live palms with above-ground trunks did not change significantly across this gradient ($r = -0.36$, $df = 7$, $P = 0.34$).

The number of tree species in plots was negatively correlated with frequency of tidal flooding (Spearman rank correlation coefficient = 0.92, $df = 11$, $P < 0.001$; Table 2). *Sabal palmetto* and *Juniperus virginiana* var. *silicicola* were the only tree species in the six most frequently flooded plots. *Sabal* was the only living tree in the most frequently flooded plot, although dead stumps of *Juniperus* were present. *Quercus virginiana* and *Celtis laevigata* occurred in less frequently flooded island plots. *Morus rubra* and *Persea palustris* were represented in plot H1 by one and two individuals <2 m tall, respectively. Plots in unbroken coastal forest (plots C1, C2, and C3) supported all of these species plus an additional 10 tree species.

TABLE 1. Palm stand structure and characteristics of the study sites on the west coast of Florida (USA) during a 37-wk census period (May 1992–January 1993). Data are arranged in order of decreasing frequency of flooding.

Plot†	<i>Sabal palmetto</i> trees (no.)‡			Elevation (m NAVD)§		Flooding (no. of weeks)
	Standing dead	Live with trunks	Trunkless	Median	Range	
D2	21	18	0	0.58	0.38–0.74	27
D3	16	10	0	0.63	0.56–0.66	26
D1	11	23	0	0.52	0.46–0.60	18
I2	6	34	1	0.67	0.63–0.72	16
I1	6	8	9	0.60	0.39–0.70	13
I3	6	24	3	0.66	0.55–0.81	10
H2	2	28	98	0.78	0.64–1.02	8
H3	1	30	62	0.80	0.71–0.92	6
H1	4	19	238	0.93	0.83–1.05	1
H0	1	19	1040	0.96	0.87–1.10	(1)
C1	0	12	1088	1.10	1.01–1.30	(1)
C2	1	14	3010	1.09	0.85–1.34	(1)
C3	6	24	308	0.69	0.60–1.03	(1)

† Plots were classified based on the status of the palm stand as decadent (D), intermediate (I), or healthy (H); plots in unbroken coastal forest were denoted “C.”

‡ Number during the initial census (1992 or 1993).

§ Elevations based on 25 measurements taken within each plot.

|| Plots H0, C1, C2, and C3 were established in 1993, after the completion of the tidal-flooding study. Because these plots were at higher elevations or farther inland than H1, the flooding frequency they experience was assumed to be equal to or less than that of H1. A plot was considered flooded when more than half of the 25 measured elevations in the plot were under water.

Trees died during the course of the study in several of the island plots (Fig. 2), changing community composition in the direction suggested by tree species zonation (Table 2). *Juniperus* was lost from two of the four most frequently flooded stands, leaving *Sabal* as the only tree species in three plots (Fig. 2). *Morus rubra* was lost from plot H1, leaving only one small *Persea*

palustris and the four tree species found in more frequently flooded plots. No change in tree species composition occurred in the highest island plot (H0) or in the three unbroken forest plots (C1, C2, and C3), but these plots were monitored for only 2 yr.

High mortality among large (>2 m tall) *Juniperus* trees in island plots (Fig. 2) resulted primarily from

TABLE 2. Zonation of tree species, by plot, indicating flooding regimes under which regenerating stands (S) and relict stands (X) occurred. The no. of weeks each plot was flooded (May 1992–January 1993) is given in parentheses below each plot; the common name for each tree species is given in parentheses after the scientific name of each tree species.

Tree species	C1 (1)	C2 (1)	C3 (1)	H0 (1)	H1 (1)	H3 (6)	H2 (8)	I3 (10)	I1 (13)	I2 (16)	D1 (18)	D3 (26)	D2 (27)
<i>Sabal palmetto</i> (Walt.) Lodd. ex Schult. (cabbage palm)	S	S	S	S	S	S	S	S	S	X	X	X	X
<i>Juniperus virginiana</i> L. var. <i>silicicola</i> (Small) Silba (southern red cedar)†	S	S	S	S	S	[S]	[S]	X	X	X	X	X	...
<i>Quercus virginiana</i> L. (live oak)‡	[X]	[X]	[X]	[X]	S	X	X
<i>Celtis laevigata</i> Willd. (sugarberry)	X	X	S	X	X	X
<i>Persea palustris</i> (Raf.) Sarg. (red bay)	X	X	X
<i>Morus rubra</i> L. (red mulberry)	X	X
<i>Quercus laurifolia</i> Michx. (swamp laurel oak)‡	[X]	...	[X]	[X]
<i>Pinus taeda</i> L. (loblolly pine)	S	...	S
<i>Acer floridanum</i> (Chapm.) Pax. (Florida maple)	S	S
<i>Ulmus alata</i> Michx. (winged elm)	...	S	S
<i>Ulmus crassifolia</i> Nutt. (cedar elm)	...	S
<i>Ulmus americana</i> L. (American elm)	S
<i>Ptelea trifoliata</i> L. (common hoptree)	...	S
<i>Diospyros virginiana</i> L. (common persimmon)	X	...	X
<i>Rhus copalina</i> L. (winged sumac)	X	X
<i>Fraxinus caroliniana</i> Mill. (Carolina ash)	...	X
<i>Gleditsia tricanthos</i> L. (honey-locust)	X

Note: Tree species are noted as present if they occurred in a stand during the initial survey (1992 for nine most frequently flooded plots, 1993 for remaining four plots). “Regenerating stands” are defined as those in which new seedlings appeared during the study.

† In plots denoted “[S],” the seedlings that appeared in 1993 and 1994 did not survive to 1995.

‡ Small plants that may have been seedlings occurred in plots denoted “[X].” They were not censused due to the difficulty of distinguishing vegetative offshoots from seedlings. Confirmed seedlings occurred in H1.

