Journal of Coastal Research	13	2	373–384	Fort Lauderdale, Florida	Spring 1997

Rates of Vegetation Succession on a Coastal Dune System in Northwest Florida

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ABSTRACT

JOHNSON, A.F., 1997. Rates of vegetation succession on a coastal dune system in northwest Florida. *Journal of Coastal Research,* 13(2), 373–384. Fort Lauderdale (Florida), ISSN 0749-0208.

Maps (1869, 1934) and aerial photographs (1953–1986) permit the dating of dune ridges on the Shell-Crooked Island barrier system, 25 km east of Panama City, Florida. Sampling of topography and vegetation along eight transects across these barrier islands allow a replacement sequence of dominant species on ridges and swales over the past 100+ yrs to be inferred. Once a foredune ridge is protected by a more seaward ridge, *Uniola paniculata* is replaced by another grass, *Schizachyrium maritimum,* within 2–17 yrs; the latter is replaced by the subshrub, *Chrysoma pauciflosculosa,* within 19–52 yrs; and this species in turn is replaced by the shrub, *Ceratiola ericoides,* within 53–117 yrs. In swales, the halophytes, *Fimbristylis castanea* and *Paspalum distichum,* are replaced by *Eragrostis elliottii* within 4 to 7 yrs after the beach tidepool is protected by a seaward dune ridge; *Eragrostis* is replaced by either *Andropogon virginicus* within 7 to 52 yrs, or by *Muhlenbergia capillaris* within 14 to 52 yrs. Development of swale vegetation over time is less predictable than is the vegetation sequence on ridges.

ADDITIONAL INDEX WORDS: *Barrier island, aerial photography, dune ridges, halophytes, coastal vegetation.*

INTRODUCTION

The study of vegetation succession on coastal dunes has attracted investigators since the early days of plant ecology (COWLES, 1899). One reason is that dune colonization is a case of primary succession where it is relatively easy to hold initial conditions, *i.e.,* substrate, topography, available flora, and climate (MAJOR, 1951), constant across sites that can reasonably be thought to differ only in time available for plant colonization. Sites undergoing secondary succession, in contrast, have a residue from the previous plant community (seed bank, soil characteristics, *etc.*) that may be difficult to match across sites. In reviewing the evolution of the concept of succession, MILES (1987) notes that after a period of attempting to find general attributes of successional sequences (*e.g.,* MARGALEFF, 1958), researchers now show a renewed focus on mechanisms and population aspects of the process (*e.g.,* PEET and CHRISTIANSEN, 1980). This trend is reflected in the succession papers cited in a recent review of research on coastal vegetation (EHRENFELD, 1990). The focus of the present study on rates of vegetation change provides a realistic timeframe for considering the mechanisms by which such change occurs. Such a timeframe also has the practical value of allowing plants to be used as indicators of recent coastal history.

Previous Studies

Several studies have described the dune vegetation and its zonation on the coast of northwest (panhandle) Florida (ANDERSON and ALEXANDER, 1985; CLEWELL, 1986; KURZ, 1942). From these descriptions, it appears that dune vegetation in panhandle Florida is very similar to that found along the coasts of Alabama and Mississippi (PENFOUND and O'NEILL, 1934; ELEUTERIAS, 1979), and differs from that found along the sandy coasts of Texas (JUDD *et al.,* 1977) and Mexico (SAUER, 1967; MORENO-CASASOLA, 1993; MORENO-CASASOLA and ESPEJEL, 1986) to the southwest, as well as from that found along the sandy Gulf coast of Florida (COOLEY, 1955; HERWITZ, 1977) to the southeast. The northeast Gulf coast from Mississippi to western Florida forms a natural unit with similar climate and substrate, isolated from sandy coasts to the southwest by the finer sediments of the Mississippi Delta, and from sandy coasts to the southeast by the marshy, limestone-floored coast along the curve ("Big Bend") of the Florida peninsula. Its dune vegetation is distinguished from that found along coasts to the southeast and southwest by several dominant species (*Ceratiola ericoides, Chrysoma pauciflosculosa*), as well as by a number of species endemic to it (*Schizachyrium maritimum,* BRUNER, 1987; *Paronychia erecta* and *Helianthemum arenicola,* JOHNSON and BARBOUR, 1990). Even the pioneer upper beach vegetation of the northeast Gulf region is distinguishable from the regions to the south (BARBOUR *et al.,* 1987), although the foredune dominant, *Uniola paniculata,* is found everywhere except on the finer sediments in the Mississippi Delta region.

Although successional pathways for dune vegetation along the northeast Gulf coast have been postulated (ELEUTERIAS, 1979), there has been no direct study of succession in this vegetation, either through time, or by comparing vegetation on known age portions of the coastal barriers. Seasonal dy-

95107 received 30 August 1995; accepted in revision 10 July 1996.

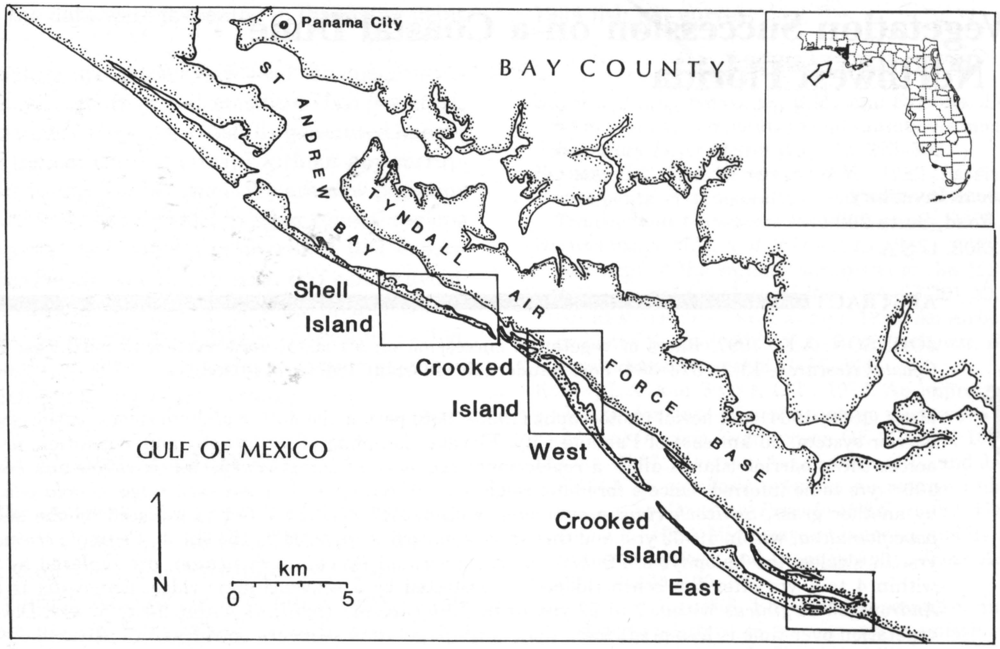

Figure 1. Location of study site. Squares outline portions where dune ridges were dated and transects were sampled.

namics of foredune vegetation in the panhandle region have been described by GIBSON and LOONEY (1992).

