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SEA-LEVEL RISE AND THE REDUCTION IN PINE FORESTS IN THE FLORIDA KEYS[1]

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Abstract. Forests dominated by *Pinus elliottii* var *densa* have undergone a reduction in area in the Florida Keys (USA). A previous investigation interpreted the presence of halophytic species in a former pine forest in Key Largo as evidence of sea-level rise. We therefore examined aerial photos and field evidence to learn how the 15-cm rise in local sea level over the last 70 yr had affected the distribution of pines on a second island, where intact pine forests still remained in 1991. The distribution of in situ dead pine stems showed that the area occupied by pines on Sugarloaf Key was 88 ha at some time prior to the earliest available aerial photographs, in 1935. The area of pine forest was reduced to 46 ha by 1935, and continued to decrease through 1991, when it covered 30 ha. The pattern of pine mortality was related to topographic position, with the areas where pines died earliest occupying the lowest elevations. Our analysis of current vegetation patterns showed that the areas of earliest pine mortality are now populated by a higher proportion of halophytic plant assemblages than areas of more recent pine mortality. We also compared the physiological responses of pines in two portions of the island: one where pine forest reduction had been most pronounced, and a second where the extent of the forest had changed little over the past 50 yr. Both groundwater and soil water salinity were higher in the area of rapid pine forest reduction, and the pines sampled there exhibited higher physiological stress, as indicated by pre-dawn water potential and stemwood carbon isotope ratios. These results suggest that the salinization of ground- and soil water that occurs as sea level rises is a major factor in the reduction of pine forests of Sugarloaf Key. If sea level continues to increase, the Florida Keys will experience a decline in both landscape and species diversity, as species-rich upland communities are replaced by simpler mangrove communities. This pattern may also occur in other low-lying island ecosystems with limited freshwater resources.

Key words: Florida Keys; geographic analysis; groundwater; limestone islands; moisture stress; Pinus elliottii *var* densa; *salinity; salt tolerance; sea-level rise; slash pine distribution; soil conductivity, stable isotopes.*

INTRODUCTION

Forests of South Florida slash pine (*Pinus elliottii* var *densa*) are currently found on ten islands in the southwesternmost (Lower) Florida Keys. Historical accounts and remnant woody materials indicate that pine forests have been completely displaced by other vegetation types on at least one other Lower Keys island, as well as on Key Largo in the Upper Keys (Alexander 1953, Dickson 1955). Furthermore, on several of the islands that presently support pines, dead snags and logs occur well beyond the perimeter of the existing forest.

Pine forests of the Florida Keys are maintained by fire, which interrupts a successional sequence leading toward more shade-tolerant, broad-leaved species (Alexander 1967, Alexander and Dickson 1972, Carlson 1989, Snyder et al. 1990). The reduction in pineland extent described above may therefore have resulted from an absence of fire ignition in recent decades, or through human suppression of those fires that did occur. Alternatively, Alexander (1976) found pine remains in areas of Key Largo currently occupied by mangroves. He proposed that sea-level rise was responsible for the disappearance of the pine forest on that island, by flooding low-lying pine communities and favoring salt-tolerant mangroves over freshwater-dependent pineland plants.

The Key Largo pine forest studied by Alexander had been reduced to scattered individuals by the 1930s, and contained no live pines by the time he first examined it in 1952 (Alexander 1953). With so little evidence, it was impossible to derive any strong inferences regarding the mechanisms of the proposed sea-level-rise effect. However, several Lower Keys islands with intact and relict pine forests side by side may represent early stages in the same process that led to the elimination of Key Largo pine forests. On such islands, comparisons of compositional and physiolog-

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ical patterns between current and former forests are a source of information that was unavailable in Key Largo. Furthermore, the temporal sequence of vegetation transformation on these islands could be documented with aerial photos, perhaps reflecting further on the mechanisms of change.

We therefore reexamined Alexander's (1976) hypothesis that sea-level rise has been a primary cause of pineland loss. Our objectives were to determine whether the reduction in pine forest in the Lower Keys has proceeded from lower to higher elevations, and whether the sequence of plant communities that have succeeded these forests reflects autogenic change toward vegetation associated with an absence of fire or allogenic change toward more salt-tolerant vegetation. We also wanted to ascertain whether living *P. elliottii* individuals adjacent to areas of high historical pine mortality exhibited evidence of physiological stress associated with high salinity in ground- or soil water. Our overall approach was to interpret current spatial patterns in environmental variables, vegetative cover, and *P. elliottii* physiology, in light of carefully documented changes in the perimeter of the pine forest over time. We concentrated on pine forests for two reasons: (1) their association with abundant freshwater resources suggests particular sensitivity to salinization effects, and (2) the distinctive canopy and wood structure of the dominant *Pinus elliottii* var *densa* facilitates mapping of their historical distributions from aerial photos and dead stems.

THE LOWER FLORIDA KEYS

The Lower Florida Keys are a series of limestone islands extending from Little Duck Key ≈60 km west to Key West (Fig. 1). The area is characterized by a dry tropical climate. Mean annual temperature at Key West is 25.2°C, with no record of freezing temperatures. Key West annual precipitation of 100 cm (compared to 118 cm at Tavernier in the Upper Keys) is highly seasonal; ≈70% is concentrated in the 6 mo between mid-May and mid-November.

Hanson and Maul (1993) recently analyzed meteorologic and sea-level records for Key West. Over the periods of record (temperature: 1850–1986; precipitation: 1886–1986) there was no directional trend in either of the climatic parameters, though temperature decreased by ≈1°C during 1880–1890, then increased gradually through 1950. However, sea level increased by an average 0.22 cm/yr between 1913 and 1986. We updated Hanson and Maul's data through 1990 (G. Maul, *personal communication*), applying a 19-yr filter to focus on the long-term trend and remove any effect of the lunar nodal cycle (Fig. 2). With the exception of a brief plateau during the 1950s, sea-level rise at Key West has been relatively steady since 1913.

The topography of the Lower Keys is low and nearly flat. Elevations >2 m above sea level are uncommon. With such modest relief, surface and subsurface hydrology are of great ecological significance. As elsewhere in the Florida Keys, Lower Keys soils and vegetation are arranged along a distinctive within-island gradient associated with elevation and the frequency of inundation by tidal waters (Davis 1942, Ross et al. 1992). In a tidal zone up to ≈50 cm elevation, relatively deep soils are continuously saturated with saline or hypersaline water. Here several mangrove species dominate floristically simple forest or shrub communities. Further upslope (to ≈80 cm elevation), an area of rocky or shallow calcareous mineral soils is frequently very dry, while at other times it is submerged in salt water. The open, relatively unproductive transitional woodlands, shrublands, or salt marshes of this zone are intermediate in plant species diversity. Finally, beyond all but the highest storm tides, the thin, predominantly organic soils of the uplands support slash pine or broadleaved forests (hammocks) that are low in stature but high in species diversity. Most of the dominant tree species are of West Indian origin, not occurring in North America outside of southern Florida (Long 1974).