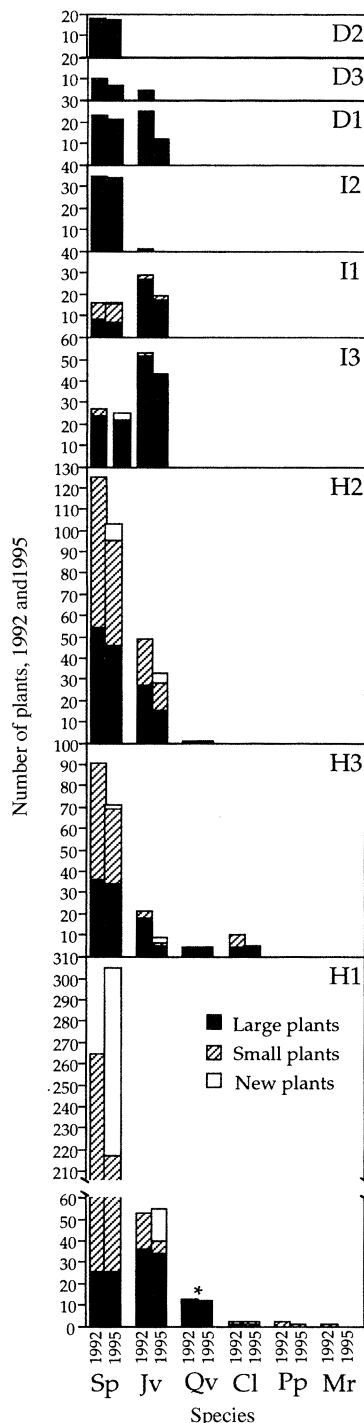


FIG. 2. Change in tree species composition over 3 yr in the nine most frequently flooded plots. Changes in number of trees between 1992 and 1995 show survival of large trees (>2 m tall or, for *Sabal palmetto*, having aboveground trunks), survival of smaller individuals, and recruitment of seedlings (open bars). Species key: Sp = *Sabal palmetto*, Jv = *Juniperus virginiana* var. *silicicola*, Qv = *Quercus virginiana*, Cl = *Celtis laevigata*, Pp = *Persea palustris*, and Mr = *Morus rubra*. The asterisk denotes that recruitment of *Q. virginiana* was not determined due to the difficulty in distinguishing seedlings from vegetative offshoots.

the effects of a violent storm that struck the study site in March 1993. This storm brought high winds, gusting to 44 m/s (85 knots) at Cedar Key, Florida (Goodbred and Hine 1995), and a storm surge >1.7 m above MHHW (mean higher high water) at our study site. However, the elimination of this species from lower plots could not be attributed solely to this storm: three of the four trees that died in plot D3 died within the first year of the study, prior to the storm.

Tree regeneration varied with frequency of tidal flooding. New seedlings of *Sabal* were observed in two of the plots classified as "intermediate" (I1 and I3, Fig. 2), but at very low densities. One seedling appeared in I1 and survived through the end of the study. Of the 10 seedlings that emerged in I3, only three survived through 1995, and by 1996 all had died. Although plots H2 and H3 were classified as "healthy" palm stands, based on high densities of "trunkless" palms, seedling establishment was relatively low during the 3 yr of study (Fig. 2). Recruitment was much higher in plots less frequently flooded by tidal waters (48–544 new seedlings by 1995 in plots H1, H0, C1, C2, and C3). The pattern for *Juniperus* was similar, with a few transient seedlings appearing in H2 and H3, and much higher numbers appearing in less frequently flooded sites. Although most new seedlings of *Juniperus* observed during the study died within the first year, plots H0, C1, C2, and C3 supported many small individuals (12–1232 individuals <2 m tall per plot) with a high survival rate (over 80% of those identified in 1993 survived to 1995).

For the four tree species that occurred in island plots (*Sabal*, *Juniperus*, *Quercus*, and *Celtis*), mature individuals existed in more frequently flooded sites than did their seedlings, suggesting that regeneration failed before mature individuals were eliminated (Table 2). The flooding frequency at which regeneration failure occurred differed among species. Seedlings of *Sabal* emerged in plots that flooded during as many as 13 wk of the 37-wk tidal flooding study (Table 2). Seedlings of *Juniperus* were encountered in plots that flooded up to 8 times, seedlings of *Quercus* existed in plots that flooded once or less, and seedlings of *Celtis* were encountered only in unbroken coastal forest (plot C3). Zonation among these species was marked, therefore, by the formation of relict stands of each species at the coastward edge of its distribution. Species zones overlapped so that relict stands of some species occurred within healthy, regenerating stands of other species.

Histories of *Sabal* palmetto recruitment and sea level

The equation used to reconstruct the history of tidal flooding (number of weeks with flooding during May–January) in the study plots was

Flooding frequency_{*i*}

$$= 41.5 - 75.1 \times (\text{elevation} + \text{MHHW}_{1992} - \text{MHHW}_i) + 50.4/\text{distance} \quad (1)$$

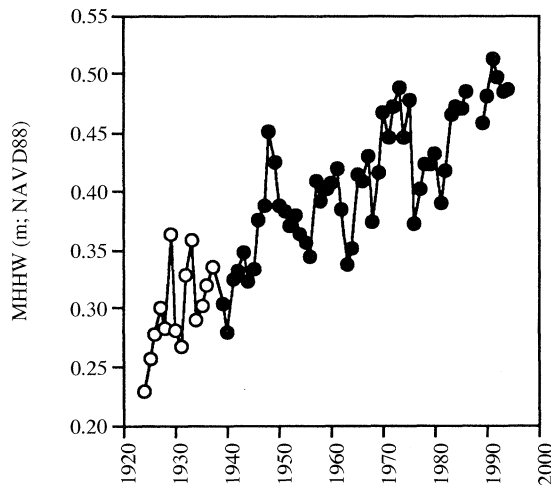


FIG. 3. Record of mean higher high water (MHHW) from Cedar Key, Florida, USA. Open symbols indicate estimates from tide records at Pensacola, Florida.

where “*i*” is the year, “elevation” indicates median plot elevation (m NAVD88), MHHW is mean higher high water for the year at Cedar Key, Florida (in meters), and “distance” is the distance (in kilometers) along tidal creeks from the Gulf of Mexico to the point closest to the forested island. This equation, based on tidal-flooding data from 1992, described tidal flooding in the eight most frequently flooded plots ($r^2 = 0.953$, $n = 8$, $P < 0.001$, 1 SE of estimate = 1.7). Flooding in higher plots was not well described by this equation, because the rare storm tides that flood these plots generally flood a large elevational range.