The Study Site

Physical Factors

The study site is located on the Shell Island-Crooked Island barrier system (30°N; 85°30′W), a 28 km stretch of unaltered coastline on Tyndall Air Force Base, 25 km east of Panama City in Bay County, Florida (Figure 1). The climate is classified as warm temperate humid (WALTER and LIETH, 1967). Panama City has a mean annual temperature of 20.6° C and mean annual rainfall of 1441 mm, evenly distributed throughout the year (25 yrs of record). The substrate is nearly pure quartz sand with less than 1% organic matter and little soil profile development on the ridges within the 50 to 100 yr period covered by this study (DUFFEE *et al.,* 1984).

Zonation of Vegetation

Zonation of dune vegetation is striking at the eastern end of Crooked Island East (Figure 2). Here four bands of vegetation can be seen, each characterized by a single dominant species, which are, from the coast inland: sea oats (*Uniola paniculata*), Gulf bluestem (*Schizachyrium maritimum*); woody goldenrod (*Chrysoma pauciflosculosa*), and Florida rosemary (*Ceratiola ericoides*). This sequence of bands might be explained by differential tolerance of the major species to coastal stresses that diminish inland from the coast, such as salt spray (OOSTING and BILLINGS, 1942) or sand burial (VAN DER VALK, 1974), or by plants having colonized progressively younger portions of the dune system as it grew seaward, or by a combination of these factors. A clue to the answer is found at the west end of Crooked Island West (Figure 1) where grassland dominated by *Schizachyrium maritimum* extends across the entire width of the barrier, from just behind the *Uniola paniculata* foredune to the marshes along the lagoon. A few km further east, still travelling parallel to the coast, the topography steepens as a series of northward-curving dune ridges are encountered, the first few ridges also covered by *S. maritimum.* As more ridges are traversed the grass gradually gives way to the subshrub, *Chrysoma pauciflosculosa,* until ridges are encountered whose crests are completely dominated the subshrub, with the grass persisting only on the edges of the swales between the dunes.

Since the latter sequence occurs parallel to, and thus without relation to distance inland from the shore, it is counterevidence for the first hypothesis that coastal stresses control vegetation zonation. The second possibility, that the sequence is related to age of the dunes, is supported by aerial photographs and topographic maps showing the portion of the dunes dominated by *Schizachyrium maritimum* to have been deposited since 1970 and the portion with increasing amounts of *Chrysoma pauciflosculosa* originating between 1970 and 1934. In order to document and further explore the relation between vegetation composition and age of the sand deposit, a series of transects across these vegetation zones were permanently staked and sampled on three portions of the Shell Island-Crooked Island barrier system (Figures 1 and 3).

Physiographic History

The Shell-Crooked Island barrier system has undergone extensive changes since the first known map of the area was

Figure 2. Zonation of dune vegetation shown in 1992 view looking southwest from near the point of attachment of Crooked Island East to the mainland. The dark rounded shrubs of *Ceratiola ericoides* in the foreground are invading the lighter band dominated by *Chrysoma pauciflosculosa* in the middle ground; *Schizachyrium maritimum* makes up the lighter band nearest the shore, seaward of the slightly darker swale vegetation which is dotted with shrubs and pines.

made in 1779 (STAPOR, 1973). This map shows a long narrow peninsula extending eastward from Shell Island to just past the present mainland point of attachment of Crooked Island West (Figure 1); to the east of this was the sickle-shaped Crooked Island, whose ends appear to have coincided with the two large trianglar bulges now present in Crooked Island East and West (Figure 1); further east were two parallel peninsulas, the outer or seaward one about the same length as the inner or landward one. About 50 yrs later, an account and map by WILLIAMS (1827), shows that the long peninsula extending eastward from Shell Island had broken into two islands, a smaller western island ("Sand Island") and a longer eastern one ("Hummock Island"), both covered only by dune grasses. Crooked Island was still present, its north end described as supporting "a considerable grove of pine trees". An 1855 map (DEMIRPOLAT *et al.,* 1987) shows that the pass between the eastern end of Crooked Island and the tip of the outer peninsula had filled in, and by 1877 (STAPOR, 1973), so had the pass between the west end of Crooked Island and Hummock Island. Thus the two islands and the outer peninsula now formed one long peninsula attached to the mainland at its eastern end and having two pronounced triangular bulges, marking the two inward-curving ends of the former Crooked island. Between 1885 and 1896 the coast was struck by four hurricanes, destroying most of the former Hummock Island except for a small piece near where it had attached to the former Crooked Island (STAPOR, 1973). These storms also left a small island off the mainland midpoint, which subsequently welded itself to the mainland. A second island, seen in about the same position in 1951 (SHEPARD and WANLESS, 1971) had by 1970 also welded itself to the mainland at the same point to form a double peninsula (STAPOR, 1973).

Since 1934 the western tip of the Crooked "Island" peninsula has built northwestward approximately 3 km and attached itself to the mainland (Figure 3); in the same time period Shell Island has built southeastward, also about 3 km. This accretion is probably at least partly due to the opening of two inlets: an artificial inlet at the west end of Shell Island, opened in the early 1930's (STAPOR, 1973) and a natural inlet, severing the Crooked Island peninsula into eastern and western halves, opened by Hurricane Eloise in 1975 (Figure 3).

