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Source: *Journal of Vegetation Science*, Vol. 11, No. 1 (Feb., 2000), pp. 101-112

Published by: Wiley

Stable URL: <http://www.jstor.org/stable/3236781>

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## The Southeast Saline Everglades revisited: 50 years of coastal vegetation change

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**Abstract.** We examined the vegetation of the Southeast Saline Everglades (SESE), where water management and sea level rise have been important ecological forces during the last 50 years. Marshes within the SESE were arranged in well-defined compositional zones parallel to the coast, with mangrove-dominated shrub communities near the coast giving way to graminoid-mangrove mixtures, and then *Cladium* marsh. The compositional gradient was accompanied by an interiorward decrease in total aboveground biomass, and increases in leaf area index and periphyton biomass. Since the mid-1940s, the boundary of the mixed graminoid-mangrove and *Cladium* communities shifted inland by 3.3 km. The interior boundary of a low-productivity zone appearing white on both black-and-white and CIR photos moved inland by 1.5 km on average. A smaller shift in this 'white zone' was observed in an area receiving fresh water overflow through gaps in one of the SESE canals, while greater change occurred in areas cut off from upstream water sources by roads or levees. These large-scale vegetation dynamics are apparently the combined result of sea level rise - ca. 10 cm since 1940 - and water management practices in the SESE.

**Keywords:** Biomass; *Cladium jamaicense*; Correspondence Analysis; *Eleocharis cellulosa*; Leaf Area Index; Periphyton; *Rhizophora mangle*; Salinity index; Sea level rise; Water management.

**Nomenclature:** Long & Lakela (1971).

**Abbreviation:** SESE = Southeast Saline Everglades.

### Introduction

Coastal wetlands reflect a dynamic hydrologic balance between the marine and upstream or upslope terrestrial ecosystems which bound them on all sides. In these transitional settings, ecological responses which arise principally as a result of changes in the marine system may be modified by physiography, management, or land use patterns in the terrestrial environment, or vice versa. One example of these interactions is found in the response of mangrove ecosystems to sea level rise, which varies in rate or even direction in different physical settings or under alternative water management scenarios (Meeder et al. 1993). At a landscape scale, the anticipated response of coastal wetlands to change in sea level is even more

complex, especially if the dramatic vegetation zonation typical of many coastal wetlands is incorporated.

Nearly 50 years ago, Dr. Frank Egler described the vegetation of the area south and east of the Atlantic Coastal Ridge in southernmost peninsular Florida, noting a conspicuous coastal zonation within the area he called the 'Southeast Saline Everglades' (Egler 1952). Egler's description was based on 1938 and 1940 aerial photographs, and on field work undertaken 1940-1948. He described the vegetation pattern in the coastal Everglades at the time as 'fossil', responding slowly to a rapidly changing environment that included a rising sea level, a decline in the level of the surface freshwater aquifer, a reduction in fire frequency, and a range of anthropogenic modifications to natural drainage patterns. Egler documented several examples of local vegetation change over the period of his study, including the invasion of the halophytic *Rhizophora mangle* into freshwater wetlands far from the coast. At the same time, he anticipated a continued interiorward shift in the vegetation gradient.

Egler's work preceded the connection of the South Dade Conveyance system to the sea via the C-111 canal. Completed in the late 1960s, this project allowed more effective drainage of the agricultural and urban lands abutting the Southeast Saline Everglades (SESE). In conjunction with roads and agricultural ditches, operation of the canal system altered fresh water delivery to SESE wetlands, starving some areas of water while augmenting the supply to others.

Five decades after Egler's ecological studies, we re-examined the vegetation of the SESE. Our objectives were (1) to describe current vegetation patterns of the area in relation to known environmental or geographic variables, and (2) to document and interpret changes in the coastal wetland vegetation since our predecessor's studies. We hypothesized that changes in SESE marshes would reflect salinization effects associated with sea level rise, and that these effects would be more severe in areas cut off from upstream water sources by canals or roads. Documentation of temporal change in SESE vegetation was derived from two sources: floristic surveys and aerial photo interpretation.

## Study area

As described by Egler (1952), the Southeast Saline Everglades (SESE) includes the broad band of wetlands extending from the southwest-curving Atlantic Coastal Ridge to the coast (Fig. 1). Our study concentrated on the coastal wetlands north of Florida Bay, but also included several sites within the Biscayne Bay drainage, east of U. S. Highway 1 (Fig. 1).

