Journal of Coastal Research	8	4	943–956	Fort Lauderdale, Florida	Fall 1992

Seasonal Variation in Vegetation Classification on Perdido Key, a Barrier Island off the Coast of the Florida Panhandle

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ABSTRACT

GIBSON, D.J. and LOONEY, P.B., 1992. Seasonal variation in vegetation classification on Perdido Key, a barrier island off the coast of the Florida panhandle. *Journal of Coastal Research*, 8(4), 943–956. Fort Lauderdale (Florida). ISSN 0749-0208.

The vegetation of 224 5 m × 2 m permanent plots located along 13 cross-island transects on the eastern end of Perdido Key, Florida, was classified using Two-Way Indicator Species Analysis. Seasonal variation in the vegetation classification was assessed using data collected in Autumn 1989, and Spring, Summer and Autumn 1990. Seven general vegetation types were recognized through the four seasons of data collection, with the greatest variation occurring within and between plots in the 'dune' vegetation type. In contrast, plots within the wooded dune and marsh vegetation types were the most stable between seasons. Four subtypes of the dune vegetation type were identified: established, disturbed, developing, and low dunes. However, consistent assignment of permanent plots to these subtypes was low and varied between seasons. Overall, the two Autumn classifications were more similar to each other than were either the Spring or Summer classifications to each other or to the Autumn classification. The problems in the development of a consistent classification of barrier island vegetation that can incorporate seasonal variations are discussed in the light of the conservation and management of coastal vegetation.

ADDITIONAL INDEX WORDS: *Barrier island, beach, dune, classification, season, vegetation.*

INTRODUCTION

The beach vegetation of the North American and Mexican Gulf Coast is floristically richer and has a broader array of dominant growth forms than either the Pacific or Atlantic coasts (Barbour *et al.*, 1985). The relatively undisturbed vegetation, occurring on the offshore barrier islands, has been well described at both the regional (Barbour *et al.*, 1987; Moreno-Casasola and Espejel, 1986; Moreno-Casasola, 1988; Castillo *et al.*, 1991) and local scale (*e.g.* Penfound and O'Neill, 1934; Eleuterius, 1979; Anderson and Alexander, 1985). The zonation of vegetation types typical of barrier islands has also been described (Doing, 1985; Burkhalter, 1987; Ehrenfeld, 1990). However, individual species phenology makes for what is, in essence, a seasonal progression of vegetation types at any one place (Cousens, 1988). This could lead to markedly different classification schemes and the identification of different indicator species (species used to discriminate vegetation types) depending upon the season. Previous classifications of barrier island vegetation have either not considered these seasonal changes (although see Cordazzo and Seeliger, 1988) or do not consider them to be of sufficient magnitude to affect an interpretation of the relationships between vegetation types (Barbour *et al.*, 1987). In these studies, classification of the plant communities may be based on data collected from a single sampling during the year. This potential problem is confounded by the observation that some vegetation types are more dynamic and more subject to seasonal change than others (Gibson *et al.*, 1990).

An understanding of the seasonal dynamics of the vegetation of coastal systems is important from a management perspective since some forms of disturbance can most readily be observed only during certain seasons and may correlate with the composition of specific plant communities (Williams and Randerson, 1989). In addition, the increasing availability and ability to interpret seasonal variation in remotely sensed data makes corresponding ground truthing necessary (Briggs and Nellis, 1991).

In this study, the effect of season upon vegetation classification was investigated on the Gulf Islands National Seashore portion of Perdido Key, a barrier island off the coast of northwest Florida. In particular, the study was designed to determine if similar vegetation types could be identified at different times of the year, and whether the same

91076 received 2 September 1991; accepted in revision 17 January 1992.

set of species were characteristic of vegetation types at different seasons.

MATERIALS AND METHODS

Study Area

The study was conducted in the Gulf Islands National Seashore at the eastern end of Perdido Key, a barrier island off the northwest coast of Florida (87°24′W, 30°18′N). The late Holocene barrier island of Perdido Key, approximately 23 km long, formed through predominant transport of sediment from the adjacent low gradient inner shelf in conjunction with material supplied by an older Holocene beach ridge complex located midway along the island (Figure 1) (STONE, 1991). The easternmost 11 km of the island is under the jurisdiction of the National Park Service as a part of the Gulf Islands National Seashore (GINS). This portion of Perdido Key is largely undeveloped except for the ruins of a WWII artillery battery on the extreme eastern end of the island. Off-road-vehicle use of the GINS was stopped in 1979 (SHABICA and COUSENS, 1983). Since that time, the only major disturbance to the vegetation was Hurricane Frederic which extensively overwashed the eastern 11 km of Perdido Key in September 1979. The hurricane flattened as much as 90% of the dunes (COUSENS, 1988). The eastern 8 km of Perdido Key has been eroding over the period 1859–1985 at a rate of 0.5 m per year (STONE, 1991; STONE *et al.*, in press). However, in 1985 and late 1990, the U.S. Army Corps of Engineers renourished approximately 1.6 km and 8 km, respectively, of beach doubling the width of the island in some places (WORK *et al.*, 1991). Sand for the renourishment project was dredged off the eastern end of Perdido Key in Pensacola Pass (Figure 1).