METHODS

Age of the Dune Ridges and Swales

Ages of dune ridges on the Shell Island-Crooked Island barrier system were determined from black and white aerial photography for 1953 and 1964, obtained from the U.S. Agricultural Stabilization and Conservation Service (1:20,000 scale), and for 1970, 1975, 1980, 1983, and 1986, obtained from the Florida Department of Transportation (FDOT; 1: 24,000). Dates of earlier ridges were obtained from DEMIRPOLAT *et al.* (1987), who re-mapped to the same scale maps of the U.S. Geological Survey (1975), maps of the U.S. Coast and Geodetic Survey (1869, 1934), and aerial photographs (1977). Arcinfo was used to digitize at the same scale the FDOT aerial photographs (1970–1986) and the map produced by Demirpolat *et al.*

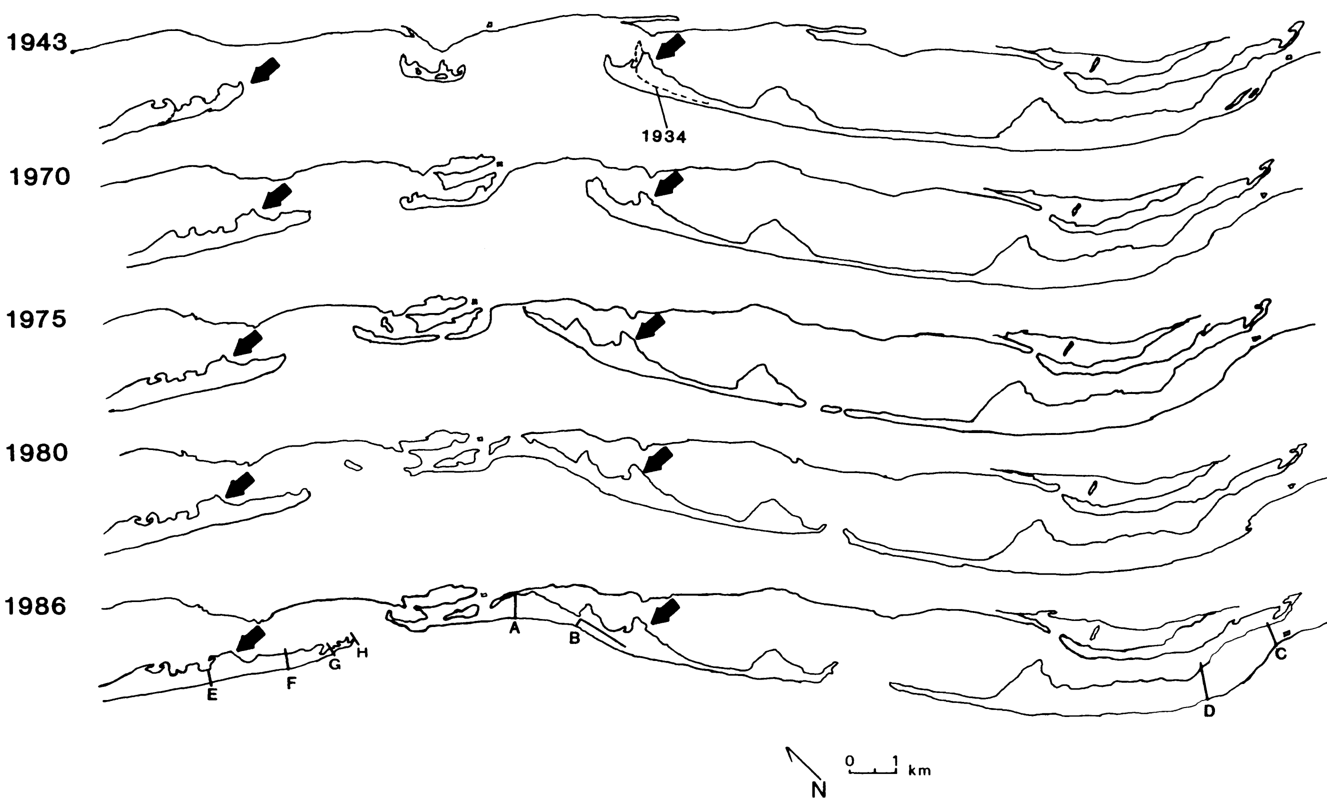

Figure 3. Schematic diagram of shoreline changes in Shell-Crooked Island barrier complex between 1934 and 1986. Arrows indicate stable points of reference. Location of transects (A–H) is shown on 1986 outline.

Vegetation/Topographic Transects

In 1987–1989 eight transects were permanently staked using 1″ diameter PVC pipe marked with numbered metal tags (Figure 3): two on Crooked Island West (A, B), two on Crooked Island East (C, D), and four on the eastern end of Shell Island (E, F, G, H). The positions of the PVC pipes marking the vegetation transects were located on blueline copies of 1986 FDOT aerial photographs (enlarged to 1″ = 400′), using landmarks in the field.

Species' cover and elevation difference along each square meter of transect line were measured using a square wooden frame (Hoyt, 1971) whose interior dimensions enclose one square meter. To measure elevation difference (cm) across each meter, the observer sights along the line formed by the top of the lower stake of the frame and the horizon to its intersection with the taller stake and reads off a cm scale on the taller stake. The frame is then laid on its side and the per cent cover of each species enclosed by the interior square meter is estimated. Transect sampling was done mostly in spring and fall (Tables 1 and 2).

Comparison of results using the frame to results using a transit level showed that errors tended to build up over longer distances (>200m) when using the frame. For this reason the elevation/distance measures in the transects should be taken as illustrative rather than absolute. Transect elevations above sea level were not corrected for tidal differences which are in the range of approximately 0.8 m in this region.

RESULTS

Transects and Aerials

Data for each of the eight transects were plotted as an elevation profile (Figure 4). Dates of the aerial photographs between which a dune ridge appeared were noted on the elevation profiles for each transect. These dates were determined by matching the foredune ridge at the shoreline on earlier maps and aerials with the same ridge as it appeared on the 1986 aerials, using both position as determined by digitization and the light and dark pattern of vegetation in the intervening swales. The result is illustrated for Crooked Island West (Figure 5).

In order to use the transect data to compare the age of a ridge with the species composition of the vegetation occupying the ridge, segments of the transects that crossed ridges are treated as plots, each one meter wide and a variable number of meters long. The plots, or ridge segments (A1, A2, B1, B2, etc.), from transects A–H are grouped by similar dominant species and the bracket of times available for colonization compared (Table 1). The same procedure is used for transect segments crossing swales (Table 2).