Mean relative sea level at Cedar Key, Florida, rose an average of 1.5 mm/yr between 1939 and 1994, a rate consistent with most estimates of global sea-level rise (Warrick and Oerlemans 1990, Davis and Mitrovica 1996). MHHW rose at a higher rate (~ 2.8 mm/yr, Fig. 3, Stumpf and Haines 1998). Sea level and MHHW during 1991 and 1992 were the highest on record.

Hindcasts of tidal flooding revealed that flooding frequency had been high enough to prevent palm regeneration in two decadent stands (D2 and D3) for all but a few brief periods during the past 50 yr (Fig. 4). Although it had been ~ 70 yr since plot D3 experienced flooding frequencies as low as those found today in currently healthy stands, the youngest palm there was even older (Fig. 4). Periods with such low flooding frequencies occurred as late as 1931 in plot D2, 1976 in plot D1, and 1982 in all plots currently classified as intermediate. The estimated age of the youngest palm in each plot correlated poorly with the number of years that had passed since flooding frequency was characteristic of healthy stands ($r = 0.68$, $n = 6$, $P = 0.07$). However, minimum-age estimates revealed that all *Sabal* in four of the six most frequently flooded plots (D3, D1, I2, and I3) established during periods when tidal flooding was either similar to that in currently healthy

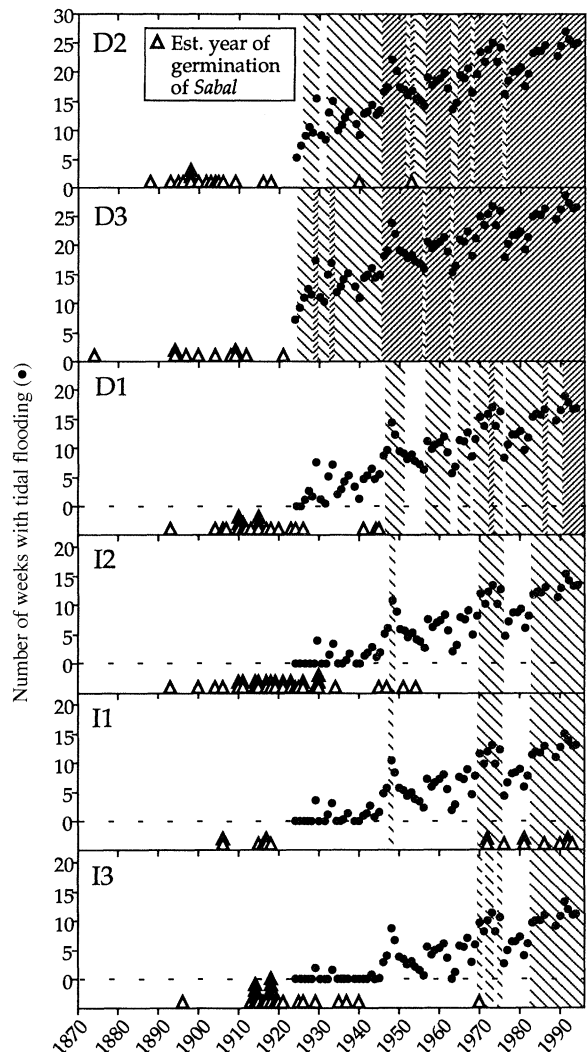


FIG. 4. Modeled history of flooding and palm recruitment at the six most frequently flooded plots. Heavy shading indicates years in which flooding frequency equaled or exceeded that experienced by “decadent” stands in 1992. Light shading indicates years in which flooding frequency was similar to that experienced by “intermediate” stands in 1992. Triangles indicate the estimated year that each *Sabal palmetto* tree in the stand germinated, based on minimum age estimates; actual germination dates may have been decades earlier (see *Methods: Histories of Sabal palmetto recruitment and sea level*).

stands or fluctuated between frequencies characteristic of healthy stands and of intermediate stands (Fig. 4). Based on the amplitude of annual sea-level variation and long-term sea-level records from Key West (1846–1992, Maul and Martin 1993), flooding in plots D2 and D3 probably fluctuated between that characteristic of healthy stands and that characteristic of intermediate stands between ca. 1890 and 1924, the beginning of the flooding record shown in Fig. 4.

Two plants in D2 and several in I1 appear to have established later than expected, based on the current

TABLE 3. Number of new leaves per plant per year (mean and range) for different size classes of *Sabal palmetto* in the 13 study sites on the west coast of Florida, USA. Leaf production data are means with the range in parentheses.

Stem height	Plots				
	D1, D2, and D3	I1, I2, and I3	H2 and H3	H1 and H0	C1, C2, and C3
0–0.5 m	2.2 (1.5–3.2)	2.3 (1.9–2.8)	4.4 (2.3–6.0)	2.1 (1.2–3.0)	3.0 (2.0–3.6)
>0.5–1.0 m	2.4 (1.9–3.4)	3.0 (2.2–4.0)	4.7 (2.5–7.7)	2.7 (2.0–3.3)	3.4 (2.0–5.7)
>1.0–2.0 m	3.0 (1.9–4.0)	3.9 (2.8–4.9)	6.3 (4.6–7.7)	3.2 (2.1–4.0)	3.8 (3.3–4.5)
>2.0–4.0 m	4.6 (2.8–6.5)	4.5 (3.4–5.9)	6.1 (2.8–8.3)	4.7 (3.6–5.7)	4.2 (3.6–5.0)
>4.0 m	5.2 (3.7–6.2)	5.3 (3.4–7.4)	6.4 (3.7–9.7)	5.7 (4.6–7.0)	5.7 (2.7–8.5)