Besides the within-island zonation discussed above, Florida Keys vegetation also changes along a northeast–southwest geographic gradient away from the mainland (Ross et al. 1992). The gradient is expressed by a decrease in forest stature and productivity from Upper to Lower Keys along with a gradual change in the species composition of upland forests. Several physical factors may contribute to these patterns, including the climatic gradient and elevation, which is generally higher in the Upper Keys. Another factor of potential importance is geology, especially through its effect on subsurface hydrology. The surficial geology of most of the Lower Keys consists of oolitic limestone of Pleistocene age. The oolitic rock is sufficiently resistant to the mixing of salt and freshwater that a lens of relatively fresh groundwater may be maintained in close proximity to an island edge. In the Upper Keys, where the high permeability of the coralline limestone promotes mixing with adjacent ocean waters, groundwater beneath most uplands is brackish except after unusually rainy periods.

The distribution of slash pine in the Keys suggests that it may be sensitive to the presence and persistence of fresh groundwater, which is generally reflected by the salinity of surface water in solution holes at the end of the dry season (M. Ross, *unpublished data*). Based on such data, slash pine forests are most abundant on islands that combine large size and stable freshwater resources (Table 1). On islands where pine forests are extensive, they are frequently found mixed with marsh communities dominated by sawgrass (*Cladium jamaicensis*) and other freshwater indicators. Carlson (1989) suggested an inverse relationship between fire return interval and island size, which may account for the limited extent of pine forests on small islands with fresh groundwater (Table 1).

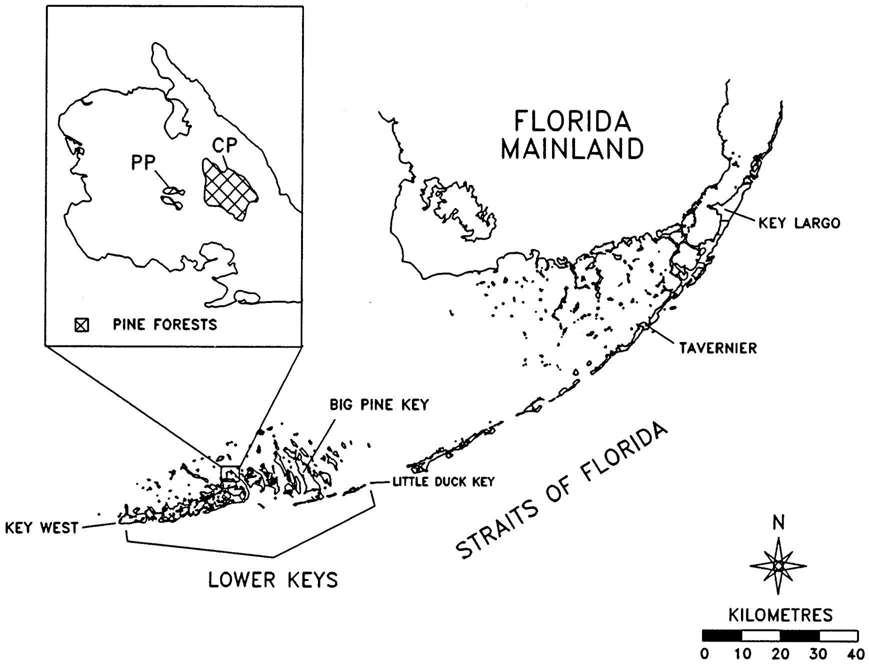

FIG. 1. Florida Keys and south Florida mainland, with upper Sugarloaf Key enlarged as an inset.

THE STUDY AREA

The study area was a 425-ha tract on the upper portion of Sugarloaf Key (24°41′ N, 81°33′ W), ≈30 km east of Key West (Fig. 1). There is little evidence of past use of the area by aboriginal people or by 19th-century settlers. A survey by the Dade County (Florida) Archaeologist in the early 1950s uncovered only fragmentary remains of a single temporary structure, probably dating to the late 19th or early 20th century. Furthermore, commercial logging has not been a significant factor in this part of the Keys (I. Eyster, *personal communication*). The northwest–southeast-oriented peninsula was platted in anticipation of development by Monroe County in the early 1970s, when a hard-surface road and a network of woods roads were established. Soon afterward, the United States Fish and Wildlife Service purchased the property as part of the Key Deer National Wildlife Refuge. Until recently, management activities were limited to controlling access to the area. In the last decade Refuge personnel have initiated a prescribed burning program, intended to reduce fuels and maintain the open pineland habitat critical for the endangered Key deer (*Odocoileus virginianus clavium*).

Despite limited topographic relief within the study area, the landscape is quite heterogeneous and typical of undeveloped portions of the Lower Florida Keys. Slightly elevated areas of pine, hammock, or transitional woodland vegetation are surrounded by a narrow supratidal fringe, all embedded in a matrix of mangroves. On the basis of electromagnetic profiling with terrain-conductivity meters, which measure the bulk electrical conductivity of the ground, Caballero (1993) recently determined that several of the upland forests on the island were underlain by a relatively fresh groundwater lens, which exhibited only minor seasonal changes in extent, depth, and salinity. The tract is further characterized by extensive areas in which dead pine trunks are clearly visible, emerging from a low broad-leaved forest canopy far from the nearest living *Pinus elliottii.*

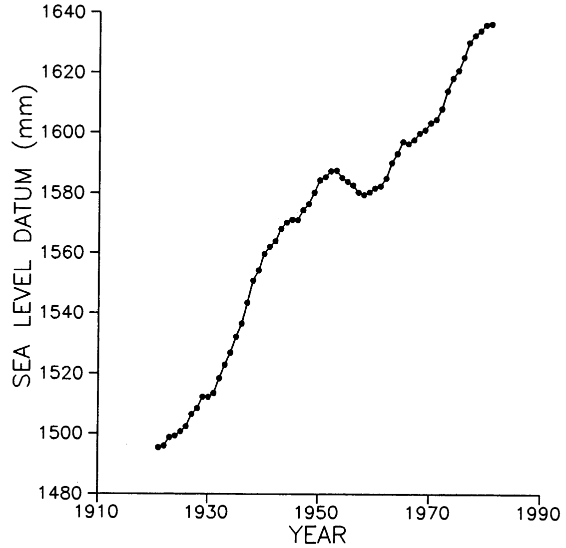

FIG. 2. Mean annual sea level at Key West, Florida. Data are 19-yr running annual means, based on monthly averages, 1913–1990 (adapted from Hanson and Maul 1992).