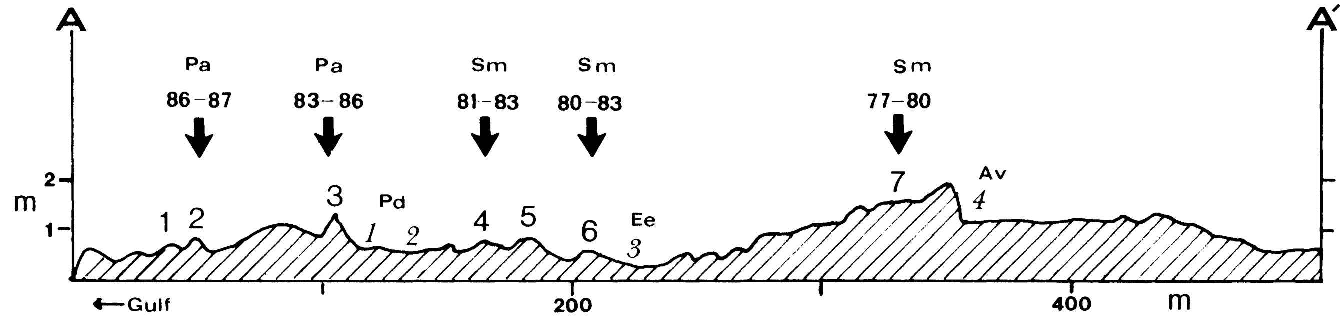

Figure 4. Transect A-A′ across a portion of Crooked Island West deposited within the last 12 yrs. Numbers above ridges and swales (italics) correspond to transect segments (A1, A2, *etc.*) in Tables 1 and 2. Numbers above arrows indicate dates of aerial photographs between which the ridge appeared. Letters indicate dominant species on each numbered ridge and swale: Pa = *Panicum amarum* var. *amarulum*, Sm = *Schizachyrium maritimum*, Pd = *Paspalum distichum*, Ee = *Eragrostis elliottii*, Av = *Andropogon virginicus*.

The procedure for calculating the maximum and minimum number of years a ridge could have been protected by a shoreward ridge is best shown by an example. Ridge A7 (Table 1) in transect A (Figure 4) is protected by ridges A4-5-6 which were not present (*i.e.* were open water) in the 1980 aerial, but were present in the 1983 aerial. Thus the earliest that A7 could have been protected by A4-5-6 is 1981, or 6 yrs before the transect was sampled in 1987, and the latest is 1983, or 4 yrs before. For ridges A1 and A2, which are at the shoreline in the 1987 transect, the maximum and minimum number of years they could have remained at the shore is 0 (*i.e.,* less than 1 year), since they are not present in the 1986 aerial and are present in the 1987 transect.

Transect A–A′ (Figures 3 and 5) crosses the youngest portion of Crooked Island West, deposited in the last 12 years (1975–1987) and is dominated by grasses; transect B–B′ (Figures 3 and 5) crosses the older portion of Crooked Island West deposited between 1934 and 1970 and shows a transition from grasses to subshrubs as dominants; transects C–C′ and D–D′ on Crooked Island East cross ridges deposited between 1869 and 1986, and show the full range of dune vegetation, with the oldest ridges dominated by a shrub species.

Transects on Shell Island recapitulate the vegetation sequence seen on Crooked Island West in the opposite direction, *i.e.,* with the oldest deposits on the west and progressively younger deposits toward the east (Figure 3). Transect E–E′ crosses a portion deposited between 1934 and 1986 and shows a mixture of grasses and subshrubs; transect F–F′ crosses a portion deposited in the last 16 years between 1970 and 1986 and is dominated by grasses; transect G–G′ crosses a portion deposited in the last 6 years, between 1980 and 1986, and is also dominated by grasses; and H–H′ crosses a portion deposited within the last 3 years, between 1986 and 1989, and is dominated by pioneer grasses and halophytes.

Community Composition

The ridge communities are simple and consistent over the barrier system, with one or two species dominating each type (Table 1). The foredune communities are dominated by two species of large grasses, *Panicum amarum* var. *amarulum* and *Uniola paniculata. Iva imbricata* and *Schizachyrium maritimum* are frequent associates. Disregarding the high and low extremes, the average number of species per plot in the foredune communities is 3 and the average percentage of bare sand is 79. Communities dominated by *Schizachyrium maritimum* have all of the major foredune species as frequent associates, except *P. amarulum* var. *amarulum.* Additional associated species are *Paronychia erecta* and *Heterotheca subaxillaris.* Average number of species per plot is 7 and per cent bare sand is 69. *Uniola, Paronychia,* and *Schizachyrium* continue to be frequent on ridges dominated by *Chrysoma pauciflosculosa.* Other frequent associates are *Cladonia leporina, Smilax auriculata,* and *Polygonella polygama.* Average number of species per plot is again 7 and average per cent bare sand is 65. Most of the plant cover in plots dominated by *Ceratiola ericoides* is made up of this shrub, with small amounts of species characteristic of the *Chrysoma* plots, plus some species also found in the older *Pinus clausa*–dominated community, such as *Cladina evansii* and *Pinus clausa* itself.

Swale communities are more diverse and variable in species composition than ridge communities (Table 2). The youngest swales are dominated by the halophytes, *Fimbristylis castanea* and *Paspalum distichum,* accompanied by several species that are also characteristic of pioneer ridge communities, such as *Panicum amarum* var. *amarulum* and *Iva imbricata.* These pioneer species are also found in the succeeding *Eragrostis*-dominated communities. Swales dominated by *Andropogon virginicus* and *Dichanthelium aciculare,* on the other hand, have a characteristic set of associated species (*Juncus polycephalus, J. scirpoides, Centella asiatica, Fuirena scirpoidea, Rhynchospora divergens*) not found on ridges. Many of these are also found in the *Muhlenbergia capillaris*-dominated swales.

