

RESPONSE OF EVERGLADES TREE ISLANDS TO ENVIRONMENTAL CHANGE

DEBRA A. WILLARD,^{1,3} CHRISTOPHER E. BERNHARDT,¹ CHARLES W. HOLMES,² BRYAN LANDACRE,¹ AND MARCI MAROT²

¹U.S. Geological Survey, 926A National Center, Reston, Virginia 20192 USA
²U.S. Geological Survey, 600 4th Street South, St. Petersburg, Florida 33071 USA

Abstract. Tree islands are centers of biodiversity within the Florida Everglades, USA, but the factors controlling their distribution, formation, and development are poorly understood. We use pollen assemblages from tree islands throughout the greater Everglades ecosystem to reconstruct the timing of tree island formation, patterns of development, and response to specific climatic and environmental stressors. These data indicate that fixed (teardrop-shaped) and strand tree islands developed well before substantial human alteration of the system, with initial tree island vegetation in place between 3500 and 500 calibrated years before present (cal yr BP), depending on the location in the Everglades wetland. Tree island development appears to have been triggered by regional- to global-scale climatic events at ~2800 cal yr BP, 1600–1500 cal yr BP, 1200–1000 cal yr BP (early Medieval Warm Period), and 500–200 cal yr BP (Little Ice Age). These periods correspond to drought intervals documented in Central and South America and periods of southward displacement of the Intertropical Convergence Zone. The records indicate a coherence of climate patterns in both subtropical North America and the Northern Hemisphere Neotropics. Water management practices of the 20th century altered plant communities and size of tree islands throughout the Everglades. Responses range from loss of tree islands due to artificially long hydroperiods and deep water to expansion of tree islands after flow reductions. These data provide evidence for the rapidity of tree island response to specific hydrologic change and facilitate prediction of the response to future changes associated with Everglades restoration plans.

Key words: climate; drought; Everglades; Florida, USA; Intertropical Convergence Zone; Little Ice Age; paleoecology; pollen; spores; tree islands; wetlands.

INTRODUCTION

Tree islands, scattered throughout the Florida Everglades, USA, serve as centers of biodiversity within the extensive, subtropical wetland. Dominated by a mixture of trees, shrubs, and ferns, tree islands are elevated slightly above the surrounding wetland and provide refugia for animals, nesting sites for wading birds, and the only habitable sites for flood-intolerant plant species (Fig. 1). These mosaics of swamp forest, transitional shrub-marsh, hammocks, and wet prairies cover up to 14% of the modern Everglades wetland, introducing variability in vegetation over different spatial scales (Brandt et al. 2000, 2002, Heisler et al. 2002). Tree islands developed as integral parts of the wetland complex due to a poorly understood combination of natural wetland processes, physical and geological setting, and climate variability. Recent changes (<50 yr) in the density, composition, and size of the Everglades have prompted efforts to answer fundamental questions on factors controlling wetland development and critical environmental parameters for tree island restoration and maintenance. Did tree islands develop due to natural succession of the subtropical

peatland (autogenic development) or did they form in response to changes in external factors, such as underlying topography and climatically induced hydrologic variability (allogenic development)? Are recent changes in tree island density, number, and size comparable to those that occurred naturally or did they result from altered water management practices? This study aims to place the well-documented changes of the past few decades into a longer temporal perspective by reconstructing long-term (centennial- to millennial-scale) trends in tree island development and assessing the relative impacts of anthropogenic and climate change on tree island communities.

In the natural system, before drainage efforts began in 1880 (Light and Dineen 1994), water depths and flow in the Everglades were governed by seasonal rainfall and underlying topography, with overflow of water from Lake Okeechobee during the wet summer season resulting in seasonal sheet flow across the Everglades. The historic Everglades covered an area of ~12 000 km² (Davis et al. 1994) and included a fringe of custard apple/cypress (*Annona glabra*/*Taxodium*) forest along the southern rim of Lake Okeechobee, a dense sawgrass (*Cladium*) plain, a ridge and slough landscape comprised of sawgrass marshes, tree islands, and waterlily (*Nymphaea*) sloughs, and mangrove forests bordering Florida Bay and the Gulf of Mexico (Fig. 2). In the mid- to late-

Manuscript received 28 October 2005; revised 11 April 2006; accepted 17 April 2006. Corresponding Editor: S. T. Jackson.

³ E-mail: dwillard@usgs.gov

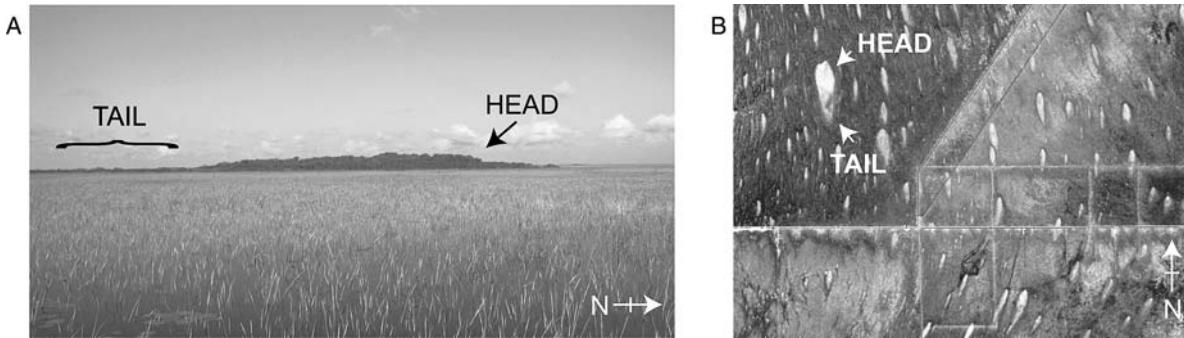


FIG. 1. Photographs of fixed tree islands of the Everglades, Florida, USA. (A) T3 tree island, Water Conservation Area 2A from the east. The highest surface elevations with the tallest trees are located at the north end of the tree island. Surface elevation and tree height taper toward the tail to the south. (Photograph courtesy of D. Willard.) (B) Aerial photograph of tree island, Water Conservation Area 3A. Note the teardrop shape of the tree island, with trees on the head at the northern (upstream) end tapering to thick stands of sawgrass and shrubs at the southern (downstream) end. (Photograph courtesy of the U.S. Geological Survey.)

20th century, the custard apple/cypress forest and much of the sawgrass plain were converted to the Everglades Agricultural Area, and urban development in southeastern Florida impinged upon the eastern ridge and slough landscape, effectively reducing the area of the Everglades by nearly half (Davis et al. 1994).

Alteration of the natural hydrologic patterns of the Everglades began early in the 20th century. Four canals linking Lake Okeechobee to the Atlantic Ocean (West Palm Beach, Hillsboro, North New River, and Miami canals; Fig. 3A) collectively drained ~607 100 ha annually, removing a volume of water more than twice the net precipitation (Sklar and van der Valk 2002). This drainage resulted in exposure of previously submerged peats and their subsidence from physical compaction, burning, and oxidation. The Hoover Dike, a 110-km long levee around Lake Okeechobee, was constructed between 1932 and 1938. The crest height of 10–11 m above the National Geodetic Vertical Datum (Army Corps of Engineers 1999, Herbert Hoover Dike Major Rehabilitation Evaluation Report, Draft Environmental Impact Statement, *available online*)⁴ provided protection against flooding in surrounding counties and reduced sheet flow southward to the Everglades. The Tamiami Trail, a highway linking Tampa and Miami, was completed in 1928. The road forms the northern boundary of Everglades National Park and was constructed atop limestone dredged from along the route. Culverts and bridges were incorporated into the design (Light and Dineen 1994), so the road did not form a complete barrier to flow.

After major hurricanes caused severe flooding and property damage in 1947–1948, additional drainage and compartmentalization of the Everglades began. A comprehensive plan to centrally regulate all phases of water distribution (the “Central and Southern Florida Project for Flood Control and other Purposes,” or C&SF Project) was signed into law by Congress in 1948.

⁴ (<http://www.saj.usace.army.mil/pd/envdocs/HHD/DEIS.html>)

The C&SF Project incorporated an extensive system of levees, canals, and pump stations to regulate freshwater availability (Fig. 3B). It ensured adequate regional water supply during droughts and the capability of storing large quantities of water to protect urbanized areas from flooding during wet years (Light and Dineen 1994). Ecologically, the C&SF Project fragmented the Everglades ecosystem into many independent units with different hydrology, nutrient status, and distribution of wetland communities (Davis 1994, Davis et al. 1994, Light and Dineen 1994). Tree islands were profoundly affected, with approximately half of them lost between 1940 and 1995 (Lodge 2005). By the late 20th century, recognition that the health of the Everglades ecosystem and the quality and availability of water affected the economy and culture of south Florida prompted development of the Comprehensive Everglades Restoration Plan (CERP). The CERP includes plans to restore natural hydroperiods, sheet flow, seasonality, and connectivity of the wetland ecosystem by modifying and removing levees and other water control structures under the assumption that the natural resilience of the wetland will allow its recovery to a more natural state.

A key to successful wetland restoration is adequate understanding of the natural processes governing wetland development. We designed this study to develop baseline data on tree island conditions prior to hydrologic changes of the 20th century and to evaluate the impact of autogenic vs. allogenic processes on Everglades development. Using paleoecological techniques, we determined the timing of tree island development and compared them to patterns observed elsewhere in the wetland and in the region. If climate is a primary factor influencing tree island development, then changes on the tree islands should be synchronous with changes elsewhere in the wetland and surrounding region. If, however, autogenic succession plays the greater role, then the timing of tree island development should be different from other sequences. We also evaluated the response of tree island communities to anthropogenic

changes of the 20th century relative to the longer-term record. The objectives of the study were to: (1) determine whether common patterns of fixed tree island development exist throughout the ecosystem; (2) determine the timing of fixed tree island formation throughout the greater Everglades ecosystem; and (3) document the response of Everglades tree islands to climatic and anthropogenic changes. These data ultimately may be incorporated into models to predict tree island response to different management schemes, thereby maximizing the likelihood of sustainable restoration.

REGIONAL OVERVIEW

The seasonal flooding necessary for wetland development occurred because of the geologic structure and climatology of south Florida. The modern Everglades basin is underlain by a limestone bedrock trough that has existed for at least the last 5×10^6 years. This depression, linking Lake Okeechobee and the Gulf of Mexico (Fig. 4A), has been subject to seasonal accumulation of water and wetlands periodically since the Pliocene, and freshwater marls similar to those presently accumulating in the southern Everglades are preserved among the older sediments. The Everglades, therefore, represent the most recent in a series of wetlands that have occupied the Everglades basin during the last few million years (Gleason and Stone 1994).

A key factor in maintenance of south Florida wetlands is the fact that precipitation and evapotranspiration rates keep the water table above the ground surface for extended periods of time. The subtropical climate is dominated by two modes of seasonal precipitation: relatively dry winters, which contribute only 25–30% of annual precipitation, and wet summers, which contribute 70–75% of annual precipitation (1900–2003 data, *available online*).⁵ There is relatively little temperature differentiation between the winters and summers, with mean daily maximum temperatures $>25^{\circ}\text{C}$ in the winter and $>27^{\circ}\text{C}$ in the summer (Deuver et al. 1994). Extended periods of drought can alter plant community composition in the short term by lowering the water table sufficiently to allow germination of seeds and establishment of different plant species. Prolonged droughts also may lower the water table sufficiently to cause the death of wetland plants and establishment of taxa characteristically found in upland environments such as tree islands (Deuver et al. 1994).