TABLE 1. Pine forest extent and surface water salinity in 17 islands in the Florida Keys, 18–20 May 1992. Values reported are for the least saline of 1–5 solution holes located in the highest part of each island.

Island	Total upland area (ha)	% of upland in pine forest	Salinity (g/kg)
Big Pine	920	76	1
No Name	213	26	1
Cudjoe	211	34	2
Upper Sugarloaf	190	20	1
Big Torch	145	0	1
Middle Torch	127	0	2
Little Pine	105	50	1
Ramrod	87	1	1
Little Knockemdown	66	0	1
Little Torch	52	0	5
Howe	45	0	1
Summerland	37	0	2
Knockemdown	21	1	5
Big Munson	10	0	4
East Water	4	0	7
Key Largo	2840	0 (<1)*	14
Lignumvitae	76	0	6

* Number in parentheses is based on minimum extent of historical pine forest.

METHODS

Current vegetation–environment relationships

South Florida slash pine forests are mid-successional communities that will give way to broad-leaved vegetation in the absence of fire, with or without an alteration in the external environment. For that reason, it was necessary to distinguish vegetation changes attributable to sea-level effects on the rooting environment of plants from autogenic successional change. In order to provide a basis for differentiating between these alternatives, we first documented the distribution of the major plant communities in the study area with respect to important environmental variables likely to be affected by sea-level rise. We stratified the vegetation of the study area using an ecological site classification (Ross et al. 1992) developed for the Florida Keys as a whole. Ecological Site Units are defined on the basis of edaphic, physiographic, and vegetation characteristics (Barnes et al. 1982), but also may serve as non-overlapping units of vegetation alone. Five of the 13 units recognized in the Florida Keys were common on Sugarloaf Key. In order to further examine vegetation–environment relationships among these five community types, two homogeneous 1-ha sampling units were randomly selected within each type in the Sugarloaf Key study area. Six additional sampling locations were selected on Big Pine Key, a large island 21 km east of Sugarloaf Key.

Vegetation in each of the 16 sites was sampled in April–May 1989 or May 1992. A variable plot sampling method (Dilworth 1975) was used to assess the crown cover of trees. At four randomly selected points at least 30 m apart, "in" trees were determined using a 10-factor (U.S. customary units) prism (for trees >7.6 cm diameter at breast height, dbh [measured at 1.4 m above the ground]) or a 5-factor prism (for trees 2.5–7.6 cm in diameter). Species, bole diameter (in centimetres), and crown diameter were determined for "in" trees, each of which represented 2923 (Prism Factor)/(bole diameter) trees/ha. Crown area of each "in" tree was multiplied by the density it represented, and the product summed by species for each point. Species cover percentages for smaller stems were estimated in 5 × 5 m quadrats centered on each prism sampling point. Cover was assessed separately in four height strata: 0–30 cm, 31 cm–1 m, 1.01–2 m, and >2 m. Total species cover was the sum of understory and overstory estimates averaged over the four sampling locations.

We identified three site variables that were apt to change with a significant rise in sea level: depth to groundwater, groundwater salinity, and soil salinity. One would expect depth to groundwater to decrease as island waters rose along with surrounding marine surface waters. The consequent reduction in freshwater recharge area would lead to an increase in groundwater salinity. The increased frequency of flooding by tidal waters and wetting from beneath by brackish subsurface waters would deposit salts in the soil matrix, and hence increase the salinity or conductivity of the soil solution. We therefore measured depth to groundwater, groundwater salinity, and soil conductivity in each site on 3 May 1992. Groundwater salinity was determined in a 3.2-cm-diameter well established at each site. Wells were drilled to a depth 30–60 cm below the groundwater surface, encased with polyvinyl chloride (PVC) plastic pipe, and cemented to the limestone bedrock. Each well was evacuated and the salinity of the water that refilled it measured with a hand refractometer. A composite A-horizon soil sample was collected from the immediate vicinity of the well, and the conductivity of a moisture saturation extract of soil determined according to the method of Jackson (1958). In order to account for the effect of the daily and semidiurnal tidal fluctuations, groundwater depth was estimated by averaging two measurements to the well water surface made 6 h apart (Ayers and Vacher 1986).

We used detrended correspondence analysis (DCA) as a preliminary technique to examine the variation among plant communities that were well represented on Sugarloaf Key. DCA is an indirect gradient analysis method that uses a reciprocal averaging algorithm to reduce the dimensionality in the species × site matrix (Gauch 1982). We subsequently applied detrended canonical correspondence analysis (DCCA) to examine the covariation of vegetation and the three environmental factors expected to be affected by sea-level rise. DCCA is a multivariate direct gradient analysis method in which the ordination axes are constrained to be linear combinations of the measured environmental variables (ter Braak 1986). Detrending was applied to both analyses to ensure that the second ordination axis was not affected by quadratic interactions with the first (the "arch" effect).

Succession

The current vegetation of the study area was mapped from a black and white 1991 aerial photo and follow-up field verification, using the classification described above. We also developed a topographic map by surveying along seven north-south and two east-west transects, recording elevations to the nearest millimetre at 20 m intervals. Surveys were also made to isolated topographic features not intersected by any transect and to a nearby USGS benchmark. A topographic map with 2-dm contours was created from the surveying data using the SURFER program (Golden Software, Inc., Golden, Colorado, USA).

Aerial photographs were used to map pine forests on Sugarloaf Key in 1935, 1959, and 1971. At the scale of these photos (1:7000 to 1:12 800), individual pine crowns were recognizable. Pine crowns were outlined as a map unit if they formed a contiguous group of at least five pine individuals, where each crown was no more than 50 m away from its nearest neighbor. The maximum verifiable extent of pine forest on the island was also outlined on the basis of physical evidence. We searched 45 parallel belt transects for the remains of dead pine trees in areas beyond existing pine forest. Transects were 10 m wide and 30 m apart, and ran from one side of the island to the other. In 30-m segments along each transect we noted the presence or absence of rooted pine stems, still identifiable on the basis of their characteristic wood structure, resinous odor, and branching pattern.