Transects were sampled at different times of the year and phenological differences may contribute to variation in presence or abundance of species in samples of the same community type. While the perennial dominants of these communities are obvious throughout the year, some of the minor species are not. Observations over several years indicate that

Table 1. *Percent cover of species[1] on dune ridges of different ages at Tyndall AFB, FL.*

	Uniola/Panicum Dunes (* = embryo dune)																	
Transect Line	A	A	A	B	B	B	B	C	D	E	E	F	F	G	G	G	H	H
Transect Segment	1*	2*	3	1*	2	3	4	1	1	1*	2	1*	2*	1*	2	3	1*	2
Area (m^2)	9	16	7	8	7	10	14	9	16	5	12	11	10	16	16	16	11	15
Month sampled	11	11	11	3	3	3	3	9	10	3	3	5	5	4	4	4	11	11
Number of species	3	3	2	3	2	2	5	4	5	2	3	2	1	3	5	6	3	2
Minimum # yrs since ridge was protected	–	–	0	–	1	1	5	–	–	–	0	–	–	–	0	3	–	0
Maximum # yrs since ridge was protected	–	–	1	–	5	5	6	–	–	–	2	–	–	–	3	5	–	2
Minimum # of years ridge has remained at shoreline	0	0	–	1	–	–	–	8	4	0	–	0	1	0	–	–	0	–
Maximum # of yrs ridge has remained at shoreline	0	0	–	5	–	–	–	11	7	2	–	10	11	3	–	–	2	–
Percent bare sand	93	80	71	97	76	71	65	77	71	88	80	90	85	92	80	63	97	55
Uniola paniculata	+	03	–	01	03	27	19	23	24	–	12	06	15	02	13	14	01	–
Panicum amarum var. *amarulum*	02	–	29	–	23	1	–	+	01	–	–	–	–	05	–	+	01	29
Schizachyrium maritimum	–	–	–	01	–	–	07	–	–	–	07	–	–	–	–	01	–	–
Oenothera humifusa	–	–	–	–	–	–	02	–	–	–	–	–	–	–	–	–	–	–
Heterotheca subaxillaris	–	–	–	–	–	–	02	03	01	–	–	–	–	–	02	02	–	–
Chrysoma pauciflosculosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cladonia leporina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Smilax auriculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polygonella polygama	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cnidoscolus stimulosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ceratiola ericoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Atriplex arenaria	–	–	–	–	–	–	–	01	–	–	–	–	–	–	–	–	–	–
Fimbristylis castanea	01	–	02	–	–	–	–	–	–	–	–	–	–	–	–	–	01	16
Iva imbricata	+	14	–	01	–	–	03	–	–	08	01	–	–	01	03	04	–	–
Sesuvium portulacastrum	–	01	–	–	–	–	–	–	–	–	–	04	–	–	–	–	–	–
Hydrocotyle bonariensis	–	–	–	–	–	–	–	–	01	–	–	–	–	–	–	–	–	–
Conyza canadensis	–	–	–	–	–	–	–	–	02	–	–	–	–	–	02	02	–	–
Chamaesyce bombensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	01	–	–	–
Cenchrus incerta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eragrostis elliottii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spartina patens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Paronychia erecta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chrysopsis godfreyi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Physalis angustifolia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polygonella fimbriata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chrysopsis gossypina var. *decumbens*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Helianthemum arenicola	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polygonella gracilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cladonia cf *pachycladodes*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pinus clausa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cladina evansii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

[1]Nomenclature follows CLEWELL, 1985

the species composition of the foredune and the older swale communities are most affected by season of sampling. On the foredunes the driftline annuals, *Atriplex pentandra* and *Cakile constricta*, germinate in winter and are most obvious during the warmer months. Some perennials, while still present, die back in winter and thus contribute less cover than if sampled in the warm months, including the trailing species, *Hydrocotyle bonariensis* and *Ipomoea stolonifera*, the suffrutescent *Iva imbricata*, and the grass, *Panicum amarum* var *amarulum*. In the relatively species-rich communities of older swales, many minor species (*e.g., Buchnera floridana, Sabatia stellata*) are not obvious except when flowering, which for most is in summer or fall.

Inferred Rate of Succession on Ridges

As long as a dune ridge remains at the shoreline (and thus is exposed to sand burial from sand blown off the beach) *Uniola paniculata* an d/or *Panicum amarum* var. *amarulum* remain dominant (Table 1). Once a foredune ridge is protected from sand burial by a new ridge forming seaward of it, other species begin to replace these foredune species and a successional sequence is initiated.

Panicum amarum var *amarulum* is often the major species on foredunes not more than 5 yrs old. However, it was not seen to persist on foredunes beyond this time, in contrast to *Uniola paniculata* which may dominate foredunes for at least 11 years, and ostensibly for as long as the ridge remains as the first dune above the beach. Within 2 to 6 years after a ridge is protected, *Uniola/Panicum* may be replaced as dominants by *Schizachyrium maritimum*, a smaller, more densely growing rhizomatous grass (Table 1). *S. maritimum* dominates ridges that have been protected between 2 and 23 years and may be replaced by *Chrysoma pauciflosculosa*, a small, short-lived woody species that bears its flowers on fleshy

Table 1. *Extended.*

Schizachyrium Dunes																			
A 4	A 5	A 6	A 7	B 5	B 6	B 7	B 8	B 9	B 10	C 2	D 2	D 3	D 4	F 3	F 4	F 5	F 6	F 7	G 4
8	17	16	30	16	9	13	13	16	21	17	16	16	16	18	13	14	16	16	16
11	12	12	12	3	3	3	4	5	5	9	10	11	11	5	5	5	5	5	4
6	7	9	7	3	4	5	6	8	9	6	8	5	7	4	7	7	9	9	7
2	2	3	4	7	14	15	16	17	19	11	4	12	14	1	8	8	8	8	6
3	3	5	6	12	14	15	16	17	23	16	7	16	16	11	12	12	12	12	8
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
84	82	77	82	64	68	73	67	48	53	39	56	50	49	88	76	61	56	52	86
–	02	01	–	12	15	09	02	08	05	08	08	10	10	05	06	–	04	03	03
01	01	02	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	03	+
09	04	12	12	17	09	13	15	35	37	35	27	24	23	05	10	22	28	32	08
–	–	–	01	02	–	01	+	+	+	–	+	–	+	–	+	01	–	+	–
02	03	02	02	02	06	02	05	01	+	05	08	07	08	–	+	+	08	07	+
–	–	–	–	–	–	–	–	–	–	–	–	–	03	–	–	–	–	–	–
–	–	–	–	–	–	–	–	+	01	–	–	–	01	–	–	–	–	–	–
–	–	–	–	–	–	–	–	02	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	+	05	10	–	–	–	–	–	–
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02	08	02	+	–	01	–	10	02	–	–	+	–	–	01	–	–	–	03	+
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	01	–	–	–	–	–	–	01	+	+	–	–	–	–	+	+	+	–
04	04	01	+	–	–	–	–	–	–	01	–	–	–	–	+	–	–	–	01
01	+	–	–	–	–	–	–	–	–	–	01	–	–	–	–	–	–	–	–
–	–	01	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	01	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	16	07	08	–
–	–	–	–	–	–	01	05	01	03	–	–	–	–	–	04	04	06	–	02
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–
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stems that die back each year, after 18 to 23 years. The subshrub *C. pauciflosculosa* dominates ridges protected for 18 to 52 years and is replaced as the dominant by the larger, longer-lived (JOHNSON, 1982) shrub, *Ceratiola ericoides,* on ridges protected for 53 to 117 years.