Data Collection and Analysis

In Autumn 1989, 224 5 m × 2 m permanent plots were established along 13 cross-island transects. The permanent plots were located at 12 m intervals along each transect for the first 120 m from mean high water and every 24 m thereafter, crossing the island from the Gulf side to the water's edge on the northern lagoon side. This yielded from 11 to 40 plots per transect. Within each plot, the vegetation was sampled by estimating cover of all species according to the Daubenmire scale (DAUBENMIRE, 1959) within 25 permanently located 0.1 m^2 quadrats. The quadrats were randomly located within the permanent plots for the first sampling and were used because the often sparse nature of the vegetation would have made species cover estimates within the large plots less

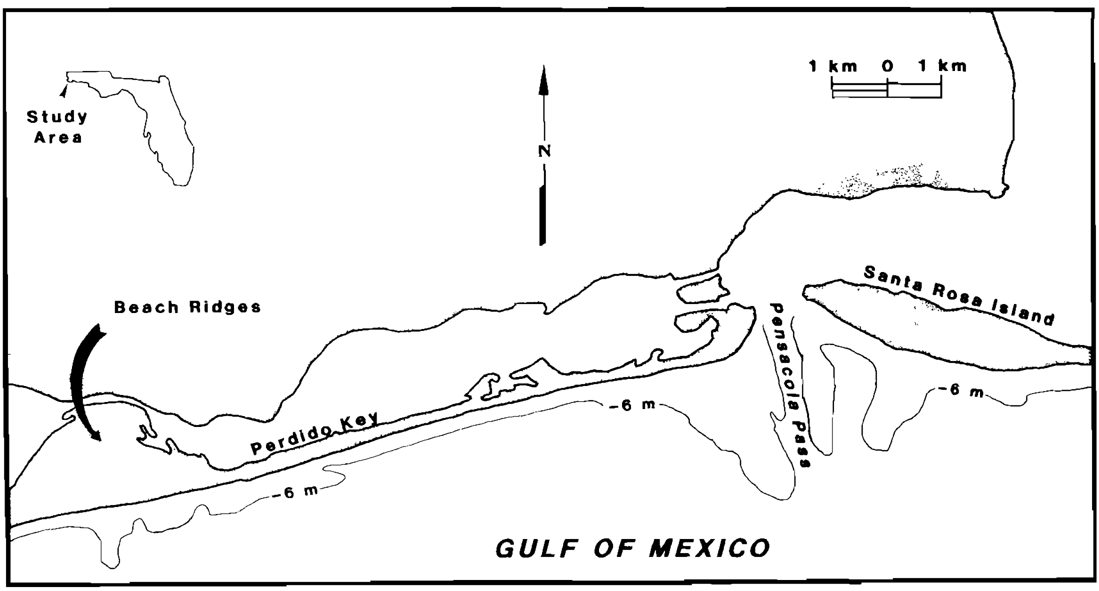

Figure 1. Eastern end of Perdido Key, Florida.

precise (DAUBENMIRE 1959, 1968). Data were collected in Autumn (October) 1989, Spring (May) 1990, Summer (July) 1990, and Autumn 1990 and initial data analysis calculated the mean species cover per permanent plot from the Daubenmire cover values per quadrat. Nomenclature for plant species follows CLEWELL (1985).