Notes: Forested islands were categorized based on the extent of decline in their *S. palmetto* population: “H” stands appeared healthy, with high density of large healthy palms and small trunkless palms (i.e., palms in the establishment phase); “I” stands had large healthy palms but low densities of trunkless palms; “D” denotes decadent stands, with high density of standing dead palms and no trunkless palms. “C” plots were in coastal forest adjacent to the marsh/forest island system. Data for healthy stands in which *Juniperus virginiana* sustained high mortality in the March 1993 storm (H2 and H3) are separated from data for less frequently flooded and less damaged healthy stands (H1 and H0).

relationship between palm establishment and tidal flooding. These results may reflect the influence of local freshwater supplies on rates of stand decline (see *Discussion*) or simply an underestimation of palm ages. The duration of the establishment phase may be longer by decades than that calculated based on the fastest growing 1% of the population (McPherson and Williams 1996), and the age of the aboveground stem would be ~40% greater than that calculated had we used mean leaf production rates to estimate age, rather than maximum leaf production rates (Table 3).

Changes in understory composition in relation to forest decline

A change in understory composition accompanied forest decline at the seaward margin of coastal forest. Whereas the tree species in frequently flooded plots were a subset of those occurring in adjacent coastal forest, the understory experienced complete species turnover (Appendix). Only two species, the epiphytes *Tillandsia recurvata* and *T. usneoides*, were widespread. Understory species characteristic of decadent forest stands were halophytic marsh species. Only one small individual of one of these (*Iva frutescens*) was found in plots in unbroken coastal forest.

Halophytic understory species appeared in the most frequently flooded “healthy” stands (Appendix). Because this pattern suggests that interference from marsh vegetation (competitive or otherwise) might play a role in the decline of tree stands, we examined the relationship between tree regeneration and the abundance of halophytic species. Our initial surveys revealed that seedling densities of *Sabal* and *Juniperus* were low in H2 and H3, indicating that population decline was already underway prior to our study and prior to the storm of March 1993 (Fig. 5). Understory species characteristic of decadent stands were present in H2 and H3, but were present at such low frequencies that interference from these species could not be considered the primary cause of poor tree regeneration (Fig. 5).

Soil redox potentials in relation to forest decline

Soil redox potentials in the centers of forested islands remained fairly high during the year of monitoring (Fig. 6). Average redox potential within a stand generally fell between 250 and 450 mV, although a few measurements made during the summer and fall were much lower. Soil redox potentials at the edges of forest stands were consistently high during the winter, but lower (usually <250 mV) during the summer (Fig. 6). Periods of anoxia and periodic denitrification probably occurred in these soils, but conditions were not sufficiently reducing to cause reduction of iron or production of H_2S (about <120 and –80 mV, respectively; Ponnampertuma 1972, Marschner 1986).

Contrary to our expectations, soil redox potential did not differ among stands in different stages of decline (Table 4). Over the six complete censuses for which data were analyzed, soil redox potentials in healthy stands showed a slight tendency to be higher than those in decadent stands ($P = 0.081$, Table 4). However, redox potentials during other censuses were often lower in healthy stands than in stands in more advanced stages of decline (Fig. 6). Unusually low redox potentials were measured in the centers of healthy stands during September and October of 1992 (Fig. 6). The causes of these low redox potentials are not completely clear. The measurements in October were taken 1 wk after the only tide to flood all islands completely during 1992, but the measurements in September were not associated with particularly high tides. These redox measurements were not part of a complete data set and therefore were not analyzed statistically. They suggest, however, that soil redox potential in apparently healthy stands may sometimes be much lower than in declining stands.

Soil redox potential was significantly higher at the centers of stands than at the edges (Table 4). Of the 140 times that soil redox potential was measured, it differed between the centers and edges of stands 88 times (t test, $P < 0.05$). Redox potential was lower in the center than on the edge only twice: in one healthy