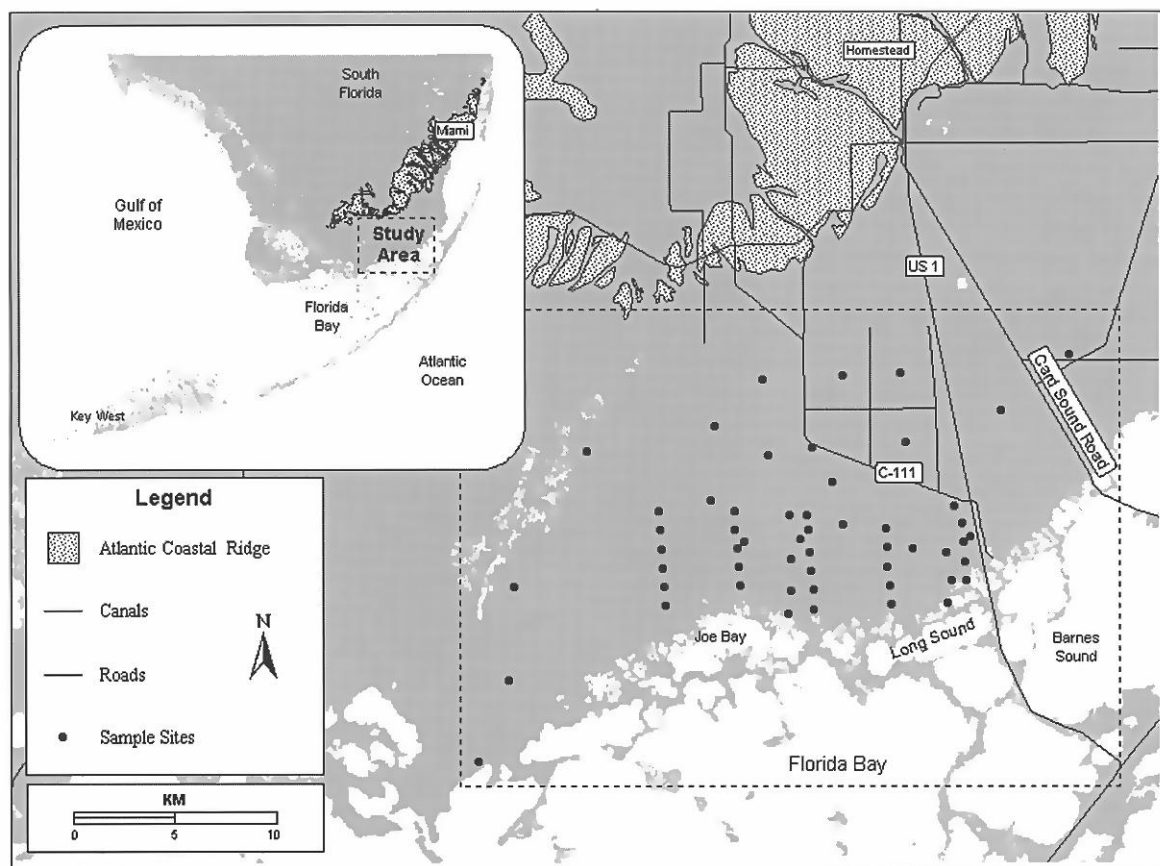
## Climate

At 25°N latitude, the SESE climate is transitional between temperate and tropical environments. Mean annual temperature is about 25 °C, with the difference between the warmest month (July) and the coolest month (January) less than 10 °C. A more significant ecological factor may be the frequency of freezing temperatures, which at the nearest long-term weather station in Homestead averaged one event per year between 1949-1987 (Duever et al. 1994). Mean annual precipitation (1951-1980) at Homestead is 1550 mm, with a distinct dry season between November and April. During many years, a large proportion of rainfall is attributable to Atlantic tropical storms and hurricanes.

## Physical environment

The SESE is a flat coastal plain which ascends from sea level to approximately one meter above sea level at the base of the uplands, more than 10 km distant throughout most of the region. Soil substrates are mostly marls produced under fresh water conditions, or peats, or some combination of the two (Leighty et al. 1965). The lower half of the SESE plain is dissected by ephemeral creeklets which range in depth from several inches in the upper reaches to several feet near the coast. Much of the variation in vegetation structure, including a profusion of tree islands, appears to be associated with these and smaller local undulations in topography.

Water levels at sites in the lower SESE respond primarily to fluctuations in the adjacent marine waters, while levels in the interior marshes are highly correlated with artificially maintained stages in the C-111 Canal. The contrast in hydrologic controls on interior and coastal sites may produce conditions where water levels are higher at either end of the SESE coastal gradient than at intermediate locations. Egler (1952) emphasized that periods of elevated salinity in the SESE are episodic, short-lived events, while background pore water salinities in most areas are low.



**Fig. 1.** South Florida and the Southeast Saline Everglades with sampling locations.

## Vegetation

Characterizations of marsh communities in the SESE are included in general treatments of South Florida vegetation (e.g. Harshberger 1914; Harper 1927; Davis 1943; Robertson 1955; Craighead 1971), but only Egler (1952) described the marshes of the SESE as a group. Egler's classification divided SESE vegetation into seven concentric belts roughly parallel to the coast. The two most interior belts, the 'Pine forest' and the 'Aristida grassland', are upland or transitional communities described in passing. In Belt 3 (Upper saline Everglades), the dominant species was *Cladium jamaicense* while *Rhizophora mangle* and *Eleocharis* spp. were notably absent. Egler recognized two variants of this marsh type: a dry, interior, species-rich phase and a wet, more coastal, species-poor phase.

In contrast, *R. mangle* was an important element in Egler's Belts 4-7. He described Belt 4 (Lower saline Everglades) as a narrow zone characterized by the general paucity of vegetation and the 'dwarfness' of many of the mangroves (Egler 1952: 256). As presented by Egler, Belt 4 marshes were a mixture of *C. jamaicense*, *R. mangle*, and *Eleocharis*, with the former the dominant species on the basis of cover. Egler considered fire regime and propagule availability to be the primary factors affecting the occurrence of *R. mangle* in Belts 3 and 4.

Egler described Belt 5 (Mangrove-sawgrass vegetation) as a mosaic of *Cladium* patches, mixed mangrove forest including *Avicennia germinans*, and open water. According to Egler, the interior border of Belt 5 represented the coastward limit of fire. In Belt 6 (mangrove - tidal marsh vegetation), *Cladium* was replaced by salt-tolerant plants such as *Batis maritima*, *Borrchia frutescens* and *Juncus roemerianus*, and *R. mangle*, *A. germinans* or *Laguncularia racemosa* were locally dominant. Finally, in the floristically simple Belt 7 (*Rhizophora* border), the salt marsh species were less extensive, and *R. mangle* was the sole significant tree species.

## Methods

### Sampling design

Vegetation and soils were sampled at 54 individual locations during the winters of 1994-95 and 1995-96 (Fig. 1). 26 sites had previously been sampled by Tabb et al. (unpubl. 1968 report), and another 21 were adjacent to hydrological stations in a network jointly maintained by Everglades National Park and the U.S. Geological Survey. 19 of the hydrologic stations consisted of wells sunk to bedrock, outfitted with water level recorders

that had been in operation since at least 1992. Seven sites along the western and coastal periphery of the study area were chosen to fill in gaps in sampling coverage.

### Vegetation sampling

To minimize observer bias among the four people involved in vegetation sampling, we determined a rank abundance for each plant species present at our 54 individual sampling locations, based upon their cover. The vegetation sampler walked ca. 50 m north from the plot center, tossed a 1.12 m diameter hoop (1 m<sup>2</sup> area enclosed) to his left, and ranked the vascular plant species rooted within the hoop in order of their shoot cover. By pacing chords of 12° arcs clockwise from the initial point, we located and sampled thirty subplots in a broad circle around the plot center. Species rank abundance at each site was equal to 100 × the sum of species abundance in the 30 subplots divided by the total abundance of all species, where the species ranked first in each plot was assigned an abundance of 10, the species ranked second an abundance of 5, the species ranked third an abundance of 2, and species ranked fourth or higher an abundance of 1. Species present in the marsh but not located in any subplot were assigned a cumulative abundance of 1.

Sampling at the 21 hydrologic stations also included an estimation of biomass and leaf area in the aboveground plant community. A 100-m transect was established, beginning within 20 m of the monitoring well and oriented perpendicular to the apparent slope direction. Within each 10-m segment of the transect, a single 0.25 m<sup>2</sup> subplot was randomly selected, and all aboveground material harvested and separated into the following components: live vascular plant tissue by species, dead standing vascular plant tissue, litter, mat periphyton, and epiphytic periphyton. Leaf and structural tissues of woody plants were also separated. Harvested material was dried to constant weight at 65 °C, and weighed. Inorganic and organic fractions of periphyton components were separated by combustion at 500 °C, and biomass expressed on the basis of the latter. Leaf area index was calculated by multiplying live leaf biomass (woody plants) or live aboveground biomass (herbaceous plants) by specific leaf area for individual species, then summing for the plot as a whole. Estimates of specific leaf area for the three most abundant plants (*C. jamaicense*: 53.58 cm<sup>2</sup>/g; S.D. = 5.03; *R. mangle*: 45.22 cm<sup>2</sup>/g, S.D. = 8.39; and *E. cellulosa*: 121.79 cm<sup>2</sup>/g, S.D. = 8.69) were based on samples of 4 - 6 leaves per plant from 10 individuals at several locations within the study area. A mean specific leaf area of 74 cm<sup>2</sup>/g was used for other species, which generally comprised less than 25% of total leaf biomass.