Two-way Indicator Species Analysis [TWINSPAN (HILL, 1979)] was used to produce an objective classification of the permanent plots for each season. TWINSPAN is a divisive, hierarchical procedure that is commonly used in vegetation analyses and has been used as an aid in coastal management projects (*e.g.* JONES and ETHERINGTON, 1989; WILLIAMS and RANDERSON, 1989). The goal of undertaking this procedure was to objectively identify vegetation types on Perdido Key along with characteristic indicator species. An indicator species (or differential species) is defined by HILL (1979) as a species with clear ecological preferences that can be used to identify particular environmental conditions. As calculated using the TWINSPAN routine, indicator species are species associated with each division in groups of sample plots that have a high frequency and cover in particular groups. An additional feature of TWINSPAN that sets it apart from most other classification procedures is that the order of samples in the final dendrogram has a statistical and ecological relevance. Thus, a direct comparison of the vegetation types can be made. In this study, separate analyses of the Autumn 1989, Spring 1990, Summer 1990 and Autumn 1990 data were undertaken so that identification of vegetation types upon a seasonal basis could be made. The data analyzed using this procedure comprised mean cover of all species per permanent plot for any one seasonal sample. BARBOUR *et al.* (1987) used a similar approach to classify strandline vegetation from stations along the northern Gulf of Mexico. Because it is a divisive classification procedure, TWINSPAN proceeds by dividing groups of samples (plots) into two, not necessarily equal, smaller groups. For this study, division of the plots using the TWINSPAN procedure was taken to three levels of division for each of the seasonal samples. This allowed a number of general vegetation types to be recognized. In each season however, between 97 and 131 plots remained at the third level of division in a single large group. A fourth level of division for this group was allowed which improved the efficacy of the resulting classification scheme (Figure 2). Each

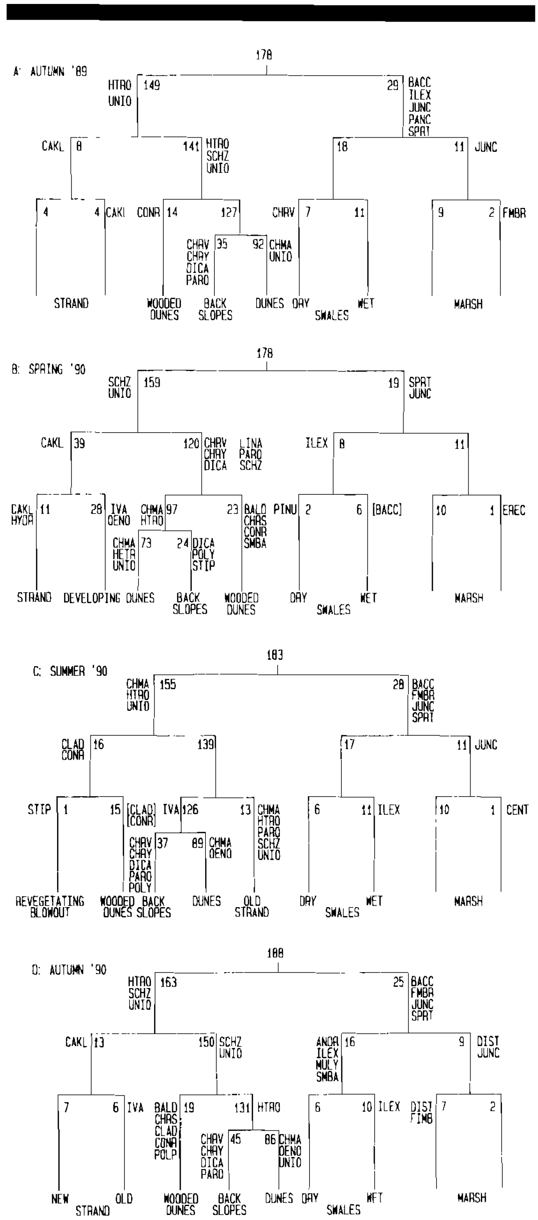

Figure 2. TWINSPAN classification of permanent plots surveyed in (a) Autumn 1989, (b) Spring 1990, (c) Summer 1990, and (d) Autumn 1990. In each analysis, division of plots continued to the third level except the back dune/dune group which was divided to the fourth level. Indicator species associated with each division are shown (codes as in Table 1). The number of permanent plots associated with each division are also shown. Vegetation types are named based on environmental characteristics of the plots comprising a vegetation type (see text).

resulting group of sample plots was labelled according to the type of vegetation and the species present, as well as factors such as location on the island relative to the Gulf shore, frequency of inundation and local topography. These criteria are similar to those used in previous studies of barrier island vegetation classification (*e.g.* RANWELL, 1972; WOODHOUSE, 1982; MORENO-CASASOLA and ESPEJEL, 1986; OLSON and VAN DER MAAREL, 1989).