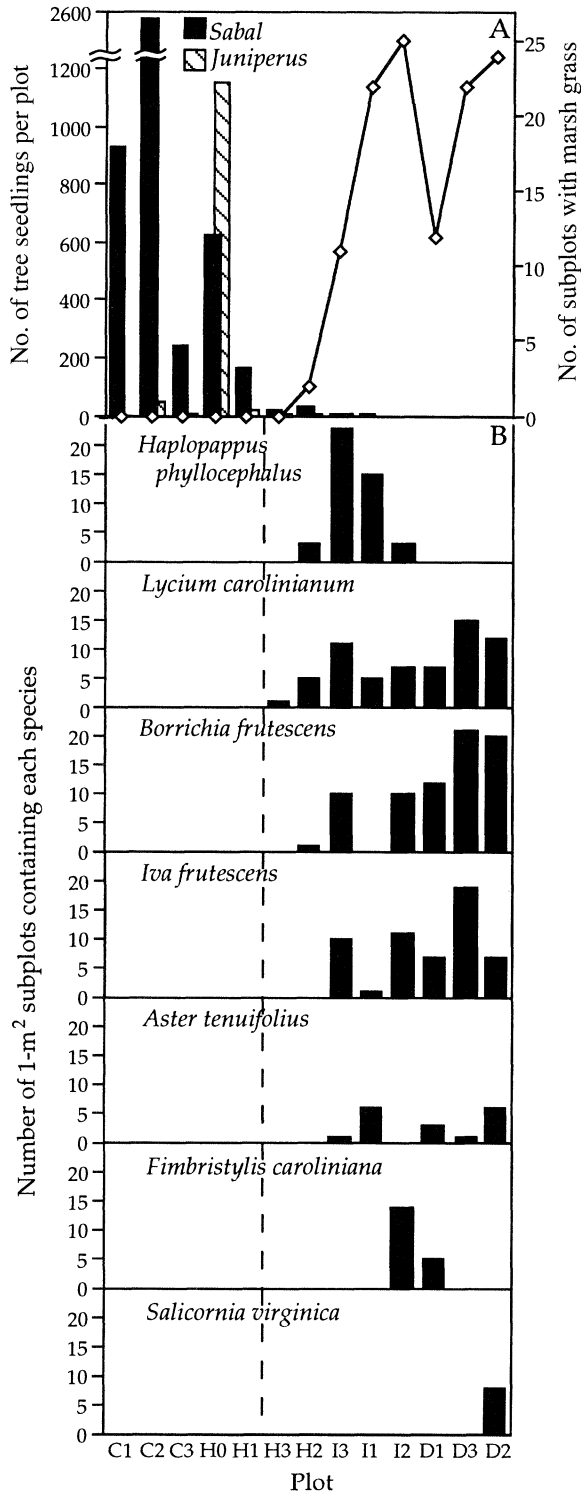


FIG. 5. Tree seedling density and distribution of understory species from decadent stands. Plots are arranged in order of increasing tidal-flooding frequency from left to right. Panel A indicates the density of *Sabal* with undivided leaves 9 mm wide (~1–4 yr old; McPherson and Williams 1996) and *Juniperus* <0.5 m tall encountered during initial plot censuses (1992–1993) and the number of 1-m² subplots (◇) in which “marsh grass,” including *Distichlis spicata*, *Spartina patens*,

stand and one intermediate stand on 3 August 1993. The intermediate stand was flooded to a depth of ~5 cm at the time of measurement, and, although standing water was not noted in the healthy stand, elevational differences between the two stands suggest that tidal waters could have been only 5–6 cm under the soil surface near the center of the stand. Thus, although redox potential did not appear to decline with stand health when existing forest stands were compared, it was often lower just outside the perimeter of trees on an island, a zone formerly occupied by forest as indicated by the presence of numerous stumps.

Substantial changes in redox potential sometimes occurred in less than a day. Of the 26 sets of repeated measurements taken in the centers of stands, soil redox potential changed significantly (*t* test, $P < 0.05$) nine times, changing 117–169 mV within a 26-h period. Soil redox potentials on stand edges were more stable; of 26 sets of repeated measurements, significant changes were detected only twice. Prolonged high tides due to onshore winds occurred on 19 May and 2–3 August, which may account for the changes observed then. On other dates, however, changes could not be related to changing temperature (temperature changes between measurements were generally <3°C), differences in tide conditions, or length of time between the two measurements. No simple relationship between tidal stage and soil redox potential could be discerned.

Groundwater salinity in relation to stand decline

The conductivity of groundwater measured in September 1997 ranged from 6 mS/cm (~4 g sea salt/L) in H1, the healthiest stand, to 32 mS/cm (~23 g sea salt/L) in D3, a stand in the final stages of forest loss. Groundwater conductivity in H1 was substantially lower than in H2 and H3 (19–22 mS/cm or ~13–15 g sea salt/L), stands that were initially classified as “healthy” but subsequently found to have low recruitment rates of both *Sabal* and *Juniperus*. Groundwater conductivity was positively correlated with relative frequency of tidal flooding as determined in 1992–1993 ($R = 0.82$, $df = 7$, $P < 0.01$, Fig. 7).

Groundwater of the decadent stand that was continuously monitored (D1) remained more saline than that of the monitored healthy stand (H1) throughout the year (1994–1995; Fig. 8A). Salinity in the tidal creek changed with the ebb and flow of the tide, and was highly variable. Rainfall caused water level in the healthy stand to rise rapidly (Fig. 8B and C) and pro-

←

and *S. spartinae*, was found during surveys of understory vegetation in 1994. Panel B indicates the frequency of other species found in decadent stands. Species that did not occur in at least two 1-m² subplots in each decadent stand are not shown. The vertical dashed line indicates the point along this gradient at which regeneration of *Sabal palmetto* falls to a low level.

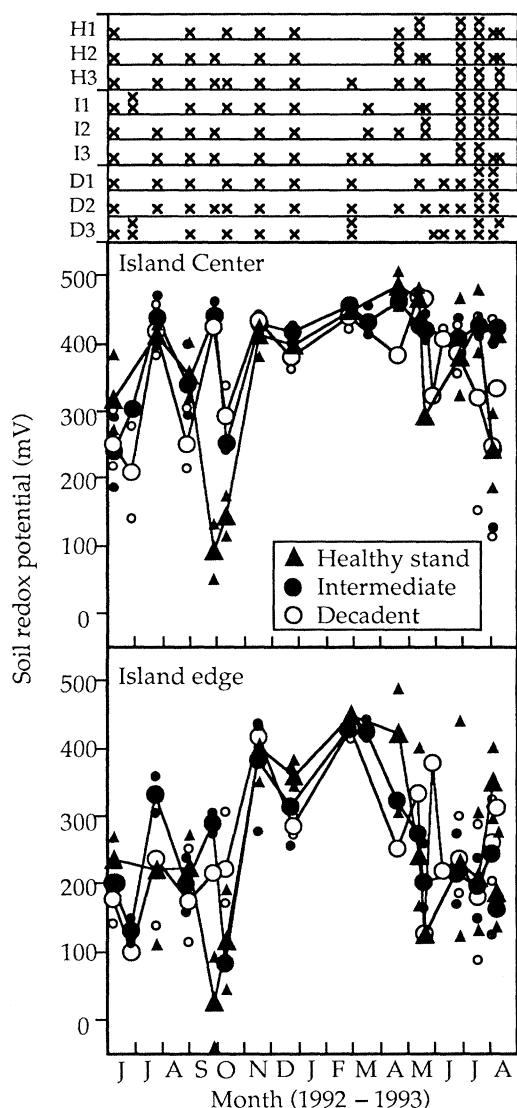


FIG. 6. Patterns in soil redox potential over a 14-mo period. The top panel indicates the dates (X) on which soil redox potential in different stands was measured. Two X's at a date indicates that soil redox potential was measured twice at this site within a 2-d period. The bottom two panels show mean redox potential (large symbols) measured in centers and at edges of stands in different stages of decline. Smaller symbols indicate the range of mean soil redox potentials measured at different sites or different times of day (15 measurements taken simultaneously at each site).