### Environmental sampling

At the 21 hydrologic sites, average elevation was calculated on the basis of a theodolite survey from the water level recorder table (whose elevation was known) to ground surface at 5-m intervals along the transect, as well as at the 10 subplot centers. At all vegetation sites, soil depth was determined as the average of 4–6 probings to bedrock with a 1-cm diameter aluminium rod. Bulk density and organic matter content were determined from surface samples (upper 3 cm) at 42 sites, according to methods outlined in DeLaune et al. (1987) and Dean (1974), respectively. From the fossil mollusc assemblage present in these surface soils, we calculated a salinity index equal to the density-weighted average of the salinity preferences of the sampled taxa. The salinity preferences of the mollusc species encountered, as well as citations for the literature on which those ratings were based, are listed in Table 1. It is recognized that this index provides an imperfect approximation of true salinity, since molluscs are also sensitive to other physical factors.

### Current patterns in marsh communities

We used a combination of classification and ordination techniques to describe the current gradients in marsh composition in SESE, taking steps to ensure that our definitions of SESE plant communities could be directly compared to Egler's (1952) study. Egler included quantitative data from two transects representative of Belt 3 marsh vegetation and one transect representative of Belt 4 species composition. His tables listed the frequency of occurrence of each species in 50 10-m<sup>2</sup> plots, and the proportion of occurrences in which it was 'rare', 'occasional', and 'abundant'. We assigned an abundance of 1, 2 and 10, respectively, to these descriptors, and calculated relative species abundance in his transects in a manner analogous to what we had done with our own data. We then applied the TWINSpan classification procedure (Hill 1979) and Detrended Correspondence Analysis (DCA) (ter Braak 1987) to a 57-site marsh data set (our 54 plots and Egler's three). After eliminating species that occurred in fewer than three sites, we transformed the relativized data into octave categories for the DCA analysis, and chose pseudospecies cut levels of 0, 2, 8, 33, and 66 for TWINSpan.

Comprehensive, spatially explicit, appropriately scaled environmental information was extremely limited for the study area. We therefore considered only a few variables in our examination of vegetation-environment interactions: the three soil variables described above (depth, organic matter percentage, bulk density), salinity index, hydroperiod, and distance to the coast. The latter was a spatial variable intended to represent

**Table 1.** Salinity rankings used to weight mollusk species abundances for calculation of salinity index, based on descriptions in Ladd 1957; Tabb & Manning 1961; Moore 1964; Turney & Perkins 1972; Abbott 1975; and Thompson 1984:

1 = freshwater species;  
1.5 = freshwater species with tolerance for low salinity;  
2 = brackish water species;  
2.5 = brackish water species that tolerate marine conditions;  
3 = restricted marine species with toleration for lower salinity;  
4 = marine species with a tolerance for low salinity;  
5 = marine species.

Species	rank	Species	rank
1 <i>Biomphalaria havanensis</i>	1	17 <i>Turbonilla</i> spp.	4.5
2 <i>Cylindrella</i> spp.	1	18 <i>Alvania</i> spp.	5
3 <i>Laevapex peninsulae</i>	1	19 <i>Anomalocardia auberiana</i>	5
4 <i>Physella cubensis</i>	1	20 <i>Bulla striata</i>	5
5 <i>Planorbella scalaris</i>	1	21 <i>Caecum pulchellum</i>	5
6 <i>Polygyra</i> spp.	1	22 <i>Carditas</i> spp.	5
7 <i>Pomacea paludosa</i>	1	23 <i>Chione cancellata</i>	5
8 <i>Littoridinops monoroensis</i>	1.5	24 <i>Chione latilirata</i>	5
9 <i>Pyrgophorus platyrachis</i>	2.5	25 <i>Corbula contracta</i>	5
10 <i>Cerithidea beattyi</i>	3	26 <i>Lima pellucida</i>	5
11 <i>Batillaria minima</i>	4	27 <i>Marginella</i> spp.	5
12 <i>Brachidontes exustus</i>	4	28 <i>Meioceras nitidum</i>	5
13 <i>Cyrenoida floridana</i>	4	29 <i>Retusa sulcata</i>	5
14 <i>Littorina angulifera</i>	4	30 <i>Rissoina catesbyana</i>	5
15 <i>Melampus coffeus</i>	4	31 <i>Strigilla carnaria</i>	5
16 <i>Terebra dislocata</i>	4.5	32 <i>Tricolia bella</i>	5

the composite effects of many unmeasured environmental factors. At the 19 sites for which continuous surface hydrologic data was available for the 1992–1994 period, we calculated hydroperiod as the mean annual number of days that average water level was more than 5 cm above the mean soil surface. Interactions between the environmental measures and SESE marsh vegetation were analysed via Canonical Correspondence Analysis (CCA), using PC-ORD version 3.11 (McCune & Mefford 1997), which incorporates the stricter convergence criteria suggested by Oksanen & Minchin (1997). The CCA analysis was applied twice: (1) to a 42-site data set in which distance to coast, the three soil variables, and salinity index were the environmental variables, and (2) to a 19-site data set in which distance to coast and hydroperiod were sole environmental variables examined. To determine the best model, we applied Monte Carlo permutation tests to variable combinations arrived at through a forward stepwise selection process.

### Change in marsh vegetation patterns – 1940 to 1994

Our analysis of changes in the SESE marsh communities intended to document the distance and direction of movement, if any, in the landward border of a "... conspicuous white band, forming a smooth arc which parallels, and is inland from, the ocean shores." (Egler 1952: 256). Egler's manuscript included copies of several 1940 aerial photos (Soil Conservation Service, CJF series), whose captions clearly illustrated the zone to

which he referred. In Egler's classification, the interior border of this white band demarcated the transition between Belts 3 and 4, and represented "...the upper limit of invasion by *Rhizophora* propagules sufficient to form a complete coverage..." (Egler 1952: 231). The white band remains remarkably prominent on current photos, with a landward boundary that remains "...distinct, but not knife-edge, definite enough so that the changeover usually occurs within half a kilometer..." (Egler 1952: 256). We therefore compared the 1940 and 1994 positions of this boundary, hereafter referred to as the 'white zone', using vegetation data from both studies as an aid in interpreting its ecological significance.