Associated species that follow the invasion patterns of the major species include *Heterotheca subaxillaris* which invades older foredunes dominated by *Uniola paniculata* and persists as the latter is replaced by *Schizachyrium maritimum*; *Paronychia erecta* which follows the invasion of *Schizachyrium maritimum*; and the ground lichen, *Cladonia leporina,* which accompanies invasion by *Chrysoma pauciflosculosa* and persists as this species is replaced by *Ceratiola ericoides.*

Inferred Rate of Succession in Swales

Once the formation of a seaward dune ridge prevents the incursion of saltwater, the pioneer species of brackish flats and tidepools on the upper beach, *Fimbristylis castanea* and *Paspalum distichum,* may be replaced within 4 to 7 years by *Eragrostis elliottii,* which in turn is replaced as a dominant within 7 to 52 years by *Andropogon virginicus* (Table 2). *Muhlenbergia capillaris* may also dominate swales between 14 and 52 yrs old and what factor determines whether *Andropogon* or *Muhlenbergia* dominates is not obvious. Swale communities are more variable and species rich than the simple communities found on ridges. Several factors other than age which undoubtedly influence the species composition of swale communities include hydroperiod (wetter swales often contain sawgrass, *Cladium jamaicense*) and salinity (higher salinity leading to dominance by *Spartina patens* or *S. spartinae*).

DISCUSSION

The species in the replacement sequence in this study dominate dunes along the northeast Gulf coast from Florida to

Table 1. *Extended.*

	Chrysoma Dunes														Ceratiola Dunes	
Transect Line	B	B	B	B	B	B	B	B	C	C	D	D	E	E	C	C
Transect Segment	11	12	13	14	15	16	17	18	3	4	5	6	3	4	5	6
Area (m^2)	21	9	16	16	15	8	16	22	16	16	16	17	16	16	16	16
Month sampled	5	5	5	6	6	6	7	7	9	9	11	1	3	3	10	10
Number of species	7	5	8	9	7	8	7	7	7	10	7	18	7	5	7	6
Minimum # yrs since ridge was protected	19	24	24	32	35	37	37	37	22	23	17	35	25	25	53	54
Maximum # yrs since ridge was protected	23	31	31	34	50	52	52	52	31	32	23	52	34	34	116	117
Minimum # of years ridge has remained at shoreline	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Maximum # of yrs ridge has remained at shoreline	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Percent bare sand	74	58	72	70	66	82	67	76	66	29	65	40	59	63	63	17
Uniola paniculata	01	01	02	02	+	01	–	01	02	03	01	02	01	–	–	–
Panicum amarum var. *amarulum*	–	–	–	01	–	–	–	–	–	–	–	–	–	–	–	–
Schizachyrium maritimum	05	01	–	01	+	05	01	01	–	02	–	06	18	18	–	–
Oenothera humifusa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Heterotheca subaxillaris	–	–	+	–	–	02	–	–	–	–	–	–	–	–	–	–
Chrysoma pauciflosculosa	08	30	15	19	27	07	18	14	29	17	25	14	09	07	01	01
Cladonia leporina	01	–	05	+	02	03	18	04	04	27	03	22	07	–	–	09
Smilax auriculata	–	–	12	05	09	–	02	06	+	02	–	04	–	–	01	–
Polygonella polygama	03	+	–	–	02	01	–	+	04	07	03	03	02	03	+	–
Cnidoscolus stimulosus	01	–	02	–	–	04	+	–	–	01	–	+	–	–	–	–
Ceratiola ericoides	–	–	–	–	–	–	–	–	–	10	11	–	–	–	32	70
Atriplex arenaria	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Fimbristylis castanea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Iva imbricata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sesuvium portulacastrum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hydrocotyle bonariensis	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Conyza canadensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chamaesyce bombensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cenchrus incerta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eragrostis elliottii	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Spartina patens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Paronychia erecta	01	01	+	01	01	03	02	01	–	01	03	03	02	01	–	–
Chrysopsis godfreyi	–	–	–	–	–	–	02	–	–	–	–	–	–	–	–	–
Physalis angustifolia	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Polygonella fimbriata	–	–	–	+	–	–	–	–	–	–	–	01	–	–	–	–
Chrysopsis gossypina var. *decumbens*	–	–	–	–	–	–	–	–	+	–	–	03	–	04	–	–
Helianthemum arenicola	–	–	–	–	–	–	–	–	–	+	01	–	–	–	+	–
Polygonella gracilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Cladonia cf *pachycladodes*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	01	–
Pinus clausa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	01
Cladina evansii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	01

Mississippi. That this sequence and rate of species replacements, at least for the ridges, if not for the swales, can be generalized to the remainder of the northeast Gulf coast is supported by observations on other portions of the Shell Island-Crooked Island complex, as well as by observations on other barrier islands along the Florida panhandle.

For example, on the double peninsula system on the central portion of the mainland between Shell and Crooked Islands, the inner peninusula, which has been stable since at least 1943 (44 yrs) is dominated by *Chrysoma pauciflosculosa*. The outer peninsula, which has changed shape continuously since it attached to the mainland in 1970, is covered on its seaward side by *Panicum amarum* var *amarulum,* and on its inland side, protected since the two peninsulas were attached in 1970 (17 yrs), by *Schizachyrium maritimum,* with *Andropogon virginicus* in the swales. These rates agree with the times bracketed for development of *Chrysoma*-dominated (18–52 yrs) and *Schizachyrium*-dominated (2–23 yrs) ridges, and *Andropogon*-dominated swales (7–52 yrs) in this study.

Another corroborating observation on the Shell-Crooked Island barrier complex is that *Ceratiola ericoides* is dominant only on those portions of the system that, according to Stapor's account (1973), have potentially been stable for at least 50 yrs, *i.e.,* the extreme eastern end of the Crooked Island East peninsula, the western end of Shell Island, and the eastern sides of the triangular bulges on Crooked Island East and West.