The maps of topography, current vegetation, and historical pine forest distribution were analyzed using a desktop geographic information system (Atlas Geographic Information System, Strategic Mapping, Inc., San Jose, California, USA). The sequential maps of pine distribution were used to outline four zones of pineland attrition (ZPAs), i.e., areas in which a pine canopy was present during one period but absent in the following period. Geographical analysis was performed by overlaying the vegetation and topographic maps on the four ZPAs. The intersections of the maps allowed the distributions of elevation and current vegetation in each ZPA to be determined. We inferred the succession of pine forest to other vegetation types by arranging the vegetative cover in the ZPAs in a series of increasing time since occupation by pine.

Physiological stress in living pine stems

The historical examinations chronicled a recession in the pine forest on Sugarloaf Key towards a core area, leaving several rapidly shrinking pine fragments behind. We reasoned that the processes underlying the forest recession might be inferred by comparing the physiological state of living trees in the pine remnants and in the core area. We therefore compared plant moisture stress (Scholander et al. 1965) and stemwood carbon isotope ratio (Farquhar et al. 1982*b*) in pines from a small peripheral pine stand (PP in Fig. 1) and from a group of trees near the center of the core pine forest (CP in Fig. 1). Several investigators (Farquhar et al. 1982*a,* Farquhar and Richards 1984, Downton et al. 1985, Guy et al. 1989) have observed that plant carbon isotope composition is determined by the ratio of internal to external carbon dioxide concentration in the leaf, a ratio largely controlled by the limitation on carbon dioxide uptake via stomatal diffusion (Farquhar et al. 1982*b*). The higher the stomatal conductance the greater the discrimination against carbon-13 during photosynthesis, resulting in lower isotope ratios (i.e., lower $\delta^{13}C$) in the carbon incorporated in plant tissue; conversely, lower stomatal conductance causes an overall increase in carbon isotope ratio. Elevated salinity contributes to reduced stomatal conductance and, consequently, to increased $\delta^{13}C$ values in a number of glycophilic and halophilic plants (Farquhar et al. 1982*a,* Ball and Farquhar 1984, Guy et al. 1989, Lin and Sternberg 1992).

We also compared the source of water utilized by pines in the two stands, on the basis of isotope ratios of hydrogen and oxygen in plant water, soil water, and groundwater. Upland glycophilic plants generally absorb and conduct water without preference for particular isotopes of hydrogen or oxygen (e.g., Dawson and Ehleringer 1991). The isotopic similarity of plant stem water to potential sources (e.g., soil water, groundwater) is therefore a good indicator of its origin when the isotope signatures of those sources differ markedly.

Prescription fires that burned the peripheral pineland (PP) and the core pineland (CP) in recent years reduced the volume of the forest floor and removed much of the hardwood subcanopy within the two areas, but they had little direct impact on the pine canopy. Ten dominant or codominant pines were randomly selected within a 20-m radius plot established in both PP and CP. A Scholander pressure bomb (PMS model 600; PMS Instruments, Corvallis, Oregon, USA) was used to determine pre-dawn water potential on a single shoot tip on each tree. Sampling occurred on 1 May and 11 May 1992, following 8 and 18 successive rainless days, respectively. On the first day samples were also collected for isotope analyses. Wood samples for carbon isotope determination were extracted from each tree at breast height, using an increment borer. Samples for hydrogen and oxygen isotope determination at each site included (a) a single 10-cm shoot section from each tree, (b) five randomly located soil samples from the A-horizon, and (c) a groundwater sample from a well established in the same manner as discussed above. We determined groundwater salinity and soil conductivity for each sample as described earlier, and soil moisture content by drying for 24 h at 110°C. The salinity of the in situ soil solution was estimated by back-calculating on the basis of a calibration relating conductivity to salinity and from the observed soil moisture contents.

Carbon isotope composition was determined on the outer 1 cm of sapwood of each tree. Monthly measurements of radial growth of pines on Sugarloaf Key between June 1990 and June 1992 (M. Ross, *unpublished data*) indicated that an average tree increased ≈1 cm in diameter every 10 yr, although individual trees varied markedly. Samples were ground in a Wiley mill and cellulose extracted by standard procedures (Sternberg 1989). Carbon isotope measurements were made by combusting the cellulose with cupric oxide at 800°C and subsequent cryogenic distillation of carbon dioxide.

Groundwater and water from stem tissue and soil were distilled as previously described (Sternberg and Swart 1987). Hydrogen isotopic composition of water was determined by passing 3–5 μL through a hot uranium furnace and collecting the liberated hydrogen gas for isotopic analysis. Oxygen isotopic composition of water was determined by the carbon dioxide equilibration method (Epstein and Mayeda 1953). Isotopic measurements of purified gases were done in a VG Prism mass spectrometer using a PDB (Peedee belemnite) standard for carbon isotope measurements and SMOW (standard mean ocean water) for oxygen and hydrogen isotopic measurements. Isotopic abundances are reported in δ units:

$$\delta = \left(\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}}\right) \times 1000,$$

where $R = {}^{18}\text{O}/{}^{16}\text{O}$, or $R = {}^{13}\text{C}/{}^{12}\text{C}$, or $R = \text{D}/{}^{1}\text{H}$ (Sternberg and Swart 1987).

RESULTS

Elevation and pine forest recession

At some time prior to 1935 the pine forest of the study area was a broad, continuous band of ≈88 ha extending along the spine of the island near its western end (Fig. 3). By 1935 this forest was divided into two large stands, and its total area was reduced by about half, to 46 ha. The replacement of 8 ha of pineland by other vegetation during the period 1935–1959 took place primarily in the smaller, western stand. The rapid loss of pine canopy between 1959 and 1971 (5.4 ha) and the slower recession between 1971 and 1991 (2.3 ha) occurred in approximately equal proportions in the two sections of the forest. By 1991 a 27-ha pine stand remained in the eastern portion of the study area, but only two pine fragments totalling 3 ha were left in the west.

Pine forest reduction occurred over a wide range of elevations during each of the four periods examined (Fig. 4). The weighted mean elevations were 62, 71, 67, and 79 cm for the pre-1935, 1935–1959, 1959–1971, and 1971–1991 ZPAs (zones of pineland attrition), respectively. Thus the overall trend was for pine mortality to occur at increasing elevation with time. When considered in relation to each other, however, the 1935–1959 and 1959–1971 ZPAs did not exhibit this pattern; a 1-ha area of pine mortality during the earlier of these periods occurred above 0.9 m, probably for reasons unrelated to sea-level change.

Weighted mean elevations for the major vegetation units over the study area as a whole in 1991 were as follows: pine rockland (0.89 m), low rockland hammock (0.78 m), transitional thorn woodland (0.53 m), supratidal scrub (0.52 m), and dwarf mangrove mudflat (0.38 m).