We first delineated the interface described above, based on the 1940 and 1994 photos. The former were the same images (1 : 24 000, black and white) used by Egler, and the latter were NAPP 18" × 18" 1 : 29 000 color infrared photos. The images were rectified using natural or anthropomorphic landmarks as control points. Using ATLAS-GIS software (Strategic Mapping Inc.), the historical and current white zone interfaces were digitized and superimposed on boundary files generated from U.S. Geological Survey 1 : 100 000 digital line graphs. Distances between the 1940 and 1994 interfaces perpendicular to the general direction of the coastline were calculated at ca. 520-m intervals along the coast, and examined graphically. Because the coastal boundary of the white zone was not clearly defined on either set of photos, we did not attempt to delineate its position.

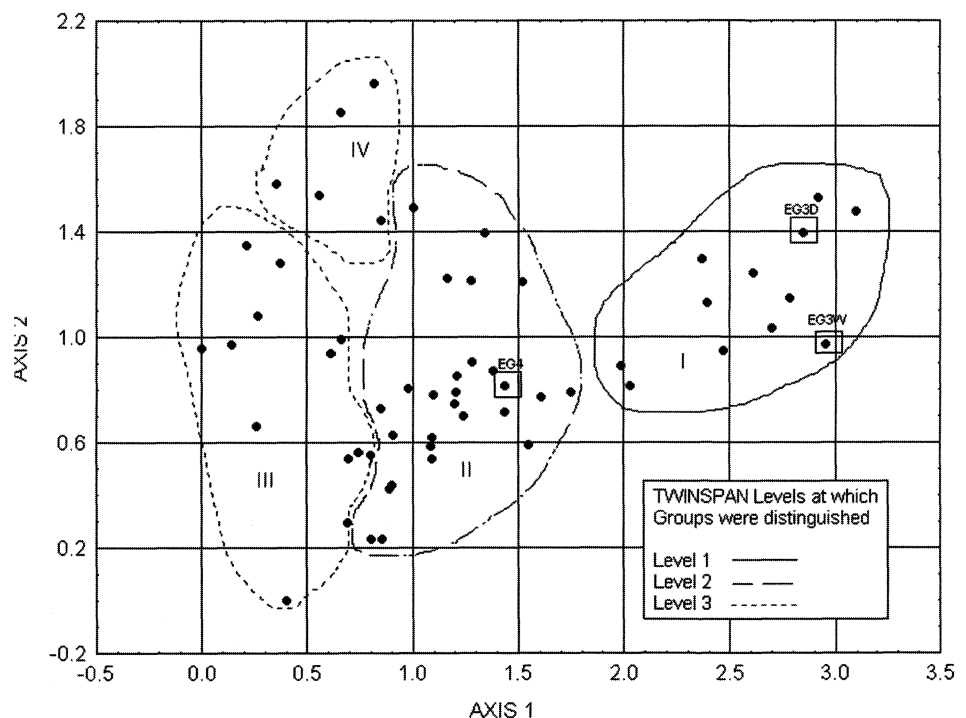
## Results

### Current marsh communities

Axis 1 of DCA explained 21% of the variation in marsh species composition, and Axis 2 accounted for an additional 9% (Fig. 2). The first and strongest division in the TWINSpan analysis (eigenvalue = 0.43) divided Group 1 from Groups 2-4, largely on the absence or presence, respectively, of a significant component of *R. mangle*. Subsequent divisions in Group 1 were weak, and the removal of individual sites commonly caused significant rearrangements in the subgroup assignments. Both of Egler's Belt 3 samples fell within Group 1. The Level 2 division distinguished Group 2 from the remaining sites (eigenvalue = 0.24), based on the presence of *C. jamaicense* and the absence of *Ruppia maritima*. Further divisions within the group (eigenvalues < 0.2) were not recognized, leaving Egler's Belt 4 site located centrally within Group 2. Level 3 division of the remaining sites distinguished Groups 3 and 4 (eigenvalue = 0.31) on the left side of Fig. 2; *R. maritima* and *Utricularia foliosa* were indicators of the former, and *Conocarpus erectus* and *Laguncularia racemosa* indicators of the latter group. Other divisions beyond Level 3 were not considered to be significant at the scale of the study area.

Based on the analyses described above, we recognized four vegetation units among SESE marshes and non-forested swamps (Table 2). *Cladium* marsh (Group

**Fig. 2.** Biplots of DCA Axis 1 and Axis 2 scores for 57 marsh samples, with TWINSpan classification groupings. Sites EG3D, EG3W, EG4 were ordinated from data supplied in Egler (1952), and represent dry and wet phases of his Belt 3, and his typical Belt 4 species assemblages, respectively. Group I = *Cladium* marsh; Group II = *Cladium-Eleocharis-Rhizophora* marsh; Group III = *Rhizophora* scrub; Group IV = Coastal prairie.



I in Fig. 2) was compositionally equivalent to Egler's Belt 3. It was characterized by the overwhelming dominance of *C. jamaicense* and the common occurrence of *E. cellulosa*, in mixture with a suite of graminoids (e.g. *Schoenus nigricans*, *Rhynchospora* spp.) and forbs characteristic of freshwater marshes further north. Group 2, *Cladium-Eleocharis-Rhizophora* marsh, was equivalent to Egler's Belt 4. The two named graminoids and *R. mangle* were of roughly equal abundance in this transitional community, while other plants characteristic of *Cladium* marsh were conspicuously absent. Groups 3 and 4 included mangrove-dominated species mixtures that Egler divided among Belts 5 through 7. In both groups, *C. jamaicense* was restricted to small patches in elevated areas adjacent to tree islands. *Rhizophora* scrub (Group 3) was a monotonous assemblage characterized by *R. mangle* shrubs, with *Eleocharis cellulosa* and/or several salt-tolerant aquatic herbs (*R. maritima*, *U. foliosa*, *U. purpurea*) in the large gaps between shrub clumps. Coastal prairie (Group 4) was characterized by the presence of *L. racemosa* and *C. erectus* shrubs in mixture with *R. mangle*, and the scattered occurrence of several halophytic herbs: *Aster tenuifolius*, *Fimbristylis castanea* and *Distichlis spicata*.

**Table 2.** Relativized rank abundance of common taxa (i.e., present in  $\geq$  three sites) in four SESE marsh community types. Parentheses enclose the number of sites in which species was recorded. C = *Cladium* marsh; CER = *Cladium-Eleocharis-Rhizophora* marsh; R = *Rhizophora* scrub; CP = Coastal prairie.