A systematic survey of the other barrier islands along the Florida panhandle (Johnson and Muller, 1992) revealed that the complete successional sequence is rarely seen at any one point along the coast. A transect on eastern Dog Island in Franklin County (Johnson, 1986, unpublished data) shows the complete sequence of ridge species, and a check of the relevant U.S. Geological Survey topographic quadrangles

Table 2. *Percent cover of species*[1] *on swales of different ages at Tyndall AFB, Florida.*

	Paspalum/Fimbristylis Swales						*Eragrostis* Swales		*Andropogon/Dicanthelium* Swales								Muhlenbergia Swale				
Transect Line	A	A	C	H	H	H	A	D	A	B	B	B	B	B	B	B	B	C	D	D	D
Transect Segment	1	2	1	1	2	3	3	1	4	1	2	3	4	5	6	11	10	3	2	3	4
Number of species	8	9	4	3	4	2	7	10	10	12	9	15	8	12	13	8	12	11	13	10	13
Area (m²)	9	10	7	15	16	14	20	15	21	14	16	13	16	12	11	12	16	14	16	8	16
Month sampled	11	11	9	11	11	11	1	10	1	4	5	5	5	5	5	7	6	9	11	11	11
Minimum number of years since swale was protected	2	2	0	0	0	0	4	4	7	17	18	18	18	19	32	37	37	24	14	17	35
Maximum number of yrs since swale was protected	3	3	1	2	2	2	6	7	11	17	22	22	22	23	34	52	52	35	16	23	52
Percent bare sand	52	67	88	54	80	77	47	28	14	40	03	02	11	17	50	47	32	57	30	46	21
Paspalum distichum	24	12	04	35	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Fimbristylis castanea	02	06	08	10	12	15	01	02	07	–	–	–	–	–	–	–	–	–	01	–	–
Eragrostis elliottii	+	+	–	–	01	–	46	62	20	07	–	02	–	–	06	03	03	13	13	02	–
Andropogon virginicus	–	–	–	–	–	–	–	01	21	27	42	50	19	46	20	04	01	01	05	01	03
Dichanthelium cf. *aciculare*	–	–	–	–	–	–	–	–	–	08	18	01	32	21	–	28	03	–	–	02	+
Muhlenbergia capillaris	–	–	–	–	–	–	–	01	–	–	–	–	–	–	–	–	63	11	38	17	46
Schizachyrium maritimum	02	02	–	–	–	–	05	06	05	18	+	–	–	–	05	–	–	08	01	–	–
Hydrocotyle bonariensis	–	01	–	–	–	–	02	+	09	–	09	04	–	–	+	–	–	01	+	–	–
Panicum amarum var. *amarulum*	07	10	–	–	05	08	01	04	–	01	–	–	–	–	+	–	–	–	01	–	–
Iva imbricata	06	02	–	–	–	–	+	02	–	–	–	–	–	–	–	–	–	–	–	–	–
Spartina patens	–	–	–	–	–	–	+	01	12	–	–	03	–	–	+	–	01	–	03	–	–
Andropogon glomeratus	–	–	–	–	–	–	–	01	20	–	–	02	–	–	–	–	–	–	05	–	–
Juncus polycephalus	–	–	–	–	–	–	–	–	01	09	01	01	01	+	–	–	–	+	01	03	01
Juncus scirpoides	–	–	–	–	–	–	–	–	02	01	–	+	01	–	–	05	–	01	–	–	01
Centella asiatica	–	–	–	–	–	–	–	–	–	–	18	25	12	08	–	04	01	–	–	–	+
Fuirena scirpoidea	–	–	–	–	–	–	–	–	–	–	13	16	12	+	–	03	–	–	17	08	+
Rhynchospora divergens	–	–	–	–	–	–	–	–	–	01	–	02	16	01	–	01	–	–	02	21	05
Limonium carolinianum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	01	–	–	–	–	–	–
Cakile constricta	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Conyza canadensis	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–
Uniola paniculata	+	02	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	06	–	–	–
Baccharis halimifolia	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Solidago stricta	–	–	–	–	–	–	–	–	+	–	–	–	–	–	01	–	–	–	–	–	–
Sesuvium portulacastrum	–	–	+	01	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lythrum lineare	–	–	–	–	–	–	–	–	–	–	–	03	–	–	–	–	–	–	–	–	–
Phyla nodiflora	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	01
Dichromena colorata	–	–	–	–	–	–	–	–	–	–	13	–	–	–	–	–	–	–	–	01	01
Cynanchum angustifolium	–	–	–	–	–	–	–	–	–	–	–	02	–	+	+	+	–	–	–	–	–
Polygala baldwinii	–	–	–	–	–	–	–	–	–	–	–	01	01	+	–	–	+	–	–	–	–
Rhynchospora microcarpa	–	–	–	–	–	–	–	–	–	–	–	01	–	03	–	–	–	–	–	–	–
Paronychia erecta	–	–	–	–	–	–	–	–	–	02	–	–	–	01	–	–	–	01	–	–	–
Polypremum procumbens	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	03	–	+	–
Cyperus lecontei	–	–	–	–	–	–	–	–	–	–	–	–	–	06	+	–	–	–	–	–	–
Setaria geniculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	19	–	–	–	–	–	–
Eustachys petraea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	01	–	+	–	–	–	–
Buchnera floridana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	01	–	–	–	–
Fimbristylis caroliniana	–	–	–	–	–	–	–	03	–	+	–	–	–	–	–	–	01	–	+	01	–
Sabatia stellaris	–	–	–	–	–	–	–	01	–	–	–	–	–	–	–	–	03	–	–	–	–
Scleria verticillata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	02	–	–	–	–
Xyris jucipai	–	–	–	–	–	–	–	–	–	01	–	–	–	–	–	–	–	–	–	–	–
Diodia teres	–	–	–	–	–	–	–	–	–	01	–	–	–	–	–	–	–	–	–	–	–
Pinus elliottii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	02
Myrica caroliniana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	28
Andropogon virginicus var. *glaucus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	01