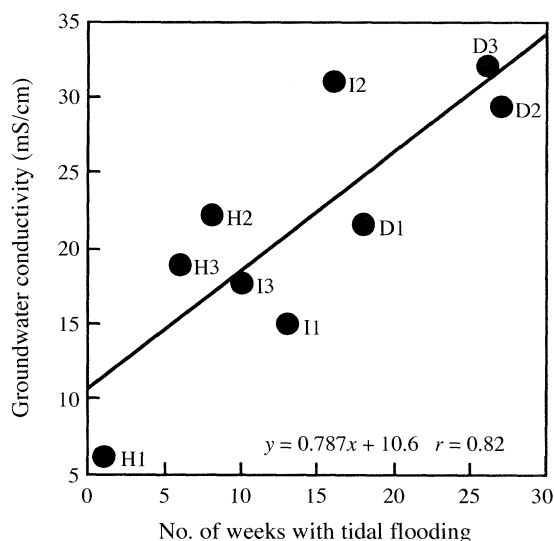


FIG. 7. Conductivity of groundwater vs. tidal-flooding frequency in forested stands. Conductivity of groundwater was sampled in September 1997. The relative frequency of tidal flooding was assessed as the number of weeks stands were flooded during a 37-wk census period (May 1992–January 1993).

duced sustained reductions in groundwater salinity (Fig. 8A). Salinity in the tidal creek often fell at the same time, reflecting basin-wide rainfall. However, local rainfall occasionally caused groundwater salinity in the healthy stand to drop without a concurrent change in salinity of the tidal creek (e.g., mid-April 1994, Fig. 8A). Groundwater in the decadent stand was less responsive to rainfall.

The water level at both D1 and H1 displayed a fortnightly oscillation, reflecting spring and neap tides, and damped short-term fluctuations, reflecting influences of the semidiurnal tides (Fig. 8B). Groundwater levels at D1 displayed only damped oscillations, despite tidal flooding of the stand during most spring tides (data not shown). In contrast, the single tide to flood the healthy stand during the monitoring period (2 October 1994) caused water levels to rise and salinity to increase in the well there (Fig. 8B). Thus, the connection between surface hydrology and groundwater through the limestone bedrock appeared to vary.

DISCUSSION

For the four most seaward-growing tree species in our study, regeneration failed before older trees were

TABLE 4. Statistical significance of differences in soil redox potential among stands in different stages of decline and between centers and edges of stands (repeated-measures ANOVA using data from the six complete censuses).

Source of variation	ss	df	F	P
Stand health	25 968	2	3.115	0.081
Position (center vs. edge of stand)	311 567	1	74.755	<0.001
Interaction (health \times position)	6 362	2	0.763	0.488
Error	50 014	12		

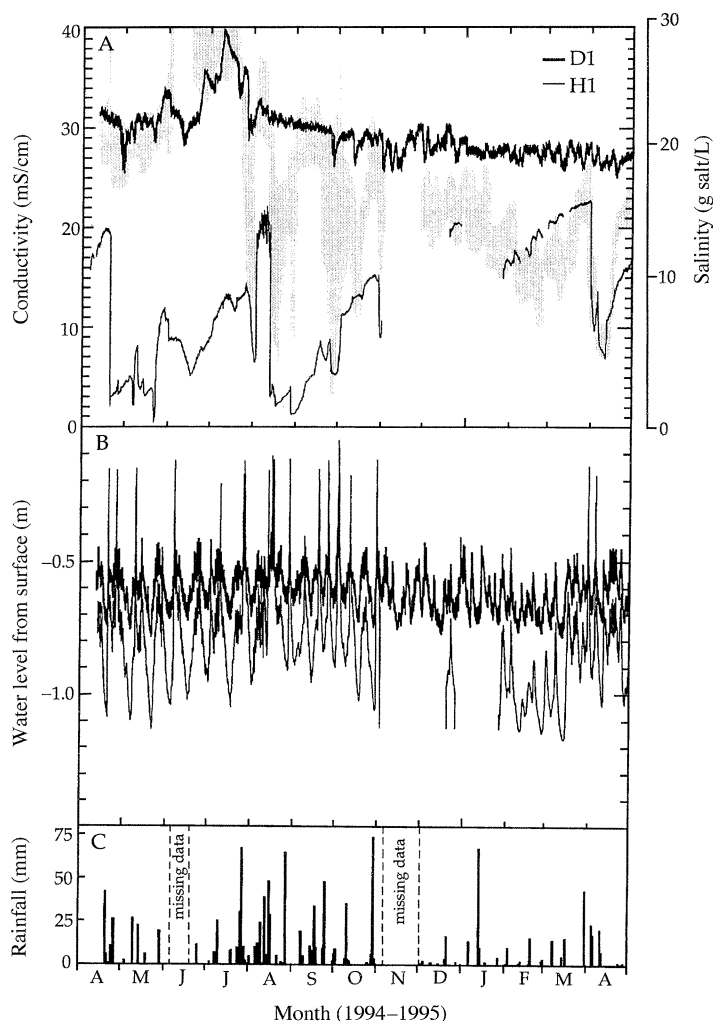


FIG. 8. (A) Groundwater conductivity and salinity and (B) water level in a healthy stand (H1) and a decadent stand (D1). Gaps in data from H1 occurred when water levels fell below the level of the sensors. Stippling in (A) indicates the range of fluctuating salinity in the tidal creek. (C) Rainfall at the study site.

eliminated from a stand. Species that were apparently more sensitive to the ocean's influence formed relict stands within healthy, regenerating stands of more tolerant tree species, a pattern that has been found among tree species in New York (Clark 1986). Whereas failure of tree regeneration in the Mississippi Delta has been linked to rising water levels and increased flooding stress (Baumann 1987, DeLaune et al. 1987, Conner and Day 1988), and failure of *Sabal* regeneration on sandy coasts has been attributed to erosion (Brown 1973), failure of tree regeneration in this system was associated with exposure to tidal water and increasing salinity of the groundwater.