Species	Community type			
	C	CER	R	CP
<i>Proserpinaca palustris</i>	0.6 (3)			
<i>Panicum tenerum</i>	1.4 (4)			
<i>Taxodium distichum</i>	1.2 (4)			
<i>Nymphaea aquatica</i>	< 0.1 (3)			
<i>Bacopa monnieri</i>	2.3 (6)			
<i>Agalinis linifolia</i>	0.2 (3)			
<i>Ludwigia</i> sp.	0.1 (3)			
<i>Rhynchospora</i> sp.	9.1 (8)	< 0.1 (1)		
<i>Oxypolis filiformis</i>	1.4 (5)			
<i>Pluchea</i> sp.	0.2 (3)			
<i>Sagittaria lancifolia</i>	1.2 (8)			
<i>Schoenus nigricans</i>	1.3 (5)	< 0.1 (1)		
<i>Eleocharis interstincta</i>	0.3 (3)			
<i>Annona glabra</i>	< 0.1 (4)			
<i>Crinum americanum</i>	0.8 (7)			
<i>Cassytha filiformis</i>	2.6 (8)	0.1 (3)		
<i>Aster tenuifolius</i>	0.6 (6)	< 0.1 (3)		0.9 (3)
<i>Cladium jamaicense</i>	49.4 (10)	43.7 (26)	< 0.1 (3)	0.8 (2)
<i>Conocarpus erectus</i>	0.1 (4)	0.8 (4)		4.9 (5)
<i>Eleocharis cellulosa</i>	20.9 (10)	30.1 (24)	46.9 (13)	53.4 (5)
<i>Utricularia purpurea</i>	5.9 (6)	6.3 (18)	19.1 (10)	2.0 (3)
<i>Utricularia foliosa</i>	0.2 (4)	0.9 (6)	5.0 (8)	1.1 (2)
<i>Fimbristylis castanea</i>		0.1 (1)		1.1 (2)
<i>Rhizophora mangle</i>	0.13 (2)	16.8 (25)	17.9 (13)	31.8 (5)
<i>Tillandsia pauciflora</i>	0.01 (1)	0.7 (11)	0.9 (7)	
<i>Tillandsia balbisiana</i>		< 0.1 (6)	0.2 (3)	
<i>Tillandsia flexuosa</i>		0.2 (8)	0.2 (7)	< 0.1 (1)
<i>Laguncularia racemosa</i>				2.7 (4)
<i>Ruppia maritima</i>			9.8 (7)	1.1 (3)

The 21 biomass sampling stations included no examples of Coastal Prairie vegetation (Table 3). Mean aboveground biomass (including dead standing material, but not litter) averaged 619 g/m<sup>2</sup> in the *Cladium* marsh, 800 g/m<sup>2</sup> in *Cladium-Eleocharis-Rhizophora* marsh, and 1072 g/m<sup>2</sup> in *Rhizophora* scrub. Differences in standing crop among the three community types were largely attributable to the relative importance of the woody plant (e.g. *Rhizophora*) component. However, leaf area index in the predominantly woody *Rhizophora* scrub (0.54 m<sup>2</sup>/m<sup>2</sup>) was little more than half that in *Cladium* marsh (0.96 m<sup>2</sup>/m<sup>2</sup>) and *Cladium-Eleocharis-Rhizophora* marsh (0.99 m<sup>2</sup>/m<sup>2</sup>).

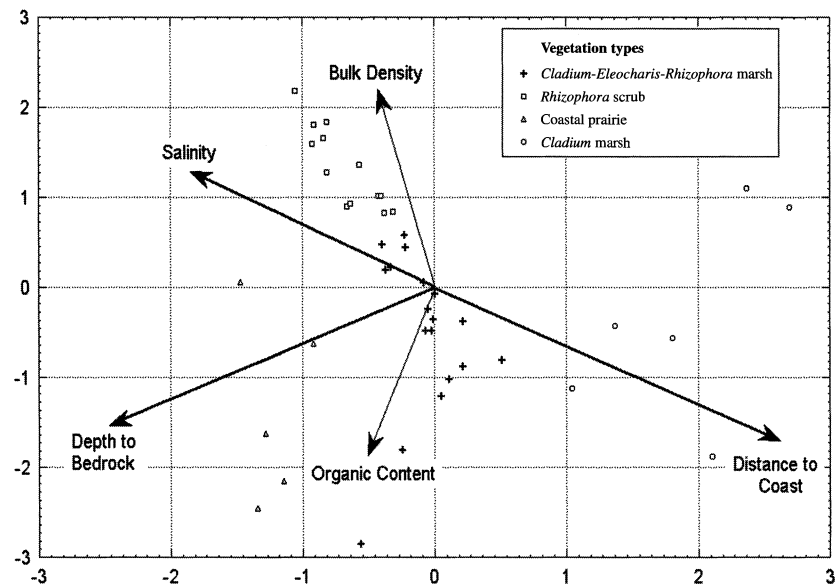
The importance of the algal component also decreased with total standing crop; total periphyton constituted 29% and 23% of total aboveground biomass in the *Cladium* and *Cladium-Eleocharis-Rhizophora* marsh, respectively, decreasing to 9% in the *Rhizophora* scrub. Finally, the high proportion of dead standing material in all three community types was in part the result of the winter sampling period and a recent (December 1989) freeze.

The Canonical Correspondence Analyses (Fig. 3) indicated that SESE marsh vegetation was arranged primarily along a gradient of distance to the coast. For the 42-site data set, linear combinations of the five environmental variables explained 29% of the variation in species composition. Distance to coast alone explained 16% of total compositional variation ( $p < 0.001$ ), and, according to the Monte Carlo permutation test, the addition of only depth to bedrock ( $p = 0.002$ ) and salinity index ( $p = 0.08$ ) improved the single-variable model

**Table 3.** Components of aboveground biomass (g/cm<sup>2</sup>) and Leaf Area Index (m<sup>2</sup>/m<sup>2</sup>) in three SESE marsh community types;  $n = 8, 11$ , and 3, respectively for C = *Cladium* marsh; CER = *Cladium-Eleocharis-Rhizophora* marsh; R = *Rhizophora* scrub; no data are available from sites classified as Coastal prairie.

Materials	Community type		
	C	CER	R
Litter	40.4	74.7	7.4
Dead standing			
<i>Rhizophora mangle</i>	0.0	12.2	317.0
Others	260.6	258.3	79.8
<b>Dead total</b>	260.6	270.5	396.7
Live materials			
<i>Cladium jamaicense</i>	96.4	126.3	0.0
<i>Eleocharis</i> spp.	16.6	10.6	7.1
<i>Rhizophora mangle</i>	22.4	182.9	553.7
<i>Utricularia</i> spp.	5.2	7.1	8.7
Others	28.1	4.1	10.4
<b>Live total</b>	168.8	331.0	579.9
Periphyton			
Attached Periphyton	50.1	37.2	35.3
Mat Periphyton	139.2	161.7	59.6
<b>Periphyton total</b>	189.3	198.9	95.0
Leaf Area Index	0.99	0.96	0.54

**Fig. 3.** Triplot of CCA analysis of SESE vegetation at 42 sites, categorized into four vegetation types. Vectors of five environmental variables are presented, with vectors indicated as significant ( $p < 0.1$ ) by a Monte Carlo permutation test (999 permutations) represented by bold lines.



further. Both depth to bedrock and salinity index were negatively correlated with distance to coast ( $r = -0.62$  and  $r = -0.52$ , respectively). However, depth to bedrock also exhibited a secondary trend of increase toward the east, and salinity index varied considerably in its rate of decrease with distance among different SESE drainage basins. Neither bulk density nor organic matter content showed a strong spatial trend across the area as a whole, and neither was significantly associated with marsh species composition. Finally, for the 19-site data set, hydroperiod was uncorrelated with coastal distance ( $r = -0.20$ ), and its inclusion did not significantly improve a model based on coastal distance alone (CCA-diagram not shown).