Initial formation of the modern Everglades wetland began with calcitic mud formation as early as 7500–7300 calibrated years before present (cal yr BP; present = AD 1950), based on radiocarbon dating of basal calcitic muds from Kreamer Island in Lake Okeechobee and Corkscrew Swamp in Collier County, Florida (Gleason and Stone 1994). In the modern Everglades wetland, calcitic mud forms in sparsely vegetated marshes, where adequate light exists for growth of calcareous algal

⁵ <http://www.dnr.state.sc.us/climate/sercc>

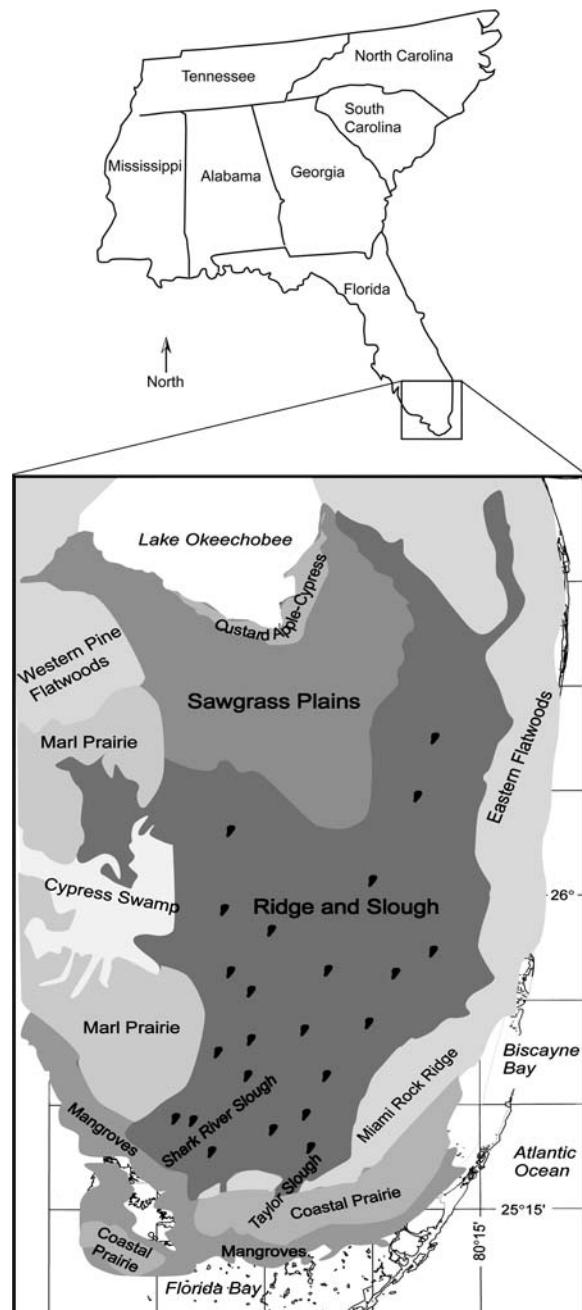


FIG. 2. Reconstructed pre-drainage distribution of vegetation types in the greater Everglades ecosystem (modified from Lodge [2005]). The map shows the location of Florida Everglades within the southeastern United States.

periphyton. These marshes typically have relatively shallow water depths (<0.5 m deep) and short hydroperiods (<6 mo) (Kushlan 1990). Initial peat accumulation began as early as 6300 cal yr BP near the southern end of Lake Okeechobee and 5800 cal yr BP in the northernmost Everglades based on basal peat dates (Gleason and Stone 1994). The oldest and thickest peats (≤ 4.3 m) occur in the northern Everglades and

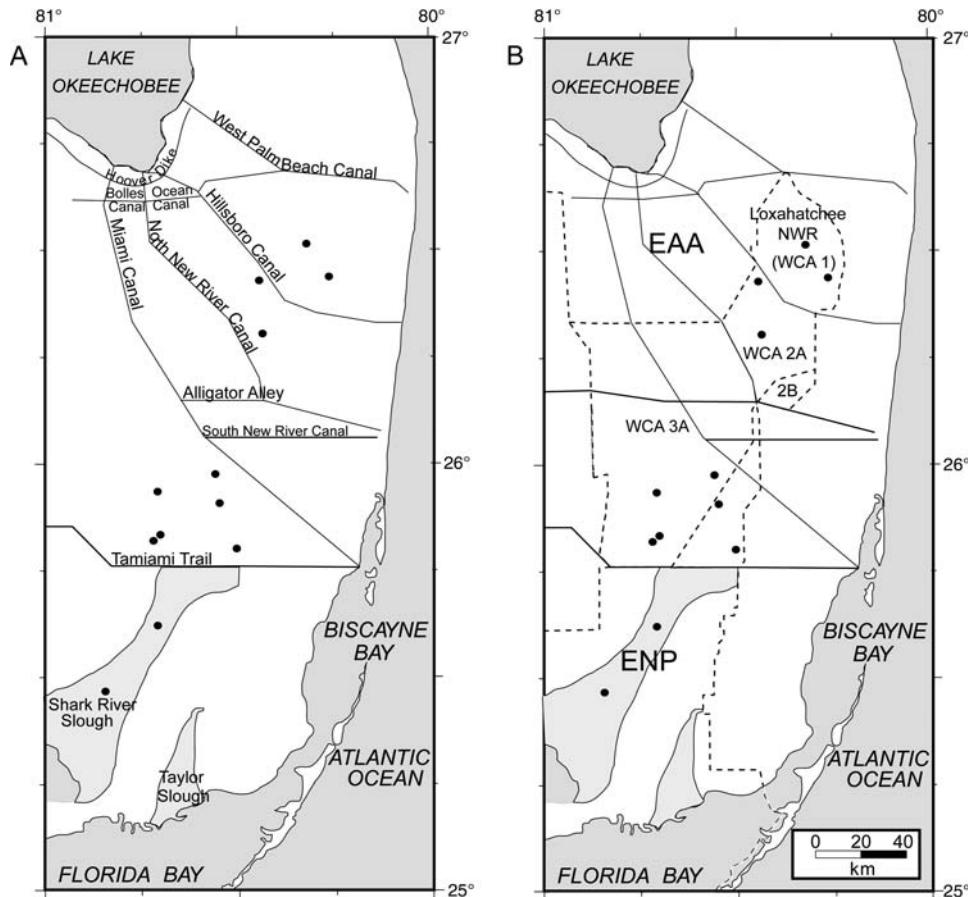


FIG. 3. Evolution of water control structures of the Florida Everglades. Black dots indicate location of tree islands sampled in this study. Dashed lines indicate boundaries of Water Conservation Areas and Everglades National Park. (A) Water control structures in place by 1930. (B) Everglades regions delineated between 1952 and 1965: Everglades Agricultural Area (EAA), Water Conservation Areas (WCA) 1–3 (WCA 1, Arthur R. Marshall Loxahatchee National Wildlife Refuge), and Everglades National Park (ENP).

correspond to the lowest bedrock elevations of the Everglades basin (Parker et al. 1955, Gleason and Stone 1994) (Fig. 4). The longer hydroperiod and deeper water depths at these low points minimized oxidation of organic material sufficiently for peat to begin accumulating. Subsequently, peat accumulation began in the central and southern Everglades, where the oldest basal peats are dated at 5100 cal yr BP (Gleason and Stone 1994).

EVERGLADES TREE ISLAND COMMUNITIES

Tree islands consist of distinct clusters of trees, shrubs, and ferns interspersed throughout sawgrass marshes and waterlily sloughs of the Everglades landscape. Soils on the tree islands typically consist of peat, although tree island heads may have mineral soils exposed on the surface. Three types of tree islands occur in the Everglades: fixed tree islands, strand tree islands, and pop-up (battery) tree islands (Fig. 5). These differ in community composition, distribution within the Everglades, and origin. This study focused entirely on

fixed and strand tree islands, and our discussion is limited to them.

Fixed tree islands are teardrop-shaped, and their long axis runs generally north to south, roughly parallel to flow. The head of the island has the greatest surface elevation (Fig. 5) and is covered by semitropical hardwoods, upland plants that cannot tolerate prolonged flooding, and many ferns. The near tail of the tree island is directly downstream of the head and includes a community with dense ferns, shrubs, aquatic plants, and semitropical hardwoods that can tolerate limited flooding. The far tail contains a mixture of flood-tolerant ferns, shrubs, sedges, and other marsh plants. Surrounding the entire tree island is a transitional zone with dense shrubs, ferns, and aquatic plants. Fixed tree islands in Water Conservation Areas (WCAs) 2 and 3 average 18 ha in area and range from 0.3 to 364 ha, and tree island heads are an average of 1.0 m higher than adjacent marshes (Heisler et al. 2002).

The primary factor controlling the spatial distribution of fixed tree islands appears to be the topography of the

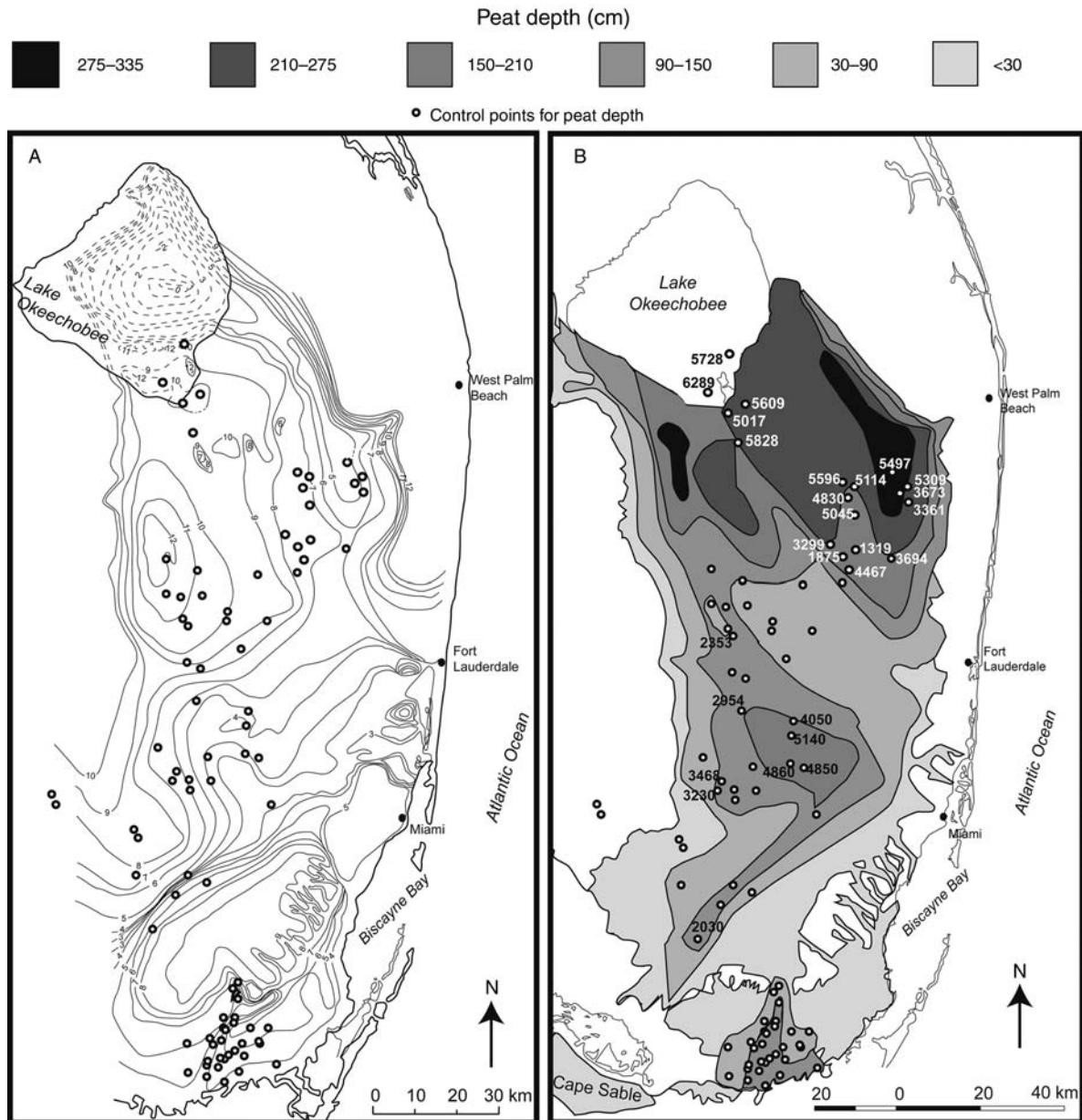


FIG. 4. Geologic and sediment characteristics of the Everglades. (A) Approximate contours on limestone surface underlying peat and marl sediments of the Everglades. Contours are drawn on top of bedrock relative to the Okeechobee datum, 4.4 m below mean sea level (MSL), U.S. Coast and Geodetic Survey. Contour interval is 1 foot (=0.30 m; modified from Parker et al. 1955). (B) Isopach map of peat thickness in the Everglades (modified from Gleason and Stone [1994], incorporating data generated during the current study) and basal dates (calibrated years before present [cal yr BP]) for peats collected throughout the Everglades (from McDowell et al. 1969, Altschuler et al. 1983, Gleason and Stone 1994, Parker et al. 1995, this study).

underlying limestone, with fixed tree islands developing over topographic highs (Loveless 1959, Heisler et al. 2002). This is consistent with palynological evidence from WCA 3B that indicates that water depths were shallower and hydroperiods were shorter on tree island heads than in the surrounding wetlands even before tree island formation (Willard et al. 2002). Tree island tails also were drier than the surrounding wetland, and the vegetational zonation evident on fixed tree islands

reflects the hydrologic gradient from driest conditions on the head to wettest conditions on the tail.