[1]Nomenclature follows CLEWELL, 1985

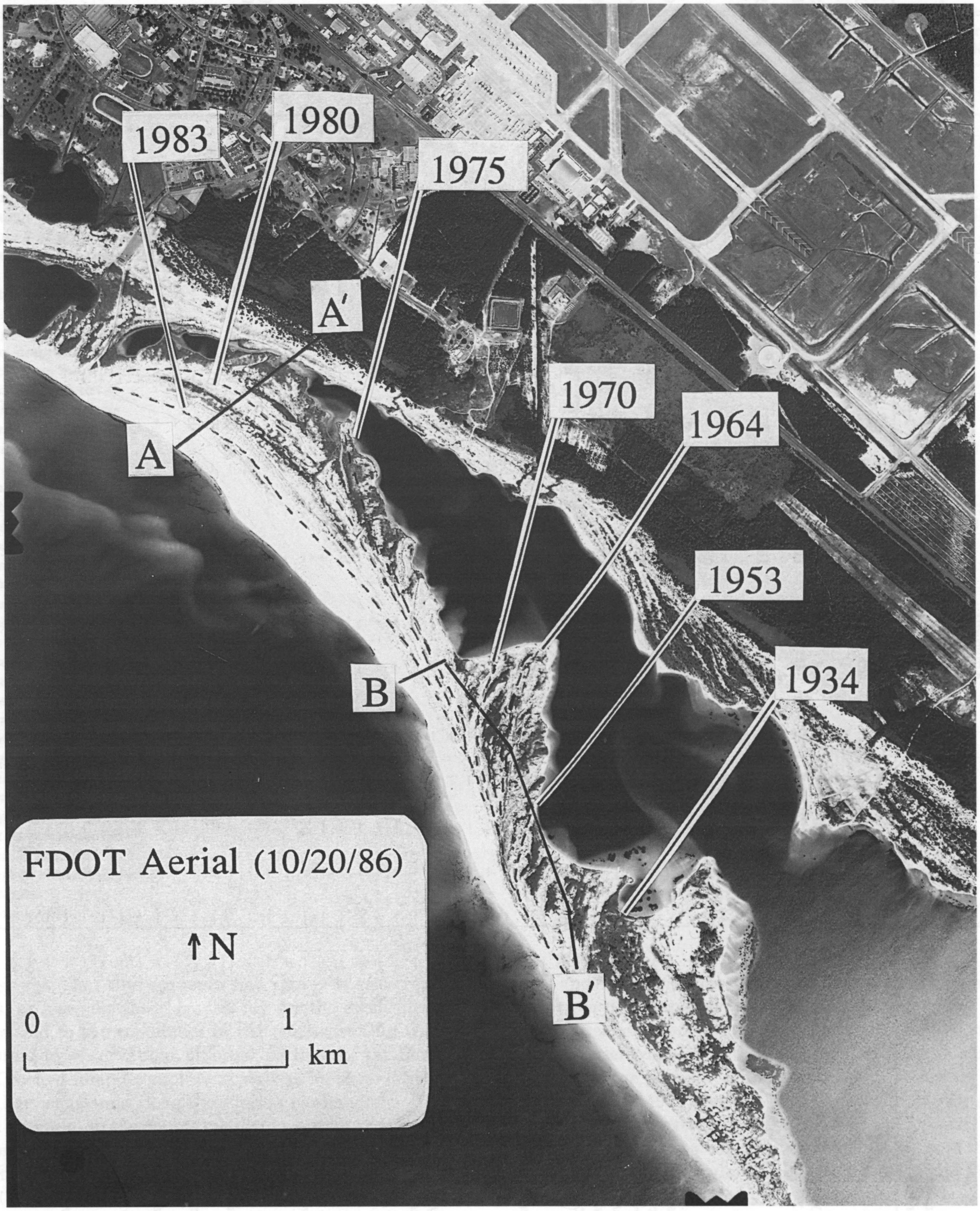

Figure 5. Florida Department of Transportion 1986 aerial photograph of a portion of Crooked Island West, showing dates of ridges (*i.e.,* date of earliest aerial on which the ridge appeared at the shoreline) and position of transects A-A′ and B-B′.

(aerial photography in 1943 and 1976) plus a 1987 FDOT aerial show that the coast there has prograded. A rough comparison of distances on the transect with location of shorelines indicates that *Ceratiola ericoides* and *Chrysoma pauciflosculosa* occupy what is probably the 1943 shoreline (43 yrs); *Schizachyrium maritimum*, the 1976 shoreline (10 yrs); and *Uniola paniculata,* the youngest portion—rates which agree with the timeframe inferred in the present study. Further east, near the tip of Dog Island, the *Ceratiola*-dominated ridge directly abuts ridges dominated by *Uniola paniculata* on the seaward side, indicating erosion and rebuilding has probably replaced the *Schizachyrium* and *Chrysoma* portion of the sequence. This is an example of why the complete sequence of vegetation zones is seldom seen along the coast: in the 50+ yrs the sequence takes to develope, storm erosion and dune re-building are likely to intervene.

The oldest portions of the Shell-Crooked Island barrier complex are occupied by pine forest communities: *Pinus clausa* with an understory of *Ceratiola ericoides*, carpets of ground lichens (*Cladonia leporina* and *Cladina evansii*), and scattered shrubs of *Quercus geminata* and *Q. myrtifolia* on the ridges; *Pinus elliottii* with an understory of *Ilex glabra* and *I. vomitoria* in the swales. These communities were not sampled in the current study because there was no way of dating when the ridges they occupied were at the shoreline.

In the six years since the initial sampling, portions of the eight permanently staked transects in the study have been periodically re-sampled to obtain a longitudinal record of changes in the same area over time. Instances of replacement of *Paspalum distichum* by *Eragrostis elliottii, Panicum amarum* var *amarulum* by *Uniola paniculata,* and *Schizachyrium maritimum* by *Chrysoma pauciflosculosa* have been observed, tending to corroborate the successional sequence inferred in the present report from spatial data. Continued re-sampling of the permanent transects should give a more detailed picture of the timing and pattern of vegetation succession on dunes along the northeast coast of the Gulf of Mexico.

ACKNOWLEDGEMENTS

I thank Tyndall Air Force Base for permission to sample on their property, and Robert Bates, Carl Petrick, Neill Hunter and other personnel of the Natural Resources Division on the base for their cooperation and logistical support. I also thank Amelie Blyth, Joseph Donoghue, John Palis, Deborah White, and Chester and Marsha Winegarner for help with sampling; Red Lamb, Scott Taylor and Mark Knoblauch for help in obtaining and digitizing maps and aerials; and the Florida Natural Areas Inventory for use of its facilities. I am grateful to Eddy van der Maarel, Robert Boyd, and three anonymous reviewers for helpful comments on the manuscript.

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