Succession in former pine forests

Axis 1 of the DCA (detrended correspondence analysis) ordination of 16 plant communities on Big Pine and Sugarloaf Keys accounted for a great deal of the among-site variation in species composition (eigenvalue = 0.91) (Fig. 5A). Sites were arranged along Axis 1 in the following order: pine forests ≤ rockland hammocks < transitional thorn woodland < supratidal scrub ≪ mangrove swamps. There was only slight overlap between pine and hammock sites on these compositional grounds. Axis 2 (eigenvalue = 0.23) provided little separation among sites, but did segregate several upland forests including an unburned site in the peripheral pine forest on Sugarloaf Key and a Big Pine Key rockland hammock.

The arrangement of sites in the DCCA (detrended canonical correspondence analysis) ordination closely resembled that produced by the DCA ordination, though there was more overlap among adjacent vegetation types (Fig. 5B). As in the DCA ordination, DCCA Axis 1 scores were low for pine and hammock forests, intermediate for transitional woodlands, and high for supratidal and mangrove communities. DCCA's Axis 1 arrangement explained nearly as much of the variation in species composition (eigenvalue = 0.85) as did Axis 1 of DCA. The three measured environmental variables were strongly correlated with one another and the overall species–environment correlation for Axis 1 was very high (0.96). High Axis 1 scores were associated with high groundwater salinity and soil conductivity and a shallow water table (Fig. 5B). Axis 2 of DCCA had little explanatory value (eigenvalue = 0.05). In general, the DCCA analysis indicated that the measured environmental variables were very closely associated with the dominant compositional gradient identified in the DCA analysis.

In 1991 a substantial proportion of the area in all four ZPAs on Sugarloaf Key was in vegetation types indicated by the above analyses to be more salt tolerant than the original pine forest (Fig. 6). Moreover, the pattern among ZPAs was generally one of increasing salt tolerance with time since pine forest attrition. The two most recent zones were occupied only by hammock and transitional woodland vegetation, but the propor-

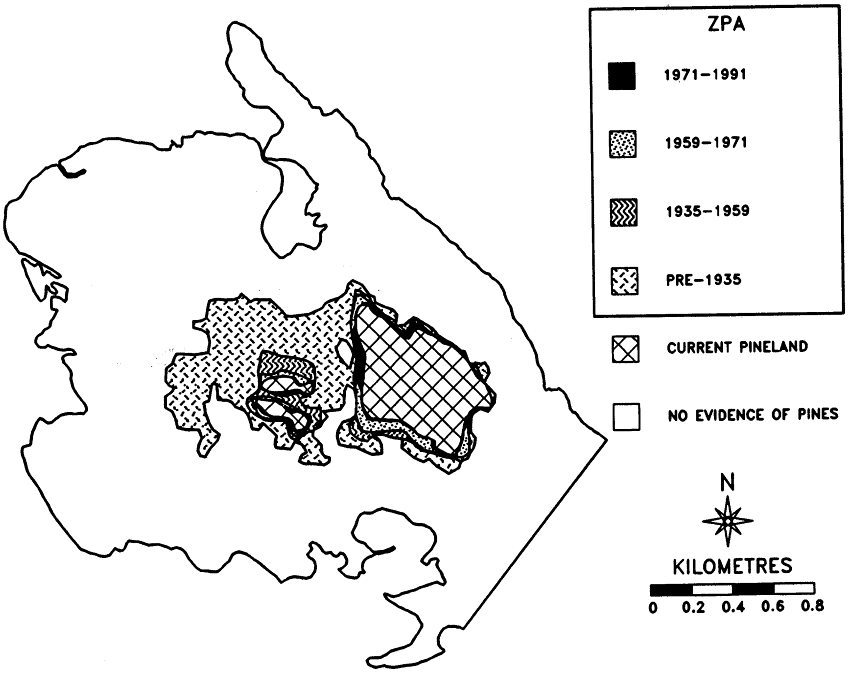

FIG. 3. Zones of pineland attrition (ZPAs) on upper Sugarloaf Key, with area of extant pine forest in 1991.

tion of the latter in the 1959–1971 ZPA was higher (26%) than in the 1971–1991 ZPA (16%). A slightly smaller proportion of the 1935–1959 ZPA was in non-hammock vegetation (23%), but some of that was supratidal scrub or mangrove swamp. Finally, in the pre-1935 ZPA, 78% of the area was in transitional woodland, supratidal scrub, or mangrove swamp, with ≈10 ha (23%) in the last two categories.

Physiological state of living pines

Groundwater salinity and soil conductivity were both higher in the peripheral pine forest (PP) than the core pine forest (CP) during the initial sampling period (Table 2). The mean salinity of the soil solution (14.8 and 5.6 g/kg for PP and CP, respectively) was higher than that of the groundwater on each site. The elevated salt concentrations observed in the ground- and soil waters of site PP were consistent with the relatively low predawn moisture potential and high $\delta^{13}C$ values found in that stand.

Like the salt concentrations, the δD and $\delta^{18}O$ values of the ground- and soil waters of the peripheral pineland were higher than those of the core pineland (Table 2). The isotopic composition of pine sap water paralleled that of the available water sources, with significantly higher δD and $\delta^{18}O$ values in PP than CP (Table 2). When plotted together, the isotopic compositions of ground-, soil, and plant water indicated that pines in both sites were using groundwater (Fig. 7). Pines in the peripheral site gave little indication of soil water use during this very dry period. Because the soil water

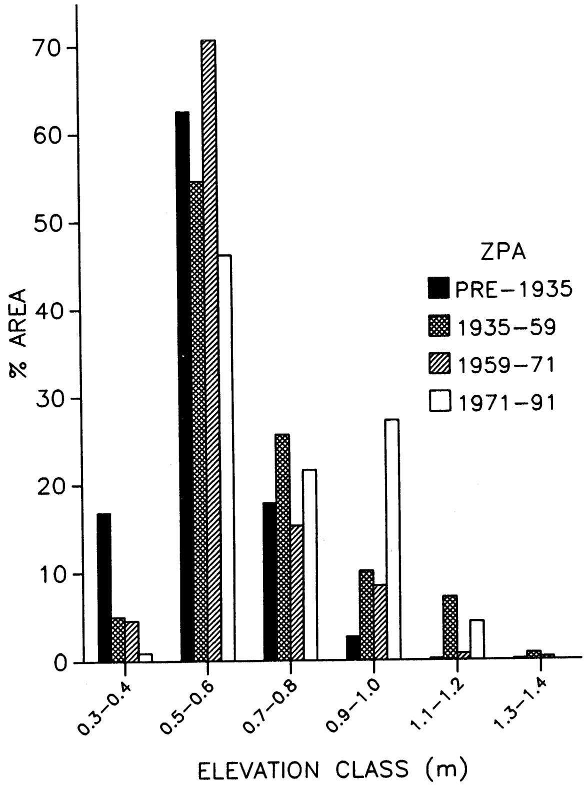

FIG. 4. Distribution of elevations in the four zones of pineland attrition (ZPAs).