Strand tree islands are found primarily in Arthur R. Marshall Loxahatchee National Wildlife Refuge (NWR). Although strand islands are elongate and oriented parallel to flow, they differ from fixed tree islands both in their shape and community composition. Strand islands taper at both the north and south ends (Fig. 5) and possess fairly uniform vegetation through-

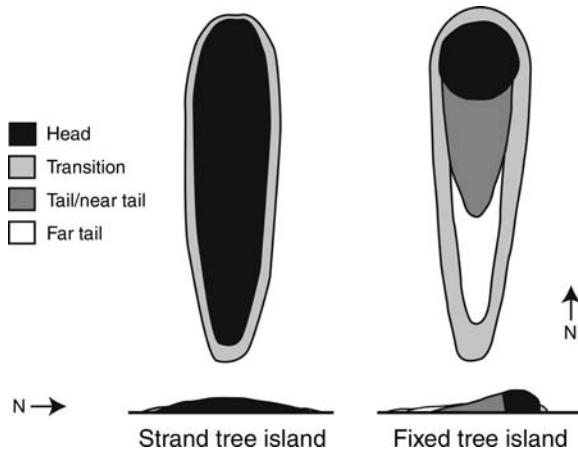


FIG. 5. Graphic representation of two tree island types in the Florida Everglades: a strand tree island and a fixed tree island.

out, lacking the north-south zonation characteristic of fixed tree islands. The central part of a strand tree island is flooded for short periods during the year, and its vegetation typically is dominated by dahoon holly (*Ilex cassine*) and ferns. Strand margins contain a mixture of shrubs and aquatic plants. The size of strand islands is quite variable, with the largest documented island covering 62 ha and others as small as 0.04 ha (Brandt et al. 2002).

Preliminary research indicates that strand tree islands may also have formed on topographic highs (Stone et al. 2002). No intensive sampling efforts have been undertaken, however, to document patterns of plant community development on strand islands. The limited pollen analyses conducted on strand tree islands show a shift from assemblages analogous to marshes and sloughs to fern-dominated assemblages. Stone et al. (2002) integrated pollen and peat petrographic data to conclude that initial strand island vegetation consisted of sawgrass marshes in elevated regions that persisted until either climate change or increased elevation of the peat surface caused sufficiently dry conditions to establish woody vegetation. Based on the shallow depth of hammock peats and occurrence of holly pollen (<15 cm depth), they concluded that strand tree islands are a recent addition to the Everglades wetland.

MATERIALS AND METHODS

Core collection, sampling, geochronology, and analysis of pollen assemblages

We analyzed pollen assemblages from sediment cores collected on 11 islands in Loxahatchee National Wildlife Refuge (NWR) and within the historic Shark River Slough drainage basin. The tree islands include two strand islands within Loxahatchee NWR, two fixed tree islands in WCA 2A, three fixed tree islands in WCA 3A, two fixed tree islands in WCA 3B, and two fixed tree islands in Everglades National Park (Fig. 6, Table 1).

We selected these sites to provide a regional overview of tree island response to climatic and hydrologic change and to provide detailed paleoenvironmental records at sites of particular interest to resource managers (such as drowned tree islands). At each tree island, we collected cores in two transects: one running the length of the tree island and one crossing the head of the tree island (Fig. 6, inset). This sampling scheme makes it possible to document spatial development of individual tree islands and to determine whether tree island size has changed through time. We also collected surface samples of sediment at various sites on the tree islands to document the modern palynological signature of different vegetation types within and adjacent to tree islands.

We collected sediment cores using a piston corer with a 10 cm diameter core barrel. The core barrel was pushed through the sediments until it contacted the underlying limestone at all sites except in Loxahatchee NWR, where peat thicknesses in excess of 2 m would require alternative coring strategies. After core collection, we extruded sediment from the core barrel and sampled it at 1-cm increments for the upper 20 cm and at 2-cm increments at greater depths. We described sediment lithology as samples were extruded. We dried samples in a 50°C oven and subsampled sediments at the base of each core and at 20-cm increments above the base for radiocarbon dating. Bulk peats were dated using conventional radiocarbon dating (Table 1).

Age models for the last century of deposition are based on lead-210 (^{210}Pb) and, where applicable, first occurrences of pollen of the exotic plant *Casuarina*, which was introduced to south Florida in the late 19th century (Langeland 1990). Lead-210 activity was measured by alpha spectroscopy using the method outlined in Flynn (1968) in which ^{210}Pb and its progeny, polonium-210 (^{210}Po), are assumed to be in secular equilibrium. Supported ^{210}Pb activity was determined by continuing measurements until activity became constant with depth. Excess ^{210}Pb activity was calculated by subtracting the supported ^{210}Pb activity from the total ^{210}Pb activity. Accumulation rates were calculated by fitting an exponential decay curve to the measured data using least-squares optimization and making the assumptions of a constant initial excess lead-210 concentration (the constant initial concentration [CIC] model).

In pre-20th century sediments, models are derived from linear interpolation between radiocarbon data points obtained on bulk sediment samples (Table 1), which were calibrated to calendar years using the Pretoria Calibration Procedure (Stuiver et al. 1998, Talma and Vogel 1993). The shorter hydroperiods and shallower water depths on tree island heads result in seasonal drying and oxidation of sediments. We have noted that radiocarbon dates from tree island head sediments appear to be artificially old relative to those in the tail and adjacent marsh. Cores collected in the near tail, directly downstream from the head, have radiocarbon dates and vegetational trends that are consistent

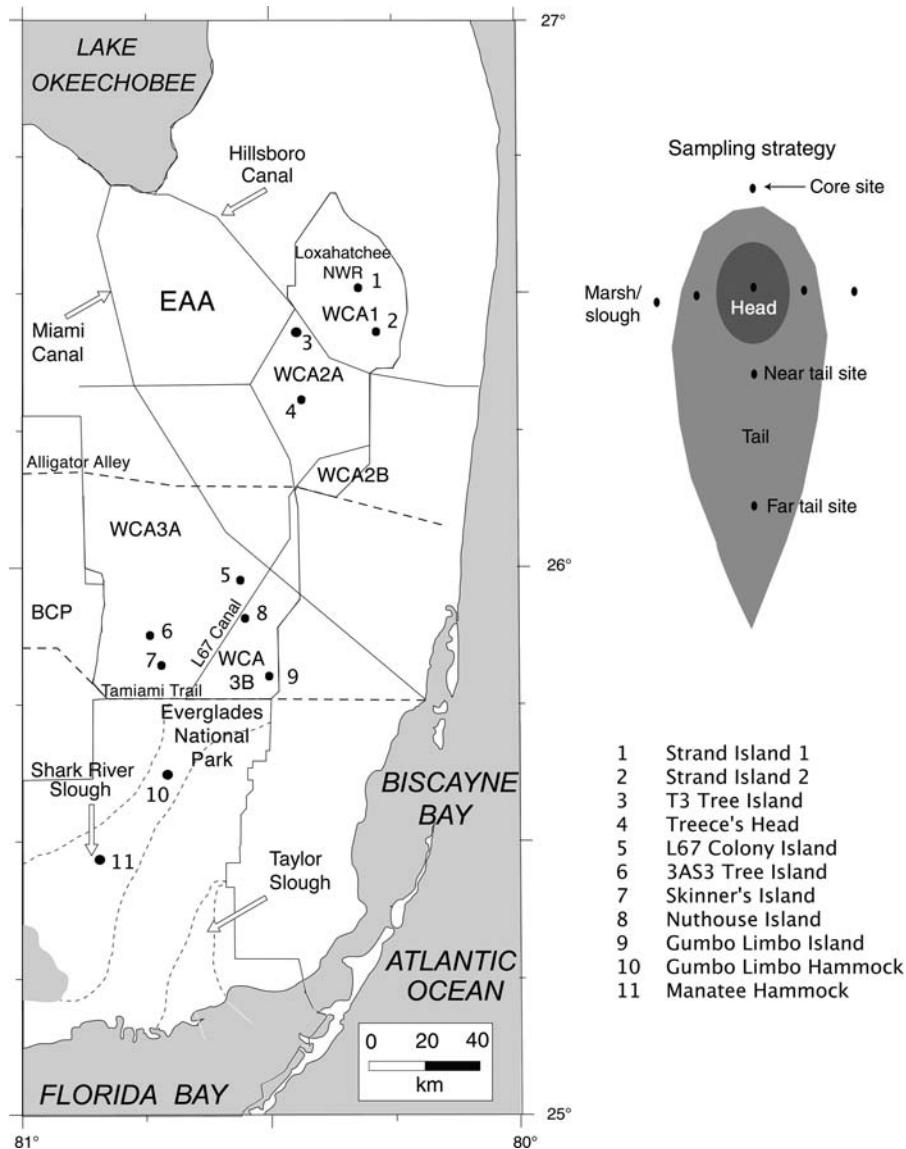


FIG. 6. Location of Everglades tree islands included in this study. The inset map indicates a typical sampling scheme for a fixed tree island. Abbreviations are: BCP, Big Cypress National Preserve; EAA, Everglades Agricultural Area; NWR, National Wildlife Refuge; WCA, Water Conservation Area.

both internally and with adjacent wetlands. Therefore, we used cores from the near tail as our representative sites to detect vegetation changes on teardrop-shaped tree islands and for comparison with patterns documented in the adjacent marsh.

Approximately 0.5–1.0 g of dry sediment was used for palynological analysis. Pollen and spores were isolated from these samples using standard palynological techniques (Traverse 1988, Willard et al. 2001a, b). After drying and weighing samples, *Lycopodium* marker tablets with known concentrations of *Lycopodium* spores were added to ~0.5 g of sediment for calculation of absolute pollen concentrations (Stockmarr 1971). The samples were first acetolyzed (9 parts acetic anhydride: 1

part sulfuric acid) in a hot-water bath (100°C) for 10 min, then neutralized and treated with 10% KOH in a hot-water bath for 15 min. Neutralized samples were sieved with 10- μ m and 200- μ m sieves, and the 10–200 μ m fraction was stained with Bismarck Brown, mixed with warm glycerin jelly, and mounted on microscope slides. Raw data for pollen samples are deposited in the North American Pollen Database (NAPD) at the World Data Center for Paleoclimatology in Boulder, Colorado, USA, and at the US Geological Survey South Florida Information Access (SOFIA) site. Pollen diagrams for all tree islands studied are available in Appendices A–L.

Pollen and spore identification (minimally 300 grains per sample) was based on reference collections of the

TABLE 1. Locality and age information for cores collected on tree islands in the Everglades, Florida, USA.