SESE marshes were zonally arranged, with the four community types falling neatly into parallel bands. Coastal prairie was closest to the shore of the SESE interior bays, followed by *Rhizophora* scrub, *Cladium-Eleocharis-Rhizophora* marsh, and *Cladium* marsh toward the interior (Fig. 4). Among the sampled sites, mean distance to the coast was 1.0, 2.1, 4.5, and 8.1 km for the four community types listed above, with some overlap between the latter two groups (Table 4). Site salinity index, highest in the two coastward community types, decreased sharply in the two types interiorward of the *Rhizophora* scrub. Soil depth in the Coastal prairie type (mean = 1.3 m) was more than twice that in *Cladium* marsh (mean = 0.5 m), with intermediate values in the two intervening zones. The other three environmental variables did not exhibit substantive differences among community types.

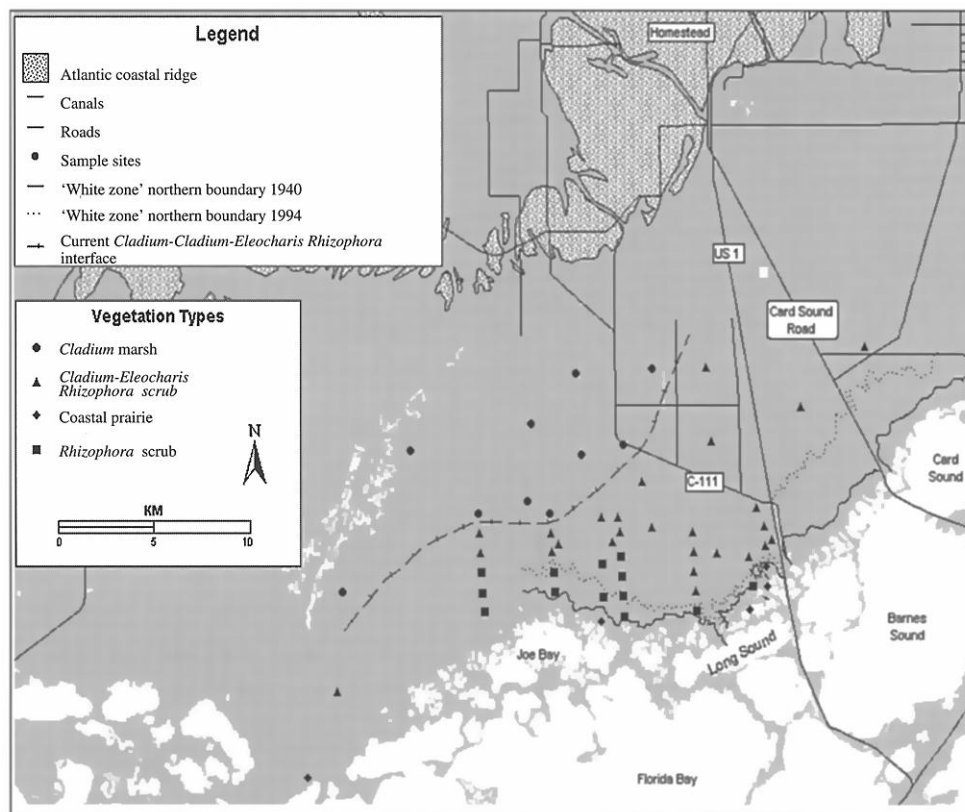
#### Historical changes in SESE vegetation

The white band discussed by Egler (1952) was a narrow coastal feature in 1940 (Fig. 5); the mean distance from its inner edge to the northern coastlines of Joe Bay, Long Sound, Barnes Sound, and Card Sound at that time was 1.13 km (range 0.56–2.22 km) (Fig. 4). By 1994, the interior boundary of this zone was, on average, 1.46 km further from the ocean (Fig. 5). In general, this trend was less pronounced west of U.S. 1 (mean = 0.82 km) than east of it (mean = 2.24 km). However,

**Table 4.** Summary of measured environmental variables in four community types. First row: mean, second row: range of values. C = *Cladium* marsh; CER = *Cladium-Eleocharis-Rhizophora* marsh; R = *Rhizophora* scrub; CP = Coastal prairie.

Environmental variables	Community type			
	C	CER	R	CP
Distance to coast (km)	8.13	4.46	2.10	1.04
	4.87 - 12.61	2.48 - 11.13	1.09 - 3.43	0.12 - 2.23
n	10	26	13	
Hydroperiod (no. of days)	259	303	300	
	133 - 335	8	116 - 360	266 - 333
n	8	9	2	
Depth to bedrock (cm)	52	94	34 - 101	134
	16 - 73	38 - 145	76	107 - 170
n	10	25	13	
Bulk density (g/cm <sup>3</sup> )	0.22	0.28	0.35	0.23
	0.12 - 0.42	0.08 - 0.78	0.06 - 0.74	0.12 - 0.32
n	6	20	13	5
Organic content (%)	14.6	24.8	16.4	19.9
	8.5 - 22.6	6.4 - 83.4	4.7 - 43.9	11.8 - 30.8
n	6	19	13	5
Salinity Index	1.0	1.2	2.3	2.7
	1.0 - 1.0	1.0 - 3.5	1.4 - 3.4	2.3 - 3.1
n	6	20	13	5





**Fig. 4.** Distribution of four marsh vegetation types in the Southeast Saline Everglades, with 1940 and 1994 positions of interior boundary of white zone.

west of U.S. 1, the interiorward shift increased with distance from the highway, while the opposite was true east of U.S. 1. Finally, while Egler's observations indicated that in 1940 the interior boundary of the white zone separated pure *Cladium* marsh to the north from the mixed *Cladium-Eleocharis-Rhizophora mangle* community, today the white zone border is near (in places south of) the boundary between *Cladium-Eleocharis-Rhizophora* marsh and *Rhizophora* scrub. Along a transect north from Joe Bay, the current interface between the *Cladium* marsh and *Cladium-Eleocharis-Rhizophora* marsh is ca. 3.3 km further inland than in 1940, while the interior border of the white zone has moved north by only 1.2 km (Fig. 4).