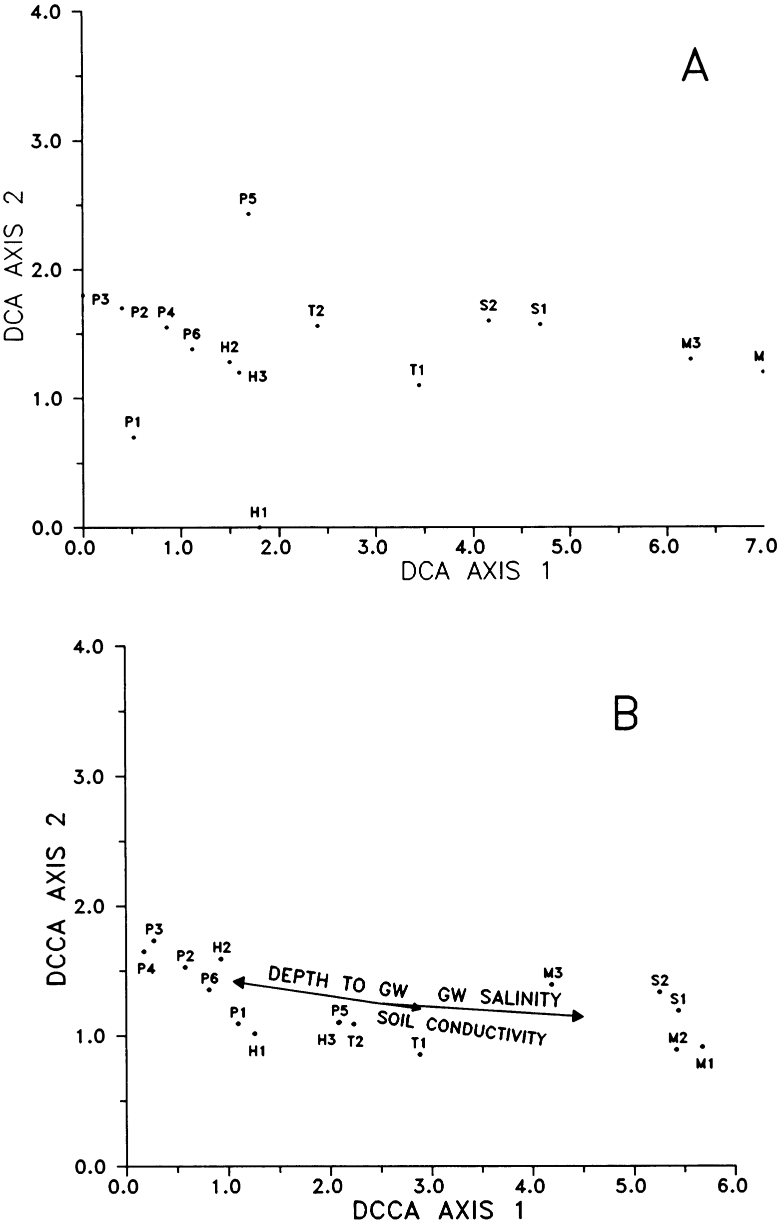

FIG. 5. (A) Detrended correspondence analysis (DCA) of 16 plant communities on Sugarloaf and Big Pine Keys, Florida. The first letter of the site code refers to vegetation type (P = pine forest, H = rockland hammock, T = transitional thorn woodland, S = supratidal scrub, M = mangrove swamp). (B) Detrended canonical correspondence analysis (DCCA) of the same sites. Length and direction of vectors represent the strength and direction of the measured environmental gradients. GW = groundwater.

signature in the core pineland was more diffuse, the pattern of water use was less definitive (Fig. 7).

Following a 10-d period without measurable precipitation, groundwater salinity and soil moisture content were unchanged (Table 2). Pre-dawn water potential was the same as it had been during the initial sampling period, with pines in PP continuing to maintain a lower pre-dawn water potential than pines in CP (Table 2). Because trees continued to transpire over the period (water potentials for all trees decreased to < -1.6 MPa by midday on both sampling dates), these results also suggest that pines in both sites were able to utilize groundwater sources.

DISCUSSION

Our results indicate that pine mortality on Sugarloaf Key proceeded from the margins of the original forest toward its center (Fig. 3), and from lower to higher elevations (Fig. 4). They further indicate that these pine forests subsequently succeeded to more halophilic vegetation types, and that the sequence advanced furthest in the areas first affected (Fig. 6). These results together signify a progressive salinization in much of the island's upland habitat during a period when sea level was rising at a fairly constant rate of ≈2.4 cm/decade (Fig. 2).

The progressive nature of the vegetation change argues against its origin in a single catastrophic incident, e.g., a hurricane or an anthropogenic event. Human impact has in fact been minimal, with no pumping, dredging, or shoreline alteration nearby. A single road was established long after the major changes in vegetation had already occurred. In light of the small (<40 cm) differences in mean elevation between pine forest and transitional woodland or supratidal scrub, the continuous transformation in the island's ecosystems are more reasonably attributed to incremental effects of sea-level rise, accumulated over a number of decades. Ecologically significant changes may have occurred in episodic events, but these episodes were sufficiently frequent to appear continuous at the level of resolution of our study.

The physical effects of sea-level rise on terrestrial environments of the Florida Keys are likely to include changes in the position of the water table, the salinity at its surface, and the salinity of the soil solution. Our vegetation analyses (Fig. 5) indicate that these three factors are very closely correlated with plant community composition and structure, and that they vary together over the landscape as a whole. Their spatial covariation is indicative of strong functional interdependence. In a scenario of rising sea level, an increase in the level of the water table would reduce freshwater recharge capacity, leading to an overall increase in groundwater salinity. In turn, higher and more saline groundwater would contribute to an increase in soil salinity through capillary wetting from beneath. The magnitude of the effect would depend on surface elevation and whether the capillary fringe rose far enough through the limestone bedrock to intersect the bottom of the soil profile.