Accession no.	Core no.	Tree island name and core location	Latitude (N)	Longitude (W)	Sample depth (cm)	$\delta^{13}\text{C}$	Conventional age (yr BP)
144706	00-3-7-1	Loxahatchee Strand, north	26°30.112'	80°18.269'	40–42	–25.5	200
144707	00-3-7-1	Loxahatchee Strand, north	26°30.112'	80°18.269'	60–62	–26.2	900
144708	00-3-7-1	Loxahatchee Strand, north	26°30.112'	80°18.269'	84–86	–25.7	1240
180426	02-05-20-2	Loxahatchee Strand 2, middle	26°26.884'	80°16.730'	64–66	–25.5	630
180427	02-05-20-2	Loxahatchee Strand 2, middle	26°26.884'	80°16.730'	48–50	–25.8	430
180428	02-05-20-2	Loxahatchee Strand 2, middle	26°26.884'	80°16.730'	20–22	–27.6	90
180429	02-05-20-3	Loxahatchee Strand 2, south	26°26.884'	80°16.730'	64–68	–27.2	630
180430	02-05-20-3	Loxahatchee Strand 2, south	26°26.884'	80°16.730'	48–50	–21.6	660
180431	02-05-20-3	Loxahatchee Strand 2, south	26°26.884'	80°16.730'	20–22	–27.5	90
180432	02-05-20-4	Loxahatchee Strand 2, marsh	26°26.884'	80°16.730'	52–54	–27.1	1080
180433	02-05-20-4	Loxahatchee Strand 2, marsh	26°26.884'	80°16.730'	36–38	–26.0	630
180434	02-05-20-4	Loxahatchee Strand 2, marsh	26°26.884'	80°16.730'	20–22	–25.8	360
180450	01-8-8-4	T3 Island, near tail	26°25.243'	80°27.206'	20–22	–26.9	380
180451	01-8-8-4	T3 Island, near tail	26°25.243'	80°27.206'	26–29	–26.5	540
180448	01-8-8-5B	T3 Island, marsh	26°25.490'	80°27.200'	20–22	–26.0	660
180449	01-8-8-5B	T3 Island, marsh	26°25.490'	80°27.200'	33–35	–26.5	1360
131982	99-3-3-2	Treece's Island, marsh	26°18.220'	80°26.254'	20–22	–27.1	140
131983	99-3-3-2	Treece's Island, marsh	26°18.220'	80°26.254'	40–42	–27.2	800
131984	99-3-3-2	Treece's Island, marsh	26°18.220'	80°26.254'	56–58	–27.1	1840
131985	99-3-3-3	Treece's Island, near tail	26°17.981'	80°26.210'	30–32	–27.1	190
150308	99-3-3-3	Treece's Island, near tail	26°17.981'	80°26.210'	50–52	–28.1	950
150309	99-3-3-3	Treece's Island, near tail	26°17.981'	80°26.210'	70–72	–26.7	1610
131986	99-3-3-3	Treece's Island, near tail	26°17.981'	80°26.210'	100–102	–27.2	2200
132409	99-3-3-3	Treece's Island, near tail	26°17.981'	80°26.210'	172–173	–27.5	4030
152791	00-3-8-1A	L67 Colony Island, head	25°57.674'	80°34.346'	20–22	–23.5	1030
152792	00-3-8-1A	L67 Colony Island, head	25°57.674'	80°34.346'	40–42	–21.9	2960
144712	00-3-9-7	Island 3AS3, near tail	25°51.348'	80°46.183'	20–22	–26.5	10
144713	00-3-9-7	Island 3AS3, near tail	25°51.348'	80°46.183'	40–42	–26.3	1110
144714	00-3-9-7	Island 3AS3, near tail	25°51.348'	80°46.183'	62–64	–27.3	1720
123299	98-4-21-H	Nuthouse Island, head	25°53.345'	80°33.750'	10–12	–27.9	134.5 pMC§
123300	98-4-21-H	Nuthouse Island, head	25°53.345'	80°33.750'	28–30	–25.5	770
120691	98-4-21-H	Nuthouse Island, head	25°53.345'	80°33.750'	50–52	–25¶	1890
120692	98-4-21-H	Nuthouse Island, head	25°53.345'	80°33.750'	60–62	–25¶	2470
123292	98-4-21-F	Gumbo Limbo Island, far tail	25°46.486'	80°30.693'	10–12	–27.8	109.2 pMC§
123293	98-4-21-F	Gumbo Limbo Island, far tail	25°46.486'	80°30.693'	30–34	–25.3	2460
120681	98-4-21-F	Gumbo Limbo Island, far tail	25°46.486'	80°30.693'	48–50	–25	3520
120682	98-4-21-F	Gumbo Limbo Island, far tail	25°46.486'	80°30.693'	68–70	–25	4290
175614	98-4-23-N	Skinner's Island, near tail	25°50.496'	80°44.306'	20–22	–27.0	20
175615	98-4-23-N	Skinner's Island, near tail	25°50.496'	80°44.306'	30–32	–26.7	330
175616	98-4-23-N	Skinner's Island, near tail	25°50.496'	80°44.306'	40–42	–26.1	810
175617	98-4-23-N	Skinner's Island, near tail	25°50.496'	80°44.306'	56–58	–26.7	1750
148013	00-8-7-1	Gumbo Limbo Hammock, near tail	25°37.68'	80°44.584'	20–22	–25.2	101.6 pMC§
148310	00-8-7-1	Gumbo Limbo Hammock, near tail	25°37.68'	80°44.584'	40–42	–26.2	990
148014	00-8-7-1	Gumbo Limbo Hammock, near tail	25°37.68'	80°44.584'	60–62	–26.6	2240
148015	00-8-7-1	Gumbo Limbo Hammock, near tail	25°37.68'	80°44.584'	74–76	–25.3	2880
155690	00-8-9-5	Manatee Hammock, near tail	25°29.640'	80°49.357'	30–32	–26.0	690
155691	00-8-9-5	Manatee Hammock, near tail	25°29.640'	80°49.357'	50–52	–26.5	1700
155692	00-8-9-5	Manatee Hammock, near tail	25°29.640'	80°49.357'	70–base	–24.7	2660
180441	00-8-9-2	Manatee Hammock, marsh	25°30.105'	80°48.760'	30–32	–27.3	2080
180440	00-8-9-2	Manatee Hammock, marsh	25°30.105'	80°48.760'	34–36	–27.3	2370
180439	00-8-9-2	Manatee Hammock, marsh	25°30.105'	80°48.760'	48–50	–26.3	2360

Notes: All dates were obtained on bulk peat sediments that underwent either acid washes or a combined acid/alkali/acid wash and were obtained by Beta Analytic (Miami, Florida, USA) using standard radiocarbon dating. Latitudes and longitudes are provided as degrees and decimal minutes relative to the WGS84 datum.

† Calibrated against the Intcal98 database after Stuiver and van der Plicht (1998), Stuiver et al. (1998), and Talma and Vogel (1993). NA, not applicable.

‡ Upper and lower limits based on two sigma errors in calibration.

§ Results for samples containing more ^{14}C than the modern reference standard are reported as “percent modern carbon” (pMC). These results indicate that the material was respiring carbon after the advent of thermo-nuclear weapons testing and is less than ~50 years old.

¶ These values were not measured but are estimates based on peat composition.

TABLE 1. Extended.

1 σ counting error	Calibration intercept (yr BP) [†]	+2 σ (yr BP) [‡]	-2 σ (yr BP) [‡]
50	285	315	0
60	790	940	690
60	1175	1285	995
70	580	680	520
70	500	550	310
70	NA		
60	580	680	530
70	650	700	530
70	NA		
50	970	1075	925
60	585	675	530
60	450	520	295
50	470	520	310
60	540	650	500
60	650	690	540
60	1280	1350	1170
60	140	300	5
60	700	895	655
60	1795	1895	1610
60	170	420	5
60	910	960	730
60	1520	1620	1360
70	2260	2345	2005
50	4467	4802	4412
90	940	1160	750
70	3140	3340	2920
60	NA		
60	985	1170	925
60	1610	1795	1515
0.9	NA		
60	680	775	645
60	1830	1945	1700
70	2650	2750	2340
0.8	NA		
60	2475	2740	2345
60	3755	3925	3635
70	4850	4995	4630
60	NA		
50	380	500	290
60	710	900	660
60	1690	1820	1530
0.7	NA		
60	927	990	760
60	2320	2350	2120
60	2980	3210	2850
60	660	710	550
60	1580	1730	1500
70	2760	2880	2720
60	2030	2300	1895
70	2350	2720	2190
70	2350	2715	2180

U.S. Geological Survey (Reston, Virginia) and Willard et al. (2004). Pollen sums were based on abundance of all identifiable taxa. Our interpretations of past plant communities are based on the quantitative method of modern analogues (Overpeck et al. 1985). We calculated squared chord distance (SCD) between down-core pollen assemblages and a suite of 197 surface samples collected throughout southern Florida in the early 1960s

and 1995–2002 (Willard et al. 2001*b* and this research) to define the similarity between each fossil and modern pollen assemblage. Internal comparison among surface samples from 10 vegetation types indicates that samples with SCD values <0.15 may be considered close analogues (Willard et al. 2001*b*). If analogues were present for a fossil assemblage, we identified the source vegetation for the fossil assemblage as one of the 12 types represented in the modern database. We divided cores into pollen zones based on a combination of visual inspection, objective zonation using CONISS (Grimm 1992), and modern analogues.

Calibration of pollen assemblages and source vegetation

We evaluated the distinctiveness of tree island assemblages relative to those of other wetland types through analysis of surface samples collected throughout the region. Tree island pollen assemblages generally are characterized by high abundances of ferns, comprising >40% of assemblages, compared to <30% in most other settings (Fig. 7). *Pinus* and *Myrica* pollen are rare on tree islands, averaging <6% and <3% of assemblages, respectively. Within the tree islands, zonation of pollen assemblages is evident based on proximity to the tree island head. Trilete ferns (excluding *Osmunda*) dominate assemblages on tree island heads, monolet spores are most common in near-tail assemblages, and far-tail assemblages are dominated by *Osmunda* spores.

In contrast to tree island assemblages, sediments collected in the marshes adjacent to tree islands contain an average of only 10% fern spores, less than the abundance of Cyperaceae and Amaranthaceae pollen, which comprise an average of 18% and 19%, respectively. In sawgrass ridges, ferns also are common (averaging 9.5%), but pollen of *Cladium*, other Cyperaceae, and Amaranthaceae are much more abundant than in tree island assemblages (Fig. 7). *Pinus* pollen, representing the background pollen rain in the Everglades wetland, also is significantly more abundant in sawgrass ridges and marshes adjacent to tree islands (averaging 34.6% and 23.3%, respectively) than on the tree islands themselves.

Because no pollen assemblages from other Everglades wetland communities approach the high abundances of fern spores characteristic of tree island assemblages (Fig. 7), ferns serve as a robust signature of the past existence of tree island vegetation in analysis of sediment cores. Although some sawgrass ridge assemblages contain up to 30% fern spores, their resemblance to incipient tree island assemblages is superficial; tree island assemblages do not contain the high abundance of *Cladium* and *Pinus* pollen preserved in sawgrass ridges. Tree species on tree islands typically are insect-pollinated, so their pollen is poorly represented in tree island sediments. Therefore, pollen assemblages from tree islands do not provide good estimates of the diversity or abundance of tree species on the tree islands, even though they provide

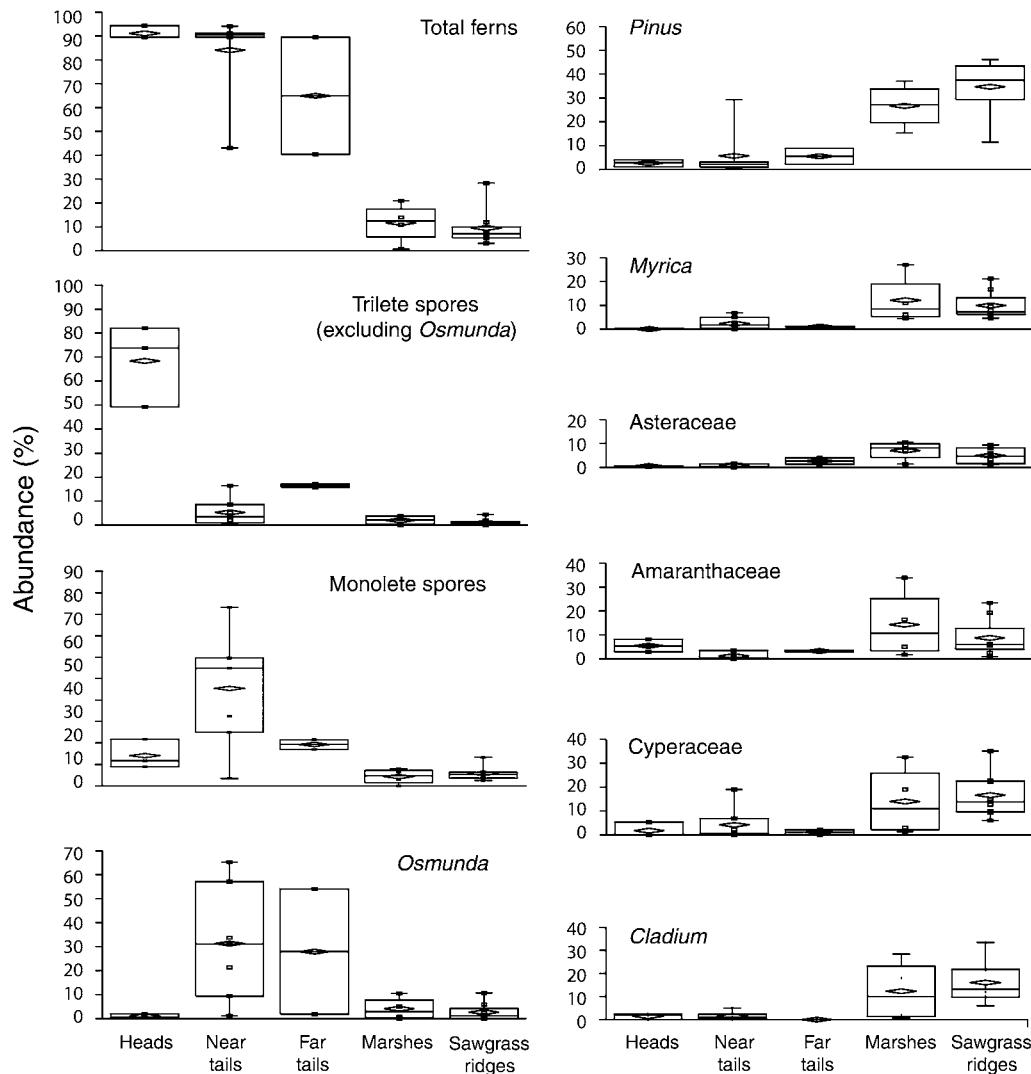


FIG. 7. Tukey box and whisker plots of abundance of palynomorphs of different plant groups in surface samples collected on tree island heads, tree island near tails, tree island far tails, sawgrass marshes near tree islands, and sawgrass ridges. Points indicate individual sample abundance, and the diamond indicates the mean. The horizontal line inside the box indicates median abundance for the vegetation type. Pollen abundance data from sawgrass ridges were obtained from Bernhardt et al. (2004).

a reliable means to distinguish the past occurrence tree island and marsh vegetation.