Although indicators of forest decline correlated with frequency of tidal flooding, associated changes in soil redox potential were modest and unlikely to stress severely many tree species in this forest. These species routinely tolerate freshwater wetland conditions. The lowest soil redox potentials were encountered in healthy stands, presumably due to the higher organic-matter content and microbial activity in these soils. The

redox potentials encountered in the root zones of declining, tidally flooded forest stands were rarely low enough to lead to formation of H_2S , which is toxic to many species. It is possible that our sampling pattern was too coarse to capture short-lived excursions of redox potential to levels low enough to damage a plant. However, we sampled most intensively in the summer, when such events were most likely to occur. Part of our failure to find low redox potentials in the root zone may stem from the geomorphology of this type of coast, where roots are restricted to shallow soil depths by an underlying limestone platform. Our failure to find very low redox potentials in most forest stands may also reflect the ability of *Sabal*, a species occurring within all stands, to oxygenate its rhizosphere via the well-developed aerenchyma in its roots. The low soil redox potentials frequently measured just outside tree stands, compared to those within stands, may be an effect of the death of the last *Sabal* trees, rather than a cause.

Groundwater salinity beneath island forest stands varied widely, being highest in forest stands in ad-

vanced stages of decline and lower in healthy stands. Salinization of groundwater appeared to occur during early to middle stages of stand decline: shallow groundwater beneath H1, where ample regeneration of *Sabal*, *Juniperus*, and *Quercus* occurred, was brackish at certain times of year (up to ~ 15 g sea salt/L several times during 1994–1995). Groundwater salinity under plots H2 and H3, where no regeneration of *Quercus* occurred and that of *Sabal* and *Juniperus* was marginal, was substantially higher than under H1 when it was measured in 1997. This pattern suggests that the salinization of groundwater could be a cause of regeneration failure. However, its role in forest decline on carbonate coasts is unclear. Ross et al. (1994) found changes in vegetation patterns in the Florida Keys that were associated with gradients in groundwater salinity and demonstrated that the mature pines there utilized groundwater. In contrast, Ish-Shalom et al. (1991) concluded that groundwater was a minor source of water for trees growing in four tropical hardwood stands in the Florida Keys. They concluded that sea-level rise would affect these coastal forest stands primarily by altering the frequency of tidal inundation, rather than by changing the salinity of groundwater. Because the first stage in forest decline appears to be seedling mortality, it is reasonable to assume that the salinity of groundwater that is inaccessible to small, shallow-rooted seedlings has little influence on the initial stages of stand decline.

Soil salinity varies across vegetational zones on the Gulf coast of Florida, generally decreasing from the *Iva*-dominated forest fringe to the coastal forest interior (Kurz and Wagner 1957). Greenhouse studies have shown that the zonation of tree species at our study site is largely consistent with the relative salt tolerance of the seedlings (Williams et al. 1998), although patterns differed slightly in the ability to tolerate constant exposure and temporary exposure to soil salinity. Of the species studied, *Sabal* and *Juniperus* were best able to maintain green leaves under conditions of continuous salt exposure, whereas *Quercus* could survive extremely high salt exposure by dying back and resprouting following salt removal. Kurz and Wagner (1957) showed that very high levels of soil salinity could occur in coastal forest after high tides and an extended period without rain (46 g/L chloride in pore water of soil in a stand dominated by *Quercus virginiana*). Thus, soil salinity displays great temporal variation across this vegetation gradient, and the ability of tree seedlings to survive various frequencies of exposure to high salinity may determine the tidal flooding regime at which regeneration of a species fails.

Both local rainfall and groundwater flow through channels in limestone may supply fresh water to forest stands on a carbonate coast. Connections between surface water and groundwater were evident at one monitoring well in this study, but not at the other. If groundwater flow reached any of our forest plots, it was in-

sufficient to offset the correlation between progression of forest decline and tidal flooding. Plot I1, however, supported an anomalously high density of both small *Sabal* and *Cladium jamaicense*, a species characteristic of freshwater or brackish marsh. The presence of *Cladium* on a frequently flooded, small (barely 0.05 ha), forested island surrounded by salt marsh may indicate subsurface freshwater subsidies that aid in the flushing of salt. Though not addressed in this study, such hydrological interactions may modify the rate at which sea-level rise eliminates forest species on karstic coastlines and merit further study.

Age structures of *Sabal* stands yielded histories of forest retreat that were broadly consistent with reconstructed rates of sea-level rise. Transplant studies have shown that seedlings of *Sabal* cannot survive in currently decadent stands (Perry and Williams 1996), and most trees in these stands appear to have germinated during periods when flooding frequencies were similar to those in currently healthy stands. Stand structures at our study site have been influenced by many natural and anthropogenic factors, but none are likely to have preferentially eliminated young trees that might have established during periods with high flooding frequency. All but the smallest seedlings appear resistant to storm damage (K. Williams, *unpublished data*), and harvesting practices spare young plants. From 1910 to 1950, *Sabal* trees with trunks >2 m tall were harvested to supply fiber for a brush factory at Cedar Key (Florida, USA). Raft landings for shipping palms to Cedar Key existed on tidal creeks near the inland boundary of our study site (L. K. Runnels, *personal communication*). This harvesting, therefore, may partly account for the lack of tall palms in island plots closest to the mainland (D1 and I1, Fig. 3; H1, data not shown). Indeed, aerial photographs show that the tree canopy in D1 increased between the 1940s and the 1970s, consistent with recovery from tree harvesting, before declining again. Past harvesting, therefore, may have affected the stand structures in each plot, but is unlikely to have eliminated trees that established after the early 1900s.