Heterogeneity in hydrology and surface topography make it less likely that sea-level-induced increases in ground- and soil water salinity will be evenly distributed in the landscape. One factor in this variation is the occurrence of significant bodies of fresh groundwater. Where a freshwater lens is present, the water table might rise in response to sea level without an immediate increase in ground- or soil water salinity, except at the lens' edges. The relatively slow rate of pine forest attrition in the eastern portion of our study area (Fig. 3) may have resulted from the mitigative effects of the large body of fresh groundwater occupying that part of the island (Caballero 1993). In the western section, where pine forest reduction was much more rapid, no such freshwater body exists today.

Whereas the presence of a freshwater lens may temporarily buffer soil and groundwater from sea-level-derived salinity changes, an increase in the frequency and extent of tidal intrusion into interior areas during storms or spring tides may accelerate the salinization process. We have observed at least 3/4 of the Sugarloaf Key study area covered by tidal waters, with salt water inundating the transitional thorn woodlands and lapping up to the edges of the hammocks and pine forests. Tidal flooding presumably deposits salts and salt-laden materials in the soil matrix, as has been reported for the high waters associated with some tropical storms and hurricanes (Blood et al. 1991). We also suspect

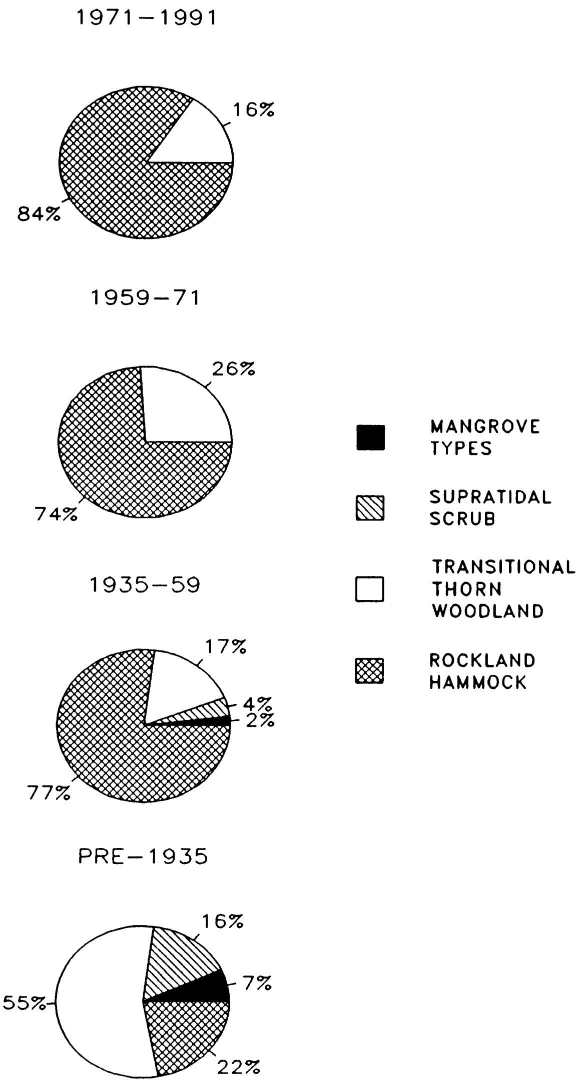

FIG. 6. Proportion of vegetation types present in the four ZPAs (zones of pineland attrition). Relative salt tolerance is highest in mangrove types, with tolerance decreasing in the following order: supratidal scrub, transitional thorn woodland, and rockland hammock.

TABLE 2. Groundwater, soil water, and *Pinus elliottii* characteristics in two stands on Sugarloaf Key, Florida, in 1992. Category means followed by different superscripts differ at $\alpha = .05$.

	Core pine forest		Peripheral pine forest	
	1 May	11 May	1 May	11May
Groundwater (n = 1)				
Salinity (g/kg)	0	27	8	10
δ^{18}O (‰)	−3.5	···	−2.2	···
δD (‰)	−20.0	···	−18.0	···
Soil (n = 5)				
Moisture content (%)	72.0^{a}	61.4^{a}	62.0^{a}	64.0^{a}
Conductivity (μS)	5150^{a}	···	$14{,}080^{b}$	···
δ^{18}O (‰)	-0.6^{a}	···	2.9^{a}	···
δD (‰)	-12.0^{a}	···	-0.2^{b}	···
Pinus elliottii (n = 10)				
Predawn water potential (MPa)	-0.68^{a}	-0.62^{a}	-0.89^{b}	-0.92^{b}
δ^{13}C of sapwood (‰)	-25.5^{a}	···	-23.8^{b}	···
δ^{18}O of sap water (‰)	-2.4^{a}	···	-1.6^{b}	···
δD of sap water (‰)	-20.9^{a}	···	-16.7^{b}	···

that ephemeral tidal water can have a long-term effect on groundwater beneath adjacent uplands. In a related situation on nearby Big Pine Key, Beaudoin (1990) demonstrated that permanent saltwater canals caused substantial reduction in the depth and extent of the adjacent freshwater lens.

The relative rates at which soil salinity and groundwater salinity are affected by sea-level rise may affect the place of hammock vegetation in the transformation of pine forest to more halophilic plant communities. The tap-rooted *Pinus elliottii* var *densa* is able to secure most of its water from groundwater sources (Table 2, Fig. 7). Its ability to use groundwater may be critical on the skeletal soils that characterize the rocklands immediately after fire, but of less significance as organic soils with increased water storage capacity build up in the absence of subsequent fire. Hammock plants, which are effective at exploiting soil water but exhibit little capacity to use groundwater (Sternberg et al. 1991, Ish-Shalom et al. 1992), may be better adapted to the deeper soils of these later stages of post-fire succession. The results of these resource exploitation strategies in a scenario of rising ocean levels would depend on the magnitude of impact on ground- and soil water salinities, as well as on the sensitivities of the plants to salt water. We are unaware of any information on the salt tolerance of the major hammock species, but have found reduced photosynthetic and growth rates in hydroponically grown *Pinus elliottii* var *densa* seedlings at salt concentrations as low as *3‰* (L. d. S. L. Sternberg, *unpublished data*).