RESULTS

Pollen assemblages from strand tree islands

We analyzed pollen assemblages from cores collected on two strand islands in the central and southeastern parts of Loxahatchee NWR (Fig. 6, sites 1–2; Table 1). Three pollen zones are identifiable in strand island assemblages: basal zone 1, representing marsh assemblages; zone 2, representing pre-drainage tree island vegetation; and uppermost zone 3, representing post-drainage tree island vegetation (Fig. 8). Zone 1 is present only in the core from central strand island 2 and is characterized by the common occurrence of

marsh plants, including *Nymphaea*, *Sagittaria*, *Amaranthaceae*, and *Poaceae* (Fig. 8A). *Pinus* and *Myrica* pollen also are common, representing the background pollen rain of the Everglades. These pollen assemblages are similar to those from sawgrass marshes, and sloughs throughout the Everglades. Zone 2 is dominated by fern spores, primarily *Blechnum*, *Thelypteris*, and *Osmunda regalis*, and greater abundance of the *Asteraceae*. Pollen of *Amaranthaceae*, *Sagittaria*, *Nymphaea*, and *Pinus* are less abundant than in zone 1. Assemblages in zone 2 are analogous to near tails and heads of tree islands. Assemblages in zone 3 are characterized by combined sums of *Myrica* and *Ilex* pollen that exceed 60% and decreased abundance of fern spores (Fig. 8). These assemblages are analogous

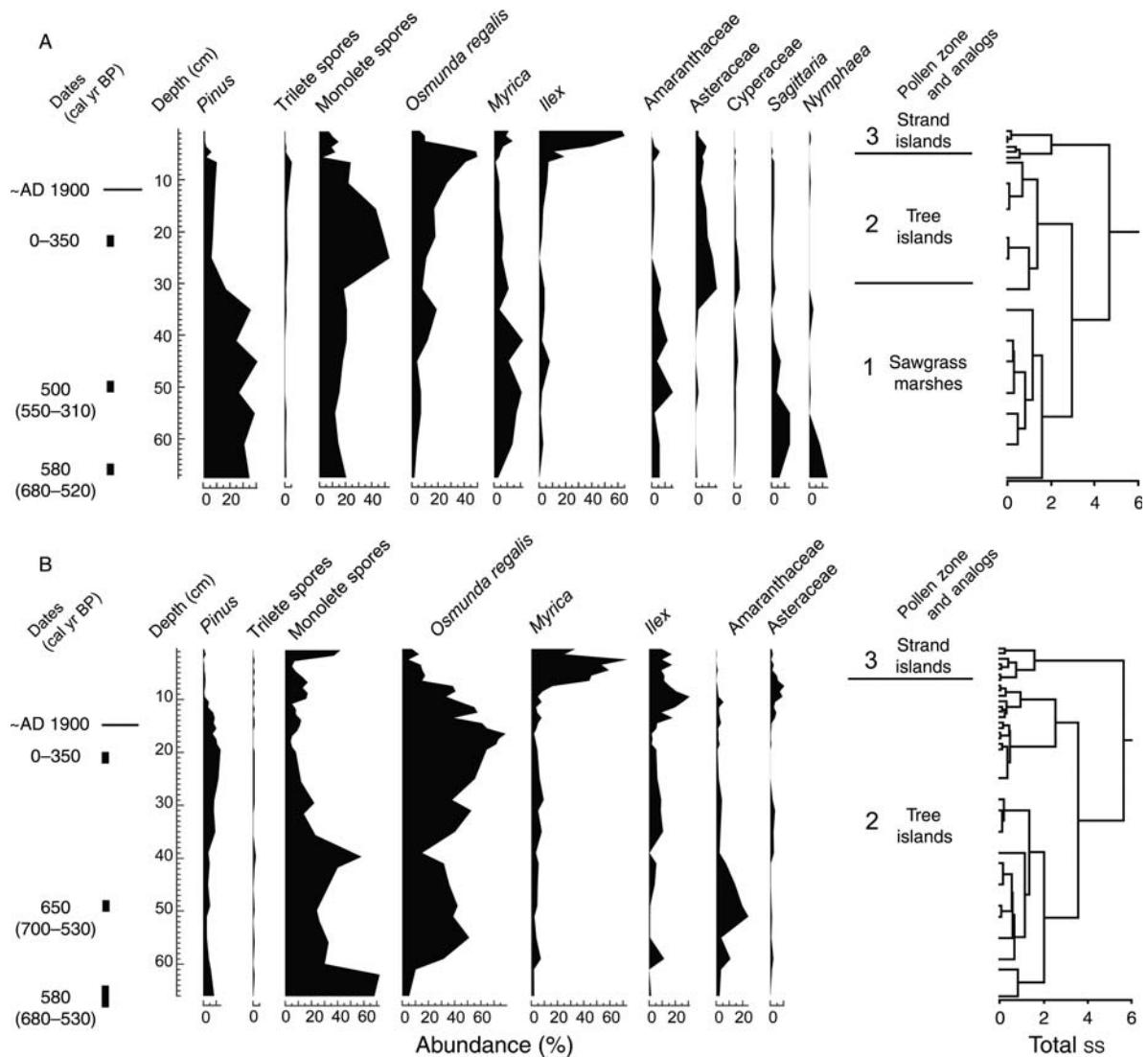


FIG. 8. Percentage abundance of pollen of major plant groups in cores collected on Loxahatchee Strand Island 2: (A) core 02-05-20-2, collected in the center of the strand; (B) core 02-05-20-3, collected in the south end of the strand. Dates are in calibrated years before present (cal yr BP). Dendrograms generated from constrained incremental sum of squares cluster analysis (CONISS; Grimm 1992) were used to define pollen zones.

to modern strand islands located throughout Loxahatchee NWR.

Pollen assemblages from fixed tree islands

We analyzed pollen assemblages from cores collected on nine fixed tree islands in WCAs 2A, 3A, 3B, and Everglades National Park (Fig. 6, sites 3–11). Pollen assemblages from all cores are divisible into three zones representing a common pattern of tree island development, although the timing and details of transitions vary with location in the Everglades wetland. We present data from two sites (Fig. 9) that are representative of patterns observed in all fixed tree island records. Pollen diagrams from other sites are available in Appendices A–L. Basal zone 1 represents marsh vegetation that occupied the

sites before initiation of tree island development. These assemblages are dominated by a combination of *Pinus* and *Amaranthaceae* pollen (Fig. 9), and *Cyperaceae*, *Cladium*, *Typha*, and *Nymphaea* are common locally. Assemblages in this zone are analogous to sawgrass marshes, ridges, and sloughs throughout the Everglades ecosystem. In zone 2, fern spores dominate assemblages. These include *Osmunda regalis*, *Acrostichum danaeifolium*, *Blechnum*, *Thelypteris*, and other fern taxa that cannot be distinguished in the palynological record (Fig. 9). *Pinus* pollen abundance is lower in zone 2, although it is common. Typically, zone 2 is divisible into two intervals: an early phase, with persistence of marsh species, and a late phase, with greater abundance of shrubs and species characteristic of shorter hydroperiods

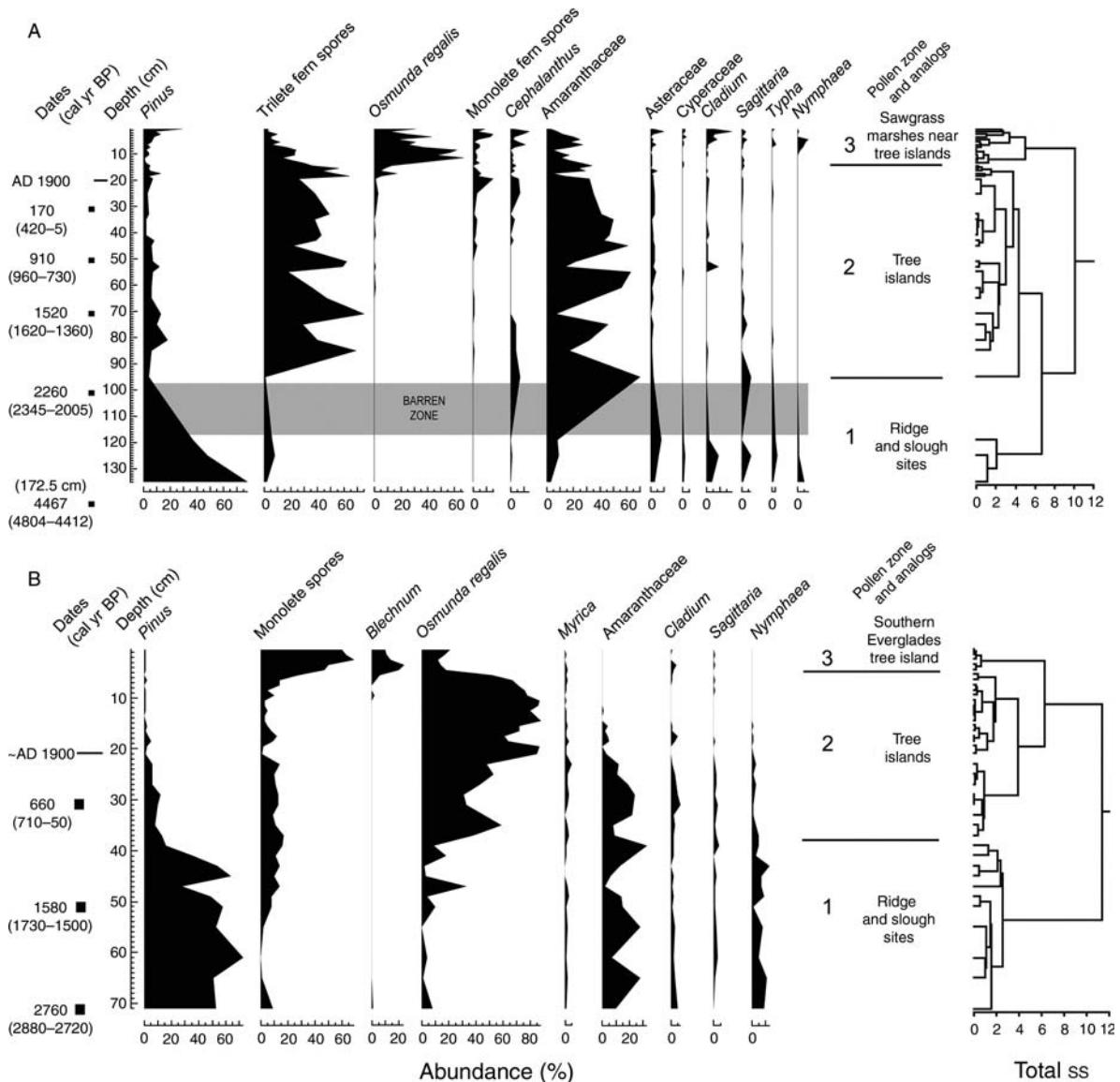


FIG. 9. Percentage abundance of pollen of major plant groups in cores collected on fixed tree islands: (A) Treece's Island, Water Conservation Area 2A; core 99-3-3-3, collected in near tail; (B) Manatee Hammock, Everglades National Park; core 00-8-9-5, collected in near tail of tree island. Dates are in calibrated years before present (cal yr BP). Dendrograms generated from constrained incremental sum of squares cluster analysis (CONISS; Grimm 1992) were used to define pollen zones.

and lower abundance of marsh species. Assemblages in zone 2 are most closely analogous to tree island sites, including heads, near tails, and far tails, but they commonly lack close modern analogues. The composition of pollen assemblages of zone 3 varies with location within the Everglades ecosystem, but this zone consistently represents a distinctive change in composition from zone 2. In some instances there is a shift in dominance of one fern species to another, such as a shift from dominance of *Osmunda regalis* to monolete fern spores produced by *Blechnum* and other fern species (Fig. 9B, Appendix F). In other cases, pollen of marsh and slough taxa such as *Cladium* and *Nymphaea* increase at

the expense of fern spores (Fig. 9A). Analogues for zone 3 vary with location in the Everglades, but they typically are analogous to the assemblages representing the present vegetation at the site.