## Discussion

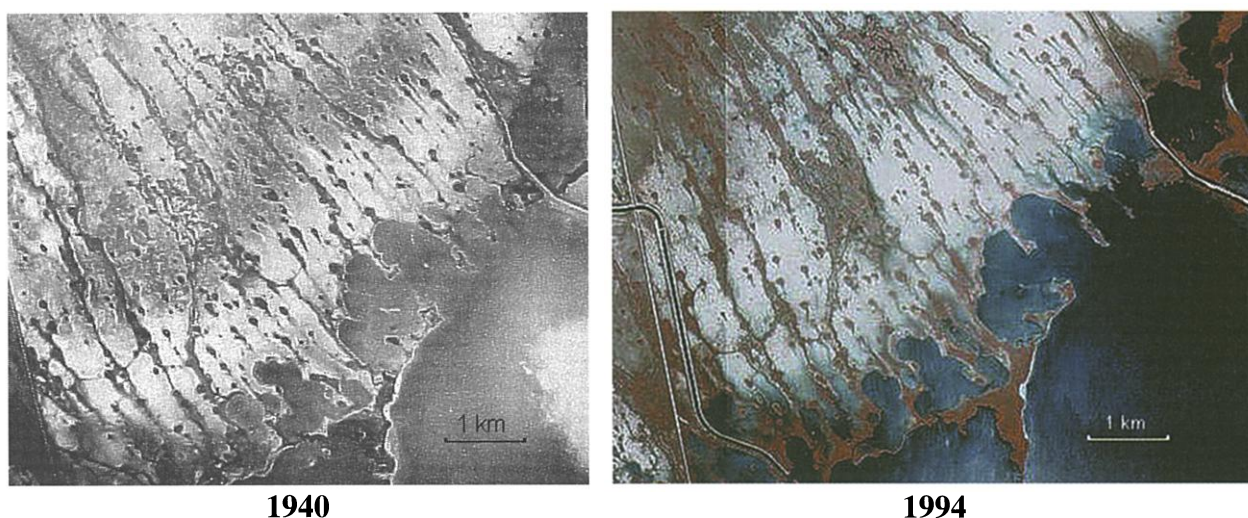
### *Environmental underpinnings of coastal zonation*

Like our predecessor (Egler 1952), we found the matrix of low vegetation in SESE to be arranged in a long gradient perpendicular to the South Florida coastline. Compositional units along this gradient were aligned in distinct zones, with little geographic overlap between

one group and the next. However, the low eigenvalues for TWINSpan divisions beyond Level 1, and the overlap in species composition among groups, suggest that these are not so much discrete units as nodal regions along a transition from mangrove-dominated coastal shrublands to *Cladium*-dominated interior grasslands.

The clinal nature of the SESE vegetation is further demonstrated by the strong coupling of species composition with distance to the coast in the CCA analysis, i.e., the position of a site with respect to the coast was a much better predictor of its plant species composition than the measured physical variables. This pattern suggests that the positional variable 'coastal distance' integrates a complex of physical factors which are strongly inter-correlated, but among which no single variable type is dominant.

Spatial variation in edaphic, hydrologic, climatic, and disturbance variables is not well-known within the SESE study area, but many of these variables are believed to change in a predictable way with distance to the coast. Soils become thinner, lower in organic matter content, and higher in bulk density with increasing distance from the coast, with attendant feedbacks on the availability of oxygen, water, and nutrients for plant growth. For instance, along a more abbreviated South



**Fig. 5.** 1940 and 1994 images of the coastal gradient between U.S. Highway 1 and Card Sound Road. Note shift in interior boundary of white zone over the period. Vertical line on left side of 1994 image results from contrast difference between NAPP photos.

Florida coastal transect that also included a transition from peat to marl, sediment phosphatase activity – a good indicator of phosphorus limitation – increased inland by nearly an order of magnitude over 500 m (Jacobsen et al. in prep.). Hydrologically, the coastal gradient is one in which marine waters and tidal processes dominate at one end, and the highly managed runoff of terrestrial water sources prevail at the other. A wide range of water quality parameters vary predictably based on site location within this mixing zone; salinity generally decreases with distance from the coast, though hypersaline conditions may develop in interior basins. Some ecologically significant climatic variables change sharply at the coast and immediately inland. Based on temperature isoclines of Thomas (1974), freeze events, which have been identified by a number of authors as important influences on vegetation patterns in South Florida (Craighead 1971; Egler 1952; Olmsted et al. 1993), may be less frequent and severe immediately adjacent to the coast than in the interior portions of the SESE. Finally, the principal natural disturbances impacting SESE ecosystems are wildfires and hurricanes. Fire frequency is presumed to parallel the distribution of fine fuels (e.g. graminoids) in increasing with distance from the coast (Egler 1952). As for hurricanes, while there is little reason to expect their occurrence within SESE to exhibit a strong spatial pattern, their characteristics may differ predictably within the study area in several ways. For instance, hurricanes accompanied by large storm surges may deposit several inches or more of mud in areas closest to the coast, causing extensive mortality in the mangrove forests (Craighead 1964).

Within the environmental complex discussed above, hydrologic variables are most directly sensitive to small

changes in sea level. One may reasonably expect sea level rise to result in surface and pore waters of more marine character throughout the SESE wetlands, along with greater water depths and longer hydroperiods. Vegetation response to elevated salinity ought to parallel the salinity tolerances of the three dominant plant species, which, though broadly overlapping, are in the order *R. mangle* > *E. cellulosa* > *C. jamaicense* (e.g. Koch 1996; Rejmankova et al. 1996; Lin & Sternberg 1993; Ross et al. unpubl.). Hydroperiod and water depth are considered to be major determinants of vegetation patterns in the exclusively fresh water portions of the Everglades (Busch et al. 1998; Newman et al. 1996; Craighead 1971; Loveless 1959), where *E. cellulosa* is generally found at more persistently and deeply inundated sites than *C. jamaicense* (McPherson 1973; Herndon et al. unpubl.). Periodicity or depth of flooding may also distinguish mangrove species composition within the relatively narrow range of salinities that characterize these coastal forests (Davis 1940). However, perhaps because of the relatively small number of sites and short period for which hydrologic data were available, interactions of hydroperiod with plant species composition were undetectable by our methods in the SESE coastal zone. We expect that more extensive sampling would show that hydroperiod effects are pertinent here as well, though they may be secondary in importance to salinity and associated water quality measures.