Because pine forests and hammocks overlap broadly in hydrologic characteristics (Fig. 5B), sea-level-induced increases in groundwater salinity are not always directly responsible for replacement of the former by the latter. Sea-level rise may play no role at all, especially at higher elevations, or its effects may be indirect, through the influence of higher water levels on

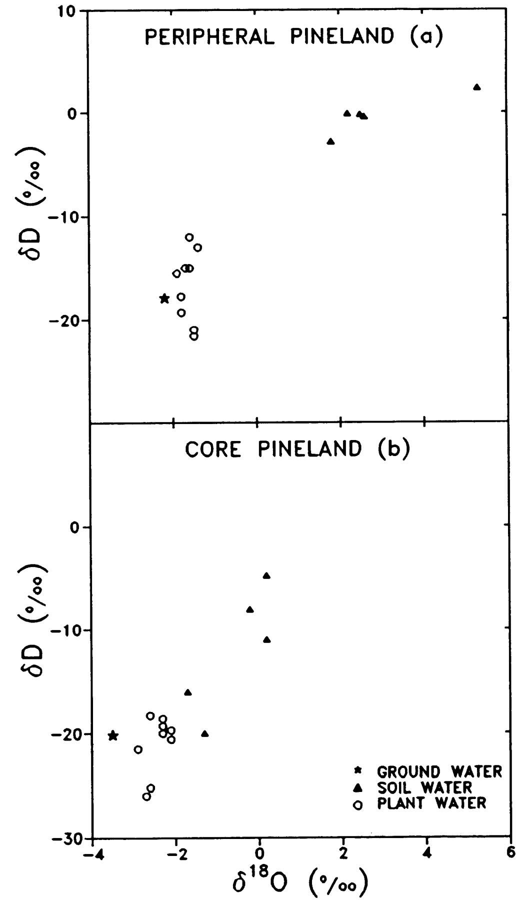

FIG. 7. δD (deuterium) and δ^{18}O of ground-, soil, and plant water in (a) peripheral pine forest, and (b) core pine forest.

fire frequency or behavior. Some pine forests do not pass through a hammock stage in their metamorphosis to more halophytic vegetation types (e.g., transitional woodlands in 1971–1991 ZPA in Fig. 6). Pine rocklands are hydrologically distinct from transitional woodlands, supratidal scrub, or mangrove swamps (Fig. 5B), and their eventual transformation to these vegetation types signifies an increase in the proximity of salts in the rooting environment. The absence of change in temperature or precipitation over the last century (Hanson and Maul 1993) suggests that the implied shift in the terrestrial hydrologic balance is a result of an increase in the level of surrounding waters.

We have argued that the observed changes in vegetation patterns on Sugarloaf Key are attributable to a progressive salinization in the rooting environment of plants, occasioned by a gradual increase in sea level. This incremental model implies that vegetation effects occur first at the lower elevations, then slowly progress upslope, with concentric bands of dead/dying and salt-stressed pine stems slowly encroaching on a nucleus of relatively unaffected pine forest. The design of our physiological studies was inadequate to test the model fully vis à vis the nature of the stress zone. However, these studies do suggest that the effects of the salinization process, if not the process itself, are ongoing. Mature pine individuals exhibited significant variation in characters indicative of both short- and long-term salt stress (pre-dawn moisture potential and stem wood $\delta^{13}C$, respectively). Stress levels were higher in a subpopulation closer to the zone of historical pine mortality where soil and groundwater salinity were both elevated (Table 2). These records provide a baseline for an expanded monitoring network, tracking future survival and salt stress. Alternatively, temporal and spatial variation in salt stress could be examined via a dendrochronological analysis based on carbon isotope composition.

Previous studies considering the effects of sea-level rise on plant communities have focused primarily on mangrove and other coastal wetland ecosystems (e.g., Ellison and Stoddart 1991; R. Parkinson and J. Meeder, *unpublished manuscript*). On low islands and along gradual shorelines, wetlands may expand, recede, or migrate upslope, depending on coastal conditions and the rate of sea-level rise. Isolated upland communities, having nowhere to migrate, retreat to a shrinking zone where conditions are suitable. For instance, K. Williams, J. Cornejo, and F. Putz (*unpublished manuscript*) reported the encroachment of coastal salt-marsh vegetation into raised *Sabal palmetto* hammocks in response to ocean levels in northern Florida. During the period 1959–1991 rockland hammock in three undeveloped areas of the Florida Keys was replaced by wetland vegetation at a rate of 1–2% per decade, while mangroves expanded in both landward and seaward directions (M. S. Ross, J. J. O'Brien, and L. J. Flynn, *unpublished manuscript*).

The chronic transformation of South Florida pine rockland forests in response to sea-level rise exacerbates the more acute problem of the loss and fragmentation of these communities due to development. Pine rockland forests support the highest plant species richness of the 13 major Florida Keys site units (Ross et al. 1992) and are critical habitat for a large proportion of South Florida endemic plant taxa (Long and Lakela 1978). The elevational distribution of the endemic herbs suggests that many are more sensitive than the dominant species to the effects of sea-level rise and are eliminated from the community relatively early in its metamorphosis to a more salt-tolerant form (J. J. O'Brien, M. S. Ross, and L. J. Flynn, *unpublished manuscript*). Where pine rocklands and other native uplands are poorly represented among terrestrial habitats, as they are in the western portions of the Lower Florida Keys, sea-level rise represents an additional threat to overall landscape diversity (sensu Romme and Knight 1982). A continuation of the current rate of sea-level rise in South Florida would place a potent constraint on conservation and restoration of low-lying upland communities, particularly if success is to be measured in the long term (e.g., >50 yr). As our results show, the protection of coastal biodiversity from the negative impacts of sea-level rise is a particularly acute problem in island ecosystems, especially those with small watersheds and minimal hydrologic buffering from surrounding marine waters.

CONCLUSION

Alexander (1976) interpreted the co-occurrence of dead pine stems in mangrove swamps as evidence of 20th century sea-level rise. In examining these relationships more closely, we followed an historical approach similar to that of our predecessor, but used modern geographical procedures, refined methods of vegetation-site analysis, and stable isotope techniques. These methods allowed us to reconstruct the historical record more completely, to interpret finer scale transformations among the entire range of plant communities, and to investigate the use of several potential water sources by slash pine. Our results strongly support Alexander's hypothesis of sea-level-induced changes. They go further, though, by linking known increments of sea-level rise with observed patterns of vegetation change, and by identifying the particular significance for slash pine of sea-level influences on groundwater salinity. Detailed description of such relationships is a first step in the development of predictive models that would allow the effects of sea-level rise to be factored into management and planning efforts. More generally, the historical approach we used might be usefully applied in other situations where the landscape effects of a progressive change in a potential forcing factor are in question, especially where (a) the natural landscape is arrayed along a single complex environmental gradient, and (b) the boundaries of one or more of the landscape units can be tracked in time, either through aerial photos or physical evidence.

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