DISCUSSION

Patterns of strand tree island development

Our preliminary paleoecological research on Loxahatchee NWR strand tree islands is suggestive of a consistent pattern of strand island development, although further studies are necessary to verify these trends. Because we collected relatively short cores (<2 m) that did not reach bedrock on the Loxahatchee

TABLE 2. Timing of tree island development and maturation in the Florida Everglades.

Map ID	Tree island and core	Location	Tree island timing (yr AD or BC)	
			Initial development	Maturation
1	Lox Strand 1	Loxahatchee NWR	pre-AD 750	NA
2	Lox Strand 2, middle	Loxahatchee NWR	AD 1500–1700	NA
2	Lox Strand 2, south	Loxahatchee NWR	pre-AD 1300	NA
3	Tree Island T3, near tail†	WCA 2A	undetermined	post-AD 1600
4	Treece's Island, near tail	WCA 2A	1050–150 BC‡	AD 1200–1400
5	L67 Colony Island, head	WCA 3A	AD 600–800	AD 1500–1600
6	Tree Island 3AS3, near tail	WCA 3A	pre-AD 300	AD 1600–1800
7	Skinner's Island, near tail	WCA 3A	AD 1200–1400	post-AD 1900
8	Nuthouse Island, head	WCA 3B	AD 300–400	AD 1200–1400
9	Gumbo Limbo Island, far tail	WCA 3B	1500–1200 BC	AD 600–800
10	Gumbo Limbo Hammock, near tail	Everglades National Park	AD 700–800	AD 1500–1700
11	Manatee Hammock, near tail	Everglades National Park	AD 750–950	AD 1200

Notes: Map ID's refer to Fig. 6. Abbreviations are: Lox, Loxahatchee; NWR, National Wildlife Refuge; WCA, Water Conservation Area.

† Highly compacted core collected at this site makes confident construction of an age model problematic.

‡ The broad range in dates is due to the occurrence of a palynologically barren zone that encompasses this transition.

strand islands, only the core from the central part of Strand Island 2 includes peat that accumulated before tree island formation. Pollen assemblages from this core indicate that sawgrass marshes and sloughs occupied the site before development of tree island vegetation. These data are consistent with observations from a single undated core analyzed by Stone et al. (2002) from another strand island in Loxahatchee NWR. Tree island vegetation, similar to that on fixed islands, succeeded the initial marsh stage. These assemblages are characterized by a diverse fern assemblage and greater abundance of the Asteraceae, *Myrica*, and *Ilex* than in initial marshes. The abundance of *Blechnum*, *Thelypteris*, and *Osmunda* spores in strand island assemblages indicates that hydrologic conditions on predrainage strand islands were comparable to those of near tails of fixed tree islands. These environments are drier than marshes that previously occupied the site, indicating that intervals of shorter hydroperiod and shallower water depth coincided with tree island initiation and development. Significant changes occurred during the 20th century, when sharp increases in abundance of *Ilex* and *Myrica* indicate a shift to the modern holly-dominated tree islands.

Although our cores are too short to determine the timing of strand island initiation at all sites, our data indicate that the initial tree island communities were established as early as AD 750 (Table 2). Analysis of multiple cores from strand island 2 also indicates a time transgressive development of tree island vegetation within a single strand island. At the southern site, tree island vegetation was established before AD 1300, but sawgrass marshes and sloughs occupied the central site at the same time. Tree island vegetation was not established there until AD 1500–1700, at least 200 years later than the southern site (Table 2). Assuming accuracy of radiocarbon dates, these data suggest that tree island vegetation in the central part of the strand island may have developed from a merger of two smaller

tree islands. Analysis of a core from the northern part of the strand island, as well as additional coring of this and other strand islands, is necessary to verify such an interpretation. The timing of the shift to tree island vegetation at the central site suggests that expansion of smaller tree islands into a strand island occurred during regional drying associated with the Little Ice Age.

Our pollen-based interpretations differ somewhat from one based on peat petrography (Stone et al. 2002). Petrographic data indicate a basal layer of waterlily peat, succeeded by a zone of sawgrass peat, and topped by a layer of forest peat in the upper 20–40 cm. Because only the thin upper layer of forest peat was interpreted as representing tree island vegetation, Stone et al. (2002) suggested that the strand tree islands of Loxahatchee NWR are geologically very young features. However, when palynological and petrographic evidence are integrated, the sawgrass peat is characterized by common occurrence of fern spores, analogous to our zone of incipient tree island vegetation, and the forest peat corresponds to the interval dominated by *Ilex* pollen. We interpret the shift from waterlily to sawgrass peat as the initiation of strand island vegetation and the shift to forest peat as evidence for the onset of post-drainage strand island vegetation.

Patterns of fixed tree island development

A consistent pattern of vegetational development occurs on all fixed tree islands studied, regardless of location in the Everglades. Prior to tree island development, marshes analogous to modern sawgrass marshes near tree islands and sawgrass ridges occupied the sites of modern tree islands. Assemblages in adjacent marshes are analogous to sloughs and sawgrass marshes, characteristic of longer hydroperiods and deeper water depths than sites of tree island formation. Incipient tree island vegetation succeeded the initial marshes, apparently consisting of a mixture of *Amaranthus*, Asteraceae, shrubs, ferns, and marsh taxa. The mature tree island

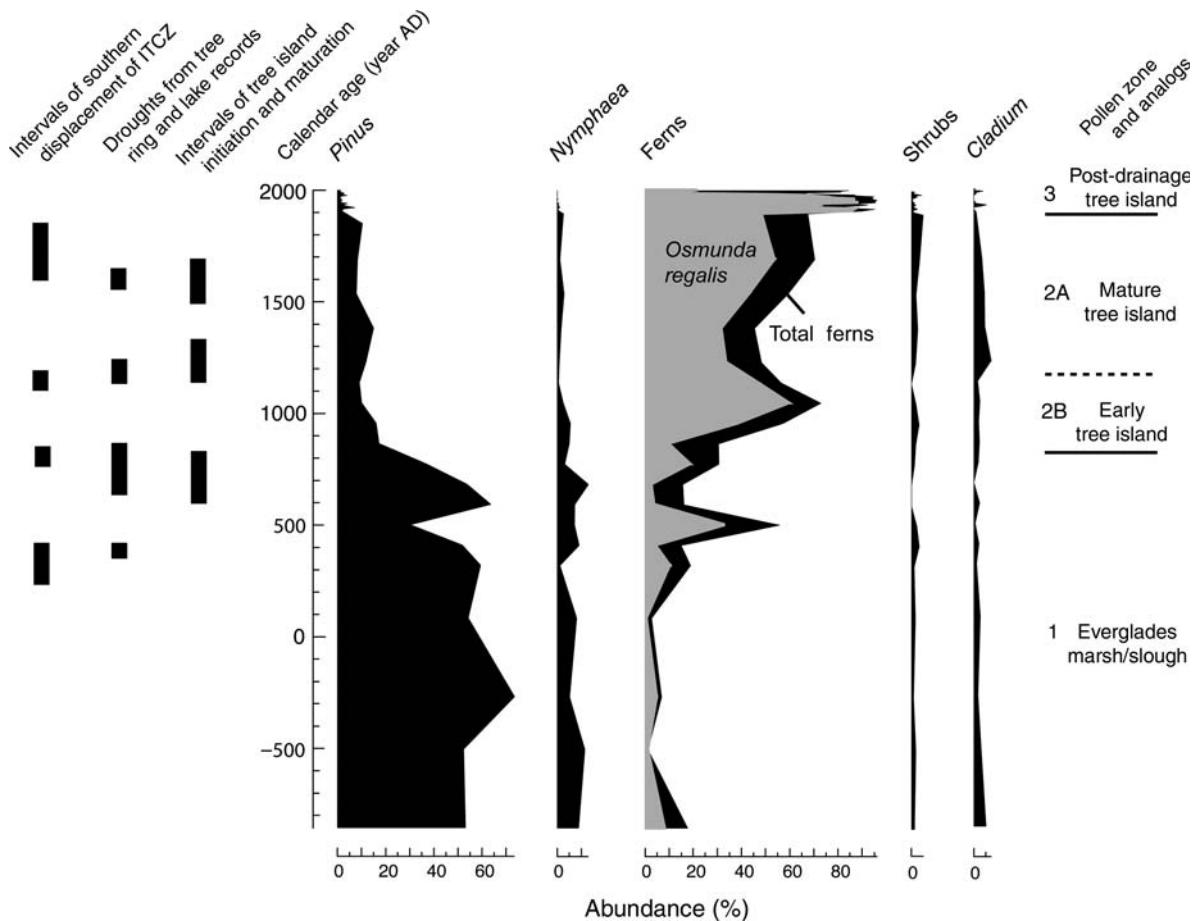


FIG. 10. Temporal trends in abundance of major plant taxa in the near tail of Manatee Hammock, Everglades National Park. Vegetation descriptions of each pollen zone are based on closest modern analogs for each fossil sample. Black bars indicate approximate duration of intervals of southern displacement of the Intertropical Convergence Zone (ITCZ) (Haug et al. 2001) and multidecadal droughts identified from tree ring and lake records (Stahle et al. 1988, Stahle and Cleaveland 1992, Hodell et al. 1995, 2005a, b; E. R. Cook and P. J. Krusic, The North American drought atlas, available online; see footnote 6). Although the timing of tree island development varies throughout the Everglades, the general trends are consistent throughout and occur during intervals of sustained drought.

phase is represented by near absence of marsh taxa, increased abundance of shrubs, and shifts in composition of fern assemblages. Trees would have been well-established in the mature phase, even though they are poorly represented in the pollen record. Mature tree island communities persisted until the early to mid-20th century, when local hydrologic changes affected community composition throughout the region (Davis et al. 1994, Light and Dineen 1994). At sites studied for both geochemistry and palynology, correlations were observed between phosphorus content and stages of tree island development. During the incipient tree island phase, phosphorus content of sediments was elevated over baseline marsh levels, and it reached the greatest concentrations during the mature tree island phase (Orem et al. 2002, Willard et al. 2002, Orem 2006). These high phosphorus concentrations may be derived from guano from the birds that began occupying sites of modern Everglades tree islands after development of

incipient tree island vegetation at the sites. Birds use tree islands for foraging, reproduction, and protection from predators (Gawlik et al. 2002), so their apparent presence on incipient and mature tree islands implies greater surface elevations and greater vegetation height than in adjacent marshes.

Impacts of climate variability on fixed tree island development

Factors that facilitate tree island formation and development have been the subject of some debate. Possible contributors include climatically induced changes in hydrology, 20th century water management practices, topographic changes due to excavation by Native Americans, and natural wetland successional patterns. Because our study has focused on cores from near tails of tree islands rather than tree island heads, we have generated no archeological evidence pertinent to occupation of the sites by Native American communi-

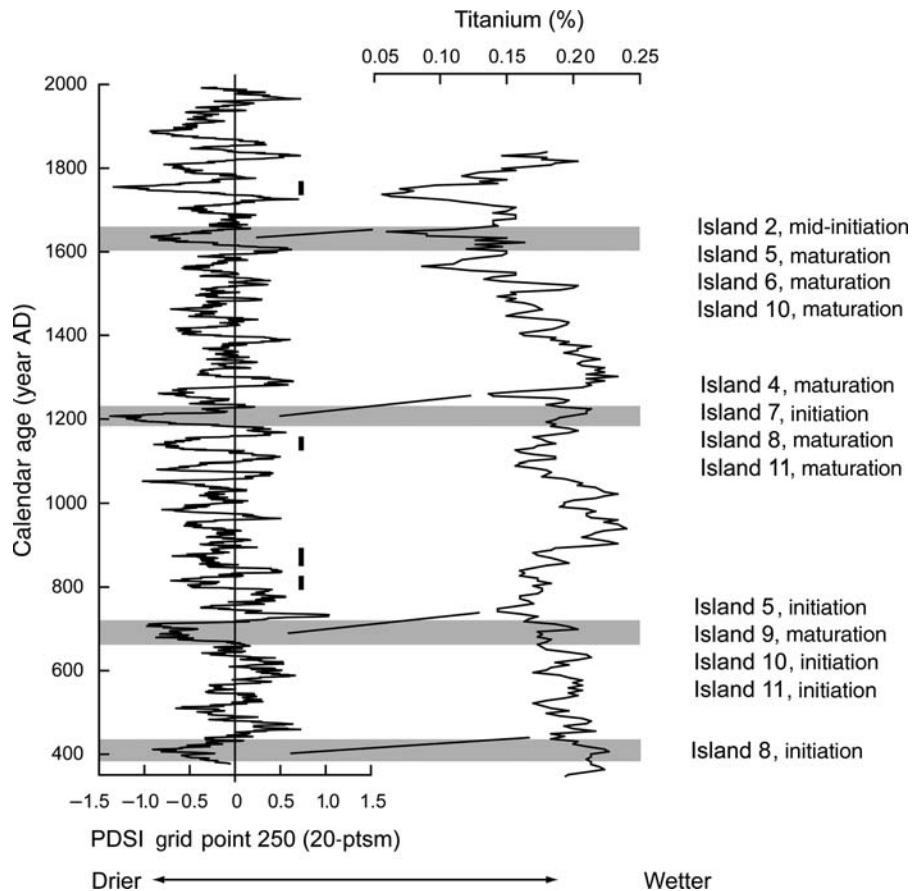


FIG. 11. Comparison of Palmer Drought Severity Index (PDSI) from site 250, southern Florida, titanium record of the position of the Intertropical Convergence Zone (ITCZ), and timing of tree island initiation and maturation (indicated by gray boxes). The PDSI record is a 20-point smooth (ptsm) of data obtained from grid point 250 of E. R. Cook and P. J. Krusic, *The North American drought atlas* (*available online*; see footnote 6). The titanium record was obtained from Haug et al. (2001). Note that the first documented interval of tree island formation (1500–1200 BC) precedes the PDSI period of record.

ties. However, our data do address the relative impacts of climate variability and anthropogenic activities on Everglades tree islands. These data indicate that the timing of tree island development has varied across the system, with the timing of initial development ranging from ~1500 BC to approximately AD 1400 (Table 2).