#### *Historical changes in SESE ecosystems*

Our analyses document two significant vegetation-related changes in the SESE over the last 50 years: (1) a movement toward the interior of a band appearing white

on both color infrared and black and white aerial photos, and (2) a similar interiorward shift in the composition of plant communities comprising the coastal gradient. In a parallel investigation of the paleoecology of the study area, we also traced a century-long increase in the proportion of marine-associated mollusk species preserved in SESE soil cores (Meeder et al. unpubl.). Several of these trends varied considerably among drainage basins of contrasting character and history, with areas cut off from upstream water sources becoming altered most rapidly. Such changes have taken place in the context of a global rise in sea level that has been 9.9 cm since 1940 at Key West (Maul & Martin 1993). We therefore believe that these are different manifestations of the same forces, i.e. the shifting balance between sea level and freshwater discharge in SESE.

#### *The white zone*

Since Egler's time, the white zone has changed from a band of mixed vegetation including approximately equal proportions of *C. jamaicense*, *E. cellulosa*, and *R. mangle*, to a monodominant community of *R. mangle*, with *C. jamaicense* virtually absent. Because the white zone community of a half century ago differed from that present today, we surmise that the characteristic appearance of this interface on aerial photos results from factors other than species composition.

Our data instead suggest that the appearance of the white zone on aerial photographs results from the combined effects of a reflective substrate and low plant cover. South and southwest of the C-111 Canal, the current white zone lies entirely within *Rhizophora* scrub vegetation, where leaf area index is less than 60% of that in the adjacent *Cladium-Eleocharis-Rhizophora* type. This contrast probably becomes accentuated during late spring or summer when new herbaceous shoots emerge in the latter. Given the low macrophyte cover, the white appearance on CIR photos may be attributable to equal reflection in green, red, and near infrared bands by the surface substrate, which is a light-colored peaty marl, or, in some areas a mixture of marl with recent storm deposits (e.g. Hurricane Andrew) (Meeder et al. unpubl.). Field observations indicate that the white zone usually does not extend into areas in which a coherent periphyton mat is at least seasonally present. Other factors which may affect the CIR appearance of SESE coastal zonation are dead biomass in the plant canopy, salt accumulation on leaf surfaces, the wetness of the soil surface, and leaf moisture content (Hardisky et al. 1986), or the species composition of the periphyton mat (Rutchev & Vilchek 1999).

Observed spatial and temporal variation in the position of the SESE white zone are consistent with the

hypothesis that hydrological variables associated with the balance of marine and fresh water sources are somehow implicated in the presence of this unproductive band of vegetation. Comparison of the 1940 and 1994 photo series indicates that the white zone has extended furthest inland in areas most deprived of access to fresh water. The areas east of U. S. 1 have long been entirely cut off from upstream sources of water by canals or roads. When these areas are flooded, it is for the most part by saline tidal waters of Barnes or Card Sound. In contrast, net outflow of fresh water through gaps in the C-111 Canal into marshes to the south (mostly Long Sound drainage) averaged about 175 000 acre-feet of water per annum during 1990-1995 (Everglades National Park unpubl.). Here, the unculverted U.S. 1 serves to intercept fresh water flow and retain it within the basin. When flooded by wind-driven tides, both Long Sound and Joe Bay drainages are inundated by estuarine Florida Bay waters whose salinity is usually less than that of open sea water. Finally, the Joe Bay drainage is open at its upper end, but the effect of water management has been to shunt water either to the east or the west.

The presence of a band of low apparent plant production midway along a coastal transect has been reported elsewhere. Montague & Wiegert (1990) described several Florida coastal sequences in which a zone of low statured vegetation, sandwiched between taller marshes or swamps, occupied a belt coastward of the mean high tide line. Carter (1988) presented general marsh profiles for Britain and eastern North America in which the zone of sparsest vegetation occupied a region near the intersection of salt and fresh water bodies. In this position, one might expect maximum variance in salinity and in other water quality parameters which differ between marine and terrestrial sources. Depending on topography, frequent wetting and drying are also likely. A plant in such an environment must function under a wide range of conditions, and the ability to do so may require physiological adaptations that result in slow growth. In developing this concept, Ball (1988) pointed out that mechanisms of salt tolerance such as salt exclusion, conservative water use, and the associated need for control of leaf temperature through leaf display adaptations all incur carbon costs. Her studies showed that mangrove species with the widest range of salinity tolerance have the slowest growth at optimal salinity. Ball's arguments were applied to interspecific variation, but similar reasoning may be relevant for variation within populations, or for variation in other environmental variables.

#### *Changes in species composition and community structure*

Based on our analyses of current and historical SESE vegetation, marsh species composition – as represented

by the interface of the *Cladium* marsh and the *Cladium/ Eleocharis/Rhizophora* marsh – has been even more sensitive to sea level rise than has the position of the white zone. Like any comparison of mapping results, this one depends on the accuracy of both modern and historical efforts, and on the equivalence of the mapping units utilized in each study. In this case we were able to address the latter point by referencing Egler's original survey data in our classification procedure.

The change in plant species composition documented in this study – an advancing wave of replacement of *C. jamaicense*-dominated marsh by low *R. mangle*-dominated mangrove swamp – signifies an extension of marine and brackish water conditions into formerly fresh water wetlands, as well as a structural shift from herbaceous to woody vegetation. The structural changes carry ecosystem consequences that may be overlooked in analyses of coastal responses to sea level rise. In shrubland ecosystems, significant proportions of fixed carbon and absorbed nutrients become tied up in stem and branch pools with relatively slow turnover rates. To a considerable extent, turnover of woody material results from periodic disturbances rather than predictable seasonal cycles. Moreover, from the perspective of associated faunal groups, low swamp communities provide a very different vertical and horizontal structure than herbaceous marshes. Algal communities are also likely to respond to structural differences that alter the light or nutrient environment at the soil surface, or that interrupt the cohesiveness of the periphyton mat. Structural impacts on hydrologic processes such as evapotranspiration or resistance to surface water flow are unknown for these ecosystems, but may be substantial. Finally, sediment accretion processes and rates differ between SESE mangrove and graminoid ecosystems (Meeder et al. unpubl.). Because the process of mangrove encroachment has been so extensive in SESE, these changes may have important impacts at the level of the south Florida ecosystem as a whole.

**Acknowledgements.** The project was funded by the South Florida Water Management District (Contract # C-4244). We especially thank Janet Ley, David Rudnick, and Rick Alleman of the District for their advice and cooperation throughout the project. Tom Armentano, Robert Fennema, Jerry Lorenz, Dewitt Smith, Alexander Sprunt, Bob Zep all provided information and discussion. Jennifer Alvord, Zachary Atlas, Allen Herndon, Luz Romero, Carmen Navedo-Cordiva, Joseph O'Brien, Kathy Rodriguez, Ana Maria Rodriguez-Urquijo, and Carl Weekley provided field assistance and plant species identification. This is contribution number 118 from the Southeast Environmental Research Center at FIU.

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Received 14 October 1998;

Revision received 2 April 1999;

Accepted 9 June 1999.

Coordinating Editor: P.S. White.