Elimination of tree regeneration may precede the death of established trees by many decades. For *Sabal*, the last tree species to be eliminated from forest stands at our study site, the stand with fewest surviving trees (D3) is estimated to have suffered complete regeneration failure starting ~ 80 yr ago. This estimate is subject to assumptions that (1) trees that grew most quickly were those that survived, and (2) after establishment, small palms were no more likely to die from exposure to sea water than larger palms. The first assumption yields minimum age estimates. The second assumption is supported by patterns in mortality observed over the course of the study: mortality was low for all but the youngest plants (those with simple, undivided, grass-like leaves), even in declining stands. Most of the mortality observed in stands in the final stages of decline

occurred among the taller, older trees. Thus, one might expect the age of the youngest palm in a stand to reflect the approximate year after which seedling establishment failed.

Characteristics of mature trees (e.g., inherent longevity, salt tolerance, and susceptibility to disturbances such as storms) affect the rapidity with which species are eliminated from stands following regeneration failure. The large number of windthrown *Juniperus* trees after the March 1993 storm suggests that storms may hasten the elimination of this species from relict stands. In stands where regeneration is possible, storms are unlikely to eliminate *Juniperus* completely, but they may increase the relative dominance of *Sabal* because of its resistance to storm damage and high leaf-production rates in storm-damaged stands (Table 3).

The long time period between failure of tree regeneration and death of the canopy trees has implications for the role of competition from marsh vegetation in the demise of tree stands. Although marsh vegetation was quite common in declining forest stands, tree regeneration appeared to fail before marsh vegetation became abundant. Although the more frequently flooded "healthy" stands (H2 and H3) supported a large number of trunkless palms, many of these individuals were >30 yr old. Regeneration of *Sabal* in these plots during the course of this study (Fig. 2) and in the years just prior to the study (Fig. 5) was poor, even though the density of marsh species was quite low. Other tree species (*Juniperus*, *Quercus*, and *Celtis*) experienced poor regeneration in even less frequently flooded plots, with even less marsh vegetation. Thus, although shading by canopy trees may discourage encroachment by marsh vegetation, as suggested by Brinson et al. (1995), such inhibition will not maintain forest stands in this area, where tree regeneration fails despite low densities of marsh vegetation.

Coastal forest retreat on this relatively undeveloped carbonate coastline, therefore, appears fully consistent with impacts of continuing sea-level rise, whereby salt exposure associated with tidal flooding eliminates tree regeneration well before mature trees die. In this area, hypoxia associated with tidal flooding is rarely severe, and interference from encroaching marsh vegetation cannot account for regeneration failure. Although sea-level rise may impose flooding stress on forest trees and seedlings near high-volume coastal springs and rivers, much of the low-lying carbonate coastlines of the world are, like our study site, less influenced by these freshwater sources. The fact that tree regeneration fails several decades before canopy trees die suggests that forest monitoring studies should focus on regeneration rather than on the health of canopy trees. Canopy trees at the forest edge may merely represent the final remnants of stands that have been functionally dead for decades. The potential for subsurface flows of fresh water to slow forest retreat requires further study. Increases in rainfall associated with global climate

change may slow coastal forest retreat in the face of sea-level rise, while the increased incidence of droughts or consumptive water use by humans may accelerate it. Lastly, the buffering effects of salt marsh (noted by Brinson et al. [1995]), whereby forest stands near open water flood more frequently than stands at similar elevations farther inland, suggest that marsh loss may hasten the retreat of coastal forest in the face of sea-level rise.

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APPENDIX Continued.

Species	C1 (1)	C2 (1)	C3 (1)	H0 (1)	H1 (1)	H3 (6)	H2 (8)	I3 (10)	I1 (13)	I2 (16)	D1 (18)	D3 (26)	D2 (27)
<i>Rubus trivialis</i> Michx.	X	X	...	X
<i>Sageretia minutiflora</i> (Michx.) Mohr	X	X	...	X
<i>Salvia lyrata</i> L.	...	X	...	X
<i>Sisyrinchium atlanticum</i> Bickn.	...	X	X	X
<i>Smilax tamnoides</i> L.	X	X
<i>Solidago fistulosa</i> Ait.	X
<i>Tillandsia bartramii</i> Ell.	X
<i>Verbesina virginica</i> L.	X	X	...	X
<i>Ampelopsis arborea</i> (L.) Koehne	X
<i>Andropogon</i> sp.	X
<i>Bignonia capreolata</i> L.	...	X
<i>Bumelia lanuginosa</i> (Michx.) Pers.	...	X
<i>Centella asiatica</i> (L.) Urban	X
<i>Crinum americanum</i> L.	X
<i>Cynanchum angustifolium</i> Pers.	X
<i>Cyperus tetragonus</i> Ell.	...	X
<i>Dichantheium laxiflorum</i> (Lam.) Gould	...	X
<i>Dyschoriste humistrata</i> (Michx.) Kuntze	X
<i>Elytraria caroliniensis</i> (J. F. Gmel.) Pers.	X
<i>Hibiscus grandiflorus</i> Michx.	X
<i>Hibiscus</i> cf. <i>aculeatus</i>	X
<i>Hibiscus</i> sp.	...	X
<i>Hydrocotyle</i> sp.	X	...	X
<i>Iris hexagona</i> Walt.	X
<i>Leitneria floridana</i> Chapm.	X
<i>Matelea suberosa</i> (L.) Shinnars	...	X
<i>Myrica cerifera</i> L.	X	...	X
<i>Phaseolus smilacifolius</i> Pollard	...	X
<i>Phlebodium aureum</i> (L.) Small.	...	X	X
<i>Samolus valerandi</i> L. subsp. <i>parviflorus</i> (Raf.) Hulten.	X
<i>Sapindus marginatus</i> Willd.	...	X
<i>Smilax smallii</i> Morong	X
<i>Vicia acutifolia</i> Ell.	X
<i>Vicia floridana</i> S. Wats.	...	X
<i>Viola sororia</i>	X
<i>Vitis rotundifolia</i> Michx.	X	X
<i>Vitis vulpina</i> L.	...	X
<i>Tillandsia recurvata</i> (L.) L.	X	X	...	X	X	...	X	...	X	X	...
<i>Tillandsia usneoides</i> (L.) L.	X	X	X	X	X	X	X	X	X	...	X	X	...