Although the timing of tree island development is variable, periods of tree island initiation and maturation correspond to intervals of sustained multidecadal drought documented elsewhere in the region (Fig. 10). Incorporating the errors inherent to age models from tree island cores, we have identified several periods of tree island development at the study sites: 1500–1200 BC, AD 300–400, AD 600–900, AD 1200–1400, and AD 1500–1800 (Fig. 11). These periods generally correspond to drought intervals documented by gypsum horizons, oxygen isotope ratios, and benthic foraminiferal assemblages in lakes of the Yucatan Peninsula of Mexico (Hodell et al. 1995, 2005a, b, Curtis et al. 1996, Rosenmeier et al. 2002) and the Cariaco Basin off the Venezuelan coast (Haug et al. 2003). When compared to

reconstructions of the Palmer Drought Severity Index (PDSI) from tree ring records in the southeastern United States for the last 1600 years (E. R. Cook and P. J. Krusic, *The North American drought atlas*, Lamont-Doherty Earth Observatory and the National Science Foundation, *available online*;⁶ Fig. 11), these intervals each encompass multidecadal droughts. These droughts lasted from 21 to 44 years and include repeated 5–12-year periods of sustained negative PDSI separated by only one- or two-year periods of positive PDSI. During these droughts, annual PDSI values are consistently less than -0.5 and typically range between -1 and -3 , indicating mild to moderate droughts. Five of these intervals are correlated with times of tree island initiation and maturation, and we identified four other intervals of multidecadal drought favorable for tree island development (Fig. 11). It seems likely that other tree islands not included in this study may have developed during any of these drought intervals.

⁶ (<http://iridl.ldeo.columbia.edu/SOURCES/.LDEO/.TRL/.NADA2004/.pdsi-atlas.html>)

Where we have complementary records from adjacent marshes, intervals of initiation and maturation of tree islands are characterized by greater abundance of pollen of drought indicators (Amaranthaceae), weedy species (Asteraceae), or trees (*Myrica*) (Appendices C, D, E; Fig. 9A). This indicates sufficient lowering of the water table for expanded abundance of weedy species in marshes and sloughs while ferns and shrubs became established on tree island sites. The apparent persistence of shallower water depths and tree island vegetation after drought intervals indicates that peat accumulation was sufficient to maintain shallower depths and shorter hydroperiods over the long term, and this pattern was repeated for eventual maturation of the tree island. The similar timing of hydrologic changes affecting tree islands and marshes and droughts in the southeastern United States and Central America indicates that climate changes had a large impact on plant communities of the Everglades. Combined with the influence of substrate topography on tree island distribution, this evidence points to allogenic processes as a dominant control on Everglades wetland development.

Comparison of the PDSI record with the titanium record of the Intertropical Convergence Zone (ITCZ) migration from the Cariaco Basin (Haug et al. 2003) shows an apparent correlation between these multi-decadal and long-term intervals of southward displacement of the ITCZ (Fig. 10). Seasonal rainfall patterns in south Florida, with wet summers and dry winters, mirror those of Central America and northern South America, and seasonal and longer-term patterns are related to fluctuations in position of the ITCZ and the strength of the North Atlantic (Azores-Bermuda) subtropical high pressure system. Droughts associated with the Little Ice Age (AD 1550–1850) previously have been documented in Everglades marshes (Willard et al. 2001a), and the onset of regionally drier conditions during this time is indicated both by changes in tree island vegetation and sharp increases in abundance of tree and shrub pollen elsewhere in the wetland. These observations are consistent with previous research (Black et al. 1999) that suggested that the ITCZ was positioned farther south than average during the Little Ice Age. The coincidence of more arid conditions in the Everglades and other circum-Caribbean sites indicates the coherence of climate patterns in both tropical and subtropical regions of North America and suggests that they resulted from broad-scale changes in atmospheric and oceanic circulation patterns.

Impacts of altered water management practices on Everglades tree islands

Physical restructuring of wetland ecosystems encompassing tree islands represents a primary stressor on the tree island biota (Wetzel 2002). Examples of such restructuring include construction of drainage ditches and levees and agricultural use of land. Such changes alter hydroperiod and water depth, fire regime, and

nutrient status, among others. In the Everglades, these changes have been underway since early in the 20th century and are divisible into those of the early 20th century (1910–1930) and those associated with the C&SF Project (1950–1970) (Fig. 3). The resulting flow reductions are due to both the direct reduction of flow through the system by water management practices and reduced precipitation due, at least in part, to land cover changes. Cumulative changes in land cover throughout the 20th century have been shown capable of reducing summer precipitation and increasing daytime temperature, consistent with observational data from the same interval (Marshall et al. 2004), magnifying the drier conditions resulting directly from water management.

The response of Everglades tree islands to each period of construction varies with their location within the ecosystem. In Loxahatchee NWR, disruption of sheet flow by the Hoover Dike and Ocean Canal in the early 20th century (Fig. 3A) resulted in minor increases in abundance of shrubby taxa. The most significant compositional changes occurred after the entire refuge was encircled by levees and canals in 1961 (Brandt et al. 2002; Fig. 3B). This effectively rerouted water from sheet flow through the marsh into canals surrounding the refuge; as a result, precipitation became the primary water source, effectively shifting from a minerotrophic to an ombrotrophic wetland. The resulting changes in hydroperiod, water depth, and possibly nutrient status allowed for greater abundance of woody species (*Ilex*, *Myrica*) on the tree islands and weedy species in the marsh (Fig. 8, Appendices A, B).

Construction of the Hoover Dike, Cross Canal, and Hillsborough Canal (Fig. 3A) in the early 20th century also influenced wetland composition in central WCA 2A. Decreased sheet flow throughout WCA 2A resulted in increased abundance of weedy species in marshes and ferns on tree islands. Completion of water control structures delineating WCA 2A in the early 1960s further altered hydroperiods. The initial water regulation scheme was set too high, and the marsh was continuously flooded between 1961 and 1980, except for drought years and one experimental drawdown (Worth 1988). On Treece's Island, pollen assemblages record these high water levels in decreased abundance of fern spores and up to an eightfold increase in abundance of *Nymphaea* pollen between 1960 and 1980 (Fig. 9A). This unprecedented increase in *Nymphaea* abundance corresponds to an interval during which tree islands began to disappear and wet prairies were converted to sloughs (Worth 1988). After 1980, a new regulation scheme, with more frequent drawdowns and periodic exposure of marsh soils, was put in place. The greater abundance of *Cladium* and Asteraceae pollen at Treece's Island (Fig. 9A, Appendix E) represents the vegetational response to the new regulation scheme, which is a closer approximation of the natural hydroperiod.

All sites in WCA 3A and 3B were affected by construction of the Miami, North New River, and

Hillsborough Canals, as well as the Bolles and Cross Canals and Hoover Dike farther north. Moderate vegetational changes, mirroring the effect of reduced hydroperiods, occurred in the early 1900s, consisting primarily of increased abundance of shrub taxa and decreased abundance of marsh species. Construction of levees demarcating WCA 3A and WCA 3B further affected the tree islands. At site 3AS3 in WCA 3A, a shift from *Osmunda* to monoete spores indicates a shift from wetter conditions, such as those found in the near tail, to drier conditions more characteristic of a tree island head (Appendix G). Farther south at Skinner's Head, the opposite pattern is observed (Appendix H); this may reflect the onset of wetter conditions after water pooled in southernmost WCA 3A, lengthening hydroperiods (Heisler et al. 2002). Similar conditions were documented in WCA 3B, where the abundance of *Osmunda* spores increased and shrub pollen abundance decreased after 1960 (Appendix I, J).

In the early 20th century, sites in Everglades National Park were affected by all the water control structures discussed above as well as the Tamiami Trail. After construction of these structures, tree island and marsh sites of Everglades National Park were characterized by decreased abundance of pollen of the Amaranthaceae and other marsh plants and greater abundance of tree and shrub pollen (Appendix L). Even more striking changes occurred after construction of the C&SF Project in the 1950s. Monoete fern spores, characteristic of tree island heads, dominated assemblages, whereas *Osmunda* abundance decreased sharply (Fig. 9B, Appendix K). The abundance of shrub species on tree islands increased, as did *Cladium* and *Myrica* in nearby marshes. These changes indicate that heads of large tree islands in Everglades National Park expanded southward in response to decreased sheetflow in the mid-20th century.

CONCLUSIONS

1) Formation of Everglades tree islands typically predates significant human alteration of wetland hydrology. Tree islands examined in this study began developing 500-3500 cal yr BP, during multidecadal intervals of sustained drought.

2) Fixed tree island development follows a common pattern throughout the Everglades. Fixed tree islands formed on topographic highs, where hydroperiods were shorter and water depths were shallower than the surrounding marsh. Initial tree island vegetation was established during periods of sustained drought and consisted of shrubs, weedy annuals, and ferns. Peat accumulation resulted in increasing elevation of the ground surface and shortening of hydroperiods, and trees and shrubs became more prominent components of the vegetation. Mature tree island vegetation was established during later sustained periods of drought. The great impact of climate variability on Everglades plant communities indicates that allogenic processes

played a dominant role in development of the Everglades wetland.

3) The multidecadal intervals of drought that triggered changes in tree island vegetation correspond to drought intervals documented in Central and South America and to periods of southward displacement of the Intertropical Convergence Zone. These correlations indicate a coherence of climate patterns in subtropical North America and the Northern Hemisphere Neotropics.

4) Hydrologic modification of the Everglades wetland during the 20th century altered composition of tree island plant communities and affected tree island size. Vegetational response depends on the location within the system and the magnitude of hydrologic change.

ACKNOWLEDGMENTS

We thank colleagues at the South Florida Water Management District, Florida Fish and Wildlife Conservation Commission, Loxahatchee National Wildlife Refuge, and Everglades National Park for guidance in site selection and extensive logistical support for field work. In particular, we are grateful to Lorraine Heisler, Tim Towles, Mike Korvela, Dan Mason, Fred Sklar, Laura Brandt, David Jones, and Tom Armentano for their guidance in the field and willingness to share their knowledge on tree island ecology. Field and laboratory support was supplied by Bill Orem, Margo Corum, Harry Lerch, David Korejwo, Lisa Weimer, Patrick Buchanan, Neil Waibel, Andrew Fagenholtz, Julie Damon, Andrew Lavenburg, Jim Murray, and Tom Sheehan. We thank Cliff Hupp, Lynn Wingard, Mark Brenner, and an anonymous reviewer for thoughtful comments of the manuscript. This research was supported by the U.S. Geological Survey South Florida Priority Ecosystem Studies Program.

LITERATURE CITED

- Altschuler, Z. S., M. M. Schnepfe, C. C. Silber, and F. O. Simon. 1983. Sulfur diagenesis in Everglades peat and origin of pyrite in coal. *Science* **221**:221-227.
- Bernhardt, C. E., D. A. Willard, M. Marot, and C. W. Holmes. 2004. Anthropogenic and natural variation in ridge and slough pollen assemblages. U.S. Geological Survey Open-file Report 2004-1448.
- Black, D., L. C. Peterson, J. T. Overpeck, A. Kaplan, M. N. Evans, and M. Kashgarian. 1999. Eight centuries of North Atlantic Ocean atmosphere variability. *Science* **286**:1709-1713.
- Brandt, L. A., K. M. Protier, and W. M. Kitchens. 2000. Patterns of change in tree islands in Arthur R. Marshall Loxahatchee National Wildlife Refuge from 1950 to 1991. *Wetlands* **20**:1-14.
- Brandt, L. A., J. E. Silveira, and W. M. Kitchens. 2002. Tree islands of the Arthur R. Marshall Loxahatchee National Wildlife Refuge. Pages 311-335 in F. H. Sklar and A. van der Valk, editors. *Tree islands of the Everglades*. Kluwer Academic, Dordrecht, The Netherlands.
- Curtis, J. H., D. A. Hodell, and M. Brenner. 1996. Climate variability on the Yucatan Peninsula (Mexico) during the past 3500 yr, and implications for Maya cultural evolution. *Quaternary Research* **46**:37-47.
- Davis, S. M. 1994. Phosphorus inputs and vegetation sensitivity in the Everglades. Pages 357-278 in S. M. Davis and J. C. Ogden, editors. *Everglades: the ecosystem and its restoration*. St. Lucie Press, Delray Beach, Florida, USA.
- Davis, S. M., L. H. Gunderson, W. A. Park, J. R. Richardson, and J. E. Mattson. 1994. Landscape dimension, composition, and function in a changing Everglades ecosystem. Pages 419-

- 444 in S. M. Davis and J. C. Ogden, editors. *Everglades: the ecosystem and its restoration*. St. Lucie Press, Delray Beach, Florida, USA.
- Deuver, M. J., J. F. Meeder, L. C. Meeder, and J. M. McCollom. 1994. The climate of south Florida and its role in shaping the Everglades ecosystem. Pages 225–248 in S. M. Davis and J. C. Ogden, editors. *Everglades: the ecosystem and its restoration*. St. Lucie Press, Delray Beach, Florida, USA.
- Flynn, W. W. 1968. The determination of low levels of polonium-210 in environmental materials. *Analytical Chimica Acta* **43**:221–227.
- Gawlik, D. E., P. Gronemeyer, and R. A. Powell. 2002. Habitat-use patterns of avian seed dispersers in the central Everglades. Pages 445–468 in F. H. Sklar and A. van der Valk, editors. *Tree islands of the Everglades*. Kluwer Academic, Dordrecht, The Netherlands.
- Gleason, P. J., and P. Stone. 1994. Age, origin, and landscape evolution of the Everglades peatland. Pages 149–197 in S. M. Davis and J. C. Ogden, editors. *Everglades: the ecosystem and its restoration*. St. Lucie Press, Delray Beach, Florida, USA.
- Grimm, E. C. 1992. CONISS: a Fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences* **13**:13–35.
- Haug, G. H., D. Gunther, L. C. Peterson, D. M. Sigman, K. A. Hughen, and B. Aeschlimann. 2003. Climate and the collapse of Maya civilization. *Science* **299**:1731–1735.
- Haug, G. H., K. A. Hughen, D. M. Sigman, L. C. Peterson, and U. Röhl. 2001. Southward migration of the Intertropical Convergence Zone through the Holocene. *Science* **293**:1304–1308.
- Heisler, L., D. T. Towles, L. A. Brandt, and R. T. Pace. 2002. Tree island vegetation and water management in the central Everglades. Pages 283–310 in F. H. Sklar and A. van der Valk, editors. *Tree islands of the Everglades*. Kluwer Academic, Dordrecht, The Netherlands.
- Hodell, D. A., M. Brenner, and J. H. Curtis. 2005a. Terminal Classic drought in the northern Maya lowlands inferred from multiple sediment cores in Lake Chichancanab (Mexico). *Quaternary Science Reviews* **24**:1413–1427.
- Hodell, D. A., M. Brenner, J. H. Curtis, R. Medina-González, E. Ildefonso-Chan Can, A. Albornaz-Pat, and T. P. Guilderson. 2005b. Climate change on the Yucatan Peninsula during the Little Ice Age. *Quaternary Research* **63**:102–121.
- Hodell, D. A., J. H. Curtis, and M. Brenner. 1995. Possible role of climate in the collapse of Classic Maya civilization. *Nature* **375**:391–394.
- Kushlan, J. A. 1990. Freshwater marshes. Pages 324–363 in R. L. Myers and J. J. Ewel, editors. *Ecosystems of Florida*. University of Central Florida Press, Orlando, Florida, USA.
- Langeland, K. 1990. Exotic woody plant control. Florida Cooperative Extension Service Circular **868**:1–16.
- Light, S. S., and J. W. Dineen. 1994. Water control in the Everglades: a historical perspective. Pages 47–84 in S. M. Davis and J. C. Ogden, editors. *Everglades: the ecosystem and its restoration*. St. Lucie Press, Delray Beach, Florida, USA.
- Lodge, T. E. 2005. *The Everglades handbook—understanding the ecosystem*. CRC Press, Boca Raton, Florida, USA.
- Loveless, C. M. 1959. A study of the vegetation in the Florida Everglades. *Ecology* **40**:1–9.
- Marshall, C. H., R. A. Pielke, Sr., L. T. Steyaert, and D. A. Willard. 2004. The impact of anthropogenic land-cover change on the Florida peninsula sea breezes and warm season sensible weather. *Monthly Weather Review* **132**:28–52.
- McDowell, L. L., J. C. Stephens, and E. H. Stewart. 1969. Radiocarbon chronology of the Florida Everglades peat. *Society of Soil Scientists of America Proceedings* **33**:743–745.
- Orem, W. H. 2006. Tree island wading bird biomarker study. Final Report for #PC P501993. South Florida Water Management District, West Palm Beach, Florida, USA, and U.S. Geological Survey, Reston, Virginia, USA.
- Orem, W. H., D. A. Willard, H. E. Lerch, A. L. Bates, A. Boylan, and M. Corum. 2002. Nutrient geochemistry of sediments from two tree islands in Water Conservation Area 3B, the Everglades, Florida. Pages 153–186 in F. H. Sklar and A. van der Valk, editors. *Tree islands of the Everglades*. Kluwer Academic, Dordrecht, The Netherlands.
- Overpeck, J. T., T. Webb, III, and I. C. Prentice. 1985. Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quaternary Research* **23**:87–108.
- Parker, G. G., et al. 1955. Water resources of southeastern Florida with special reference to the geology and ground water of the Miami area. U.S. Geological Survey Water-Supply Paper **1255**:1–965.
- Rosenmeier, M. F., D. A. Hodell, M. Brenner, and J. H. Curtis. 2002. A 4000-year lacustrine record of environmental change in the southern Maya lowlands, Petén, Guatemala. *Quaternary Research* **57**:183–190.
- Sklar, F., and A. van der Valk. 2002. *Tree islands of the Everglades: an overview*. Pages 1–18 in F. H. Sklar and A. van der Valk, editors. *Tree islands of the Everglades*. Kluwer Academic, Dordrecht, The Netherlands.
- Stahle, D. W., and M. K. Cleaveland. 1992. Reconstruction and analysis of spring rainfall over the southeastern U.S. for the past 1000 years. *Bulletin of the American Meteorological Society* **73**:1947–1961.
- Stahle, D. W., M. K. Cleaveland, and J. G. Hehr. 1988. North Carolina climate changes reconstructed from tree rings: A.D. 372 to 1985. *Science* **240**:1517–1519.
- Stockmarr, J. 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores* **13**:615–621.
- Stone, P. A., P. J. Gleason, and G. L. Chmura. 2002. Bayhead tree islands on deep peats of the northeastern Everglades. Pages 71–116 in F. H. Sklar and A. van der Valk, editors. *Tree islands of the Everglades*. Kluwer Academic, Dordrecht, The Netherlands.
- Stuiver, M., P. J. Reimer, E. Bard, J. W. Beck, G. S. Burr, K. A. Hughen, B. Kromer, G. McCormac, J. van der Plicht, and M. Spurk. 1998. INTCAL98 radiocarbon age calibration, 24,000–0 cal BP. *Radiocarbon* **40**:1041–1083.
- Stuiver, M., and H. van der Plicht. 1998. Editorial comment. *Radiocarbon* **40**:xii–xiii.
- Talma, A. S., and J. C. Vogel. 1993. A simplified approach to calibrating C14 dates. *Radiocarbon* **35**:317–322.
- Traverse, A. 1988. *Paleopalynology*. Unwin-Hyman, Boston, Massachusetts, USA.
- Wetzel, P. R. 2002. Tree island ecosystems of the world. Pages 19–70 in F. H. Sklar and A. van der Valk, editors. *Tree islands of the Everglades*. Kluwer Academic, Dordrecht, The Netherlands.
- Willard, D. A., C. E. Bernhardt, L. E. Weimer, S. R. Cooper, D. Gamez, and J. Jensen. 2004. Atlas of pollen and spores of the Florida Everglades. *Palynology* **28**:175–227.
- Willard, D. A., C. W. Holmes, M. S. Korvela, D. Mason, J. B. Murray, W. H. Orem, and D. T. Towles. 2002. Paleocological insights on fixed tree island development in the Florida Everglades: I. Environmental controls. Pages 117–151 in F. H. Sklar and A. van der Valk, editors. *Tree islands of the Everglades*. Kluwer Academic, Dordrecht, The Netherlands.
- Willard, D. A., L. M. Weimer, and C. W. Holmes. 2001a. The Florida Everglades ecosystem: climatic and anthropogenic impacts over the last two millennia. *Bulletins of American Paleontology* **361**:41–55.
- Willard, D. A., L. M. Weimer, and W. L. Riegel. 2001b. Pollen assemblages as paleoenvironmental proxies in the Florida Everglades. *Review of Palaeobotany and Palynology* **113**: 213–235.
- Worth, D. F. 1988. Environmental response of WCA-2A to reduction in regulation schedule and marsh drawdown. South Florida Water Management District Technical Publication 88-2.

APPENDIX A

Percentage abundance of pollen and spores of major plant taxa, Core 00-3-7-1, collected on Strand Island 1, A. R. Marshall Loxahatchee National Wildlife Refuge, Florida, USA (*Ecological Archives* M076-021-A1).

APPENDIX B

Percentage abundance of pollen and spores of major plant taxa, Core 02-5-20-4, collected in the marsh adjacent to Strand Island 2, A. R. Marshall Loxahatchee National Wildlife Refuge, Florida, USA (*Ecological Archives* M076-021-A2).

APPENDIX C

Percentage abundance of pollen and spores of major plant taxa, Core 01-8-8-4, collected in the near tail of Tree Island T3, Water Conservation Area 2A, Florida, USA (*Ecological Archives* M076-021-A3).

APPENDIX D

Percentage abundance of pollen and spores of major plant taxa, Core 01-8-8-5, collected in the marsh adjacent to Tree Island T3, Water Conservation Area 2A, Florida, USA (*Ecological Archives* M076-021-A4).

APPENDIX E

Percentage abundance of pollen and spores of major plant taxa, Core 99-3-3-2, collected in the marsh adjacent to Treece's Island, Water Conservation Area 2A, Florida, USA (*Ecological Archives* M076-021-A5).

APPENDIX F

Percentage abundance of pollen and spores of major plant taxa, Core 00-3-8-1, collected in the head of L67 Colony Island, Water Conservation Area 3A, Florida, USA (*Ecological Archives* M076-021-A6).

APPENDIX G

Percentage abundance of pollen and spores of major plant taxa, Core 00-3-9-7, collected in the near tail of Tree Island 3AS3, Water Conservation Area 3A, Florida, USA (*Ecological Archives* M076-021-A7).

APPENDIX H

Percentage abundance of pollen and spores of major plant taxa, Core 98-4-23, collected in the near tail of Skinner's Island, Water Conservation Area 3A, Florida, USA (*Ecological Archives* M076-021-A8).

APPENDIX I

Percentage abundance of pollen and spores of major plant taxa, Core 98-4-21-NHH, collected on the head of Nuthouse Island, Water Conservation Area 3B, Florida, USA (*Ecological Archives* M076-021-A9).

APPENDIX J

Percentage abundance of pollen and spores of major plant taxa, Core 98-4-21-GLFT, collected in the far tail of Gumbo Limbo Island, Water Conservation Area 3B, Florida, USA (*Ecological Archives* M076-021-A10).

APPENDIX K

Percentage abundance of pollen and spores of major plant taxa, Core 00-8-7-1, collected in the near tail of Gumbo Limbo Hammock, Everglades National Park, Florida, USA (*Ecological Archives* M076-021-A11).

APPENDIX L

Percentage abundance of pollen and spores of major plant taxa, Core 00-8-9-2, collected in the marsh adjacent to Manatee Hammock, Everglades National Park, Florida, USA (*Ecological Archives* M076-021-A12).