The distribution of different life forms within the group of indicator species was investigated by calculating the number of species of a life form that would be expected by random chance drawing from the 323 species known for the GINS portion of Perdido Key (LOONEY, unpublished). For example, 33 C_4 perennial grasses are known for the study site, thus in a sample of 35 indicator species 6 would be expected by random chance. Chi-square was calculated comparing the observed to the expected number of indicator species in each life form category for all vegetation classifications, and between seasons.

RESULTS

General Classification

Starting with the Autumn 1989 classification, seven general vegetation types were recognized; *i.e.*, strand, wooded dunes, back slopes, dunes, dry and wet swales, and marsh (Figure 2a). The distribution of these seven vegetation types from the left to the right side of the dendrograms reflects a moisture gradient from the dry condition of the strand to the continuously wet conditions of the marsh. Characteristics of the seven vegetation types are described below with indicator species named in Table 1 and the cover of the dominant species shown in Table 2. Comparison with the classifications of WOODHOUSE (1982), DOING (1985), and MORENO-CASASOLA and ESPEJEL (1986) are made where appropriate and are shown in Table 3.

Strand

Plots present on the very front of the beach consisting primarily of bare sand dominated by either *Cakile constricta* or *Iva imbricata* were classified as strand.

Wooded Dunes

These were fixed dunes similar to inland scrub (MYERS, 1990) and characterized by woody perennials such as *Conradina canescens* and *Quercus geminata*. In general, this vegetation type was found at greater than 240 m from the Gulf MHW.

Back Slopes

Low areas on the northern or lagoon-facing slopes of dunes were classified as back slopes. These were characterized by a large number of species per plot, and high cover of *Schizachyrium maritimum, Uniola paniculata,* and *Polypremum procumbens.* Indicator species were *Paronychia erecta, Dicanthelium sabulorum,* or *Chrysopsis godfreyi,* and *C. Godfreyi* f. *viridis.*

Dunes

The largest, most complex and seasonally changing vegetation type was classified as dunes. *Uniola paniculata* reached its greatest cover in the dunes, while *Heterotheca subaxillaris* had high cover and was also an indicator species. This vegetation type was subdivided into three or four subtypes (see below and Figure 3).

Dry Swales

Swales (slacks of other authors, *e.g.* RANWELL, 1972) were low areas with fresh water close to the surface. The presence of only small amounts of *Juncus roemerianus* distinguished swales from the closely related marshes. *Ilex vomitoria* was also a common species of swales. Dry swales were characterized by high cover of *Spartina patens, Schizachyrium maritimum,* and *Dicanthelium sabulorum.*

Wet Swales

Distinguished from dry swales by higher cover of *Muhlenbergia capillaris, Ilex vomitoria,* and *Smilax* spp.

Marsh

Seasonally or constantly innundated areas bordering the lagoons at the back of Perdido Key were classified as marsh. Some areas were removed from tidal influence and the water had low salinity. The marsh vegetation type was characterized by high cover of the dominant *Juncus roemerianus,* an indicator species in three out of four seasons. *Distichlis spicata* was only found in the marsh and wet swales with its highest cover in the marsh.

Dune Classification

Classification of the dune vegetation type (Figure 2) through two additional TWINSPAN di-

Table 1. *Indicator species (codes in parentheses) for main vegetation types and dune vegetation types determined by TWINSPAN classification of permanent plots for Autumn 1989, and Spring, Summer, and Autumn 1990.*

	General Classification				Dune Classification			
	1989	1990			1989	1990		
Species Name	Autumn	Spring	Summer	Autumn	Autumn	Spring	Summer	Autumn
Andropogon virginicus (ANDR)[3]	-	–	–	+	–	–	–	–
Baccharis halmifolia (BACC)[7]	+		+	+	–	–	–	–
Balduina angustifolia (BALD)[4]		+	–	+	–	–	–	–
Cakile constricta (CAKL)[4]	+	+	–	+	–	–	–	–
Centella asiatica (CENT)[5]	–	–	+	–	–	–	–	–
Chamaesyce ammanioides (CHMA)[6]	+	+	+	+	–	+	+	+
Chrysoma pauciflosculosa (CHRS)[7]	–	+	–	+	–	–	–	–
Chrysopsis godfreyi (CHRY)[5]	+	+	+	+	–	+	–	+
C. godfreyi f. viridis (CHRV)[5]	+	+	+	+	–	+	–	–
Cladonia spp. (CLAD)[1]	–		+	+	–	–	–	–
Conradina canescens (CONR)[7]	+	+	+	+		–	–	–
Dicanthelium sabulorum (DICA)[2]	+	+	+	+	–	–	–	–
Distichlis spicata (DIST)[3]	-	–	–	+	–	–	–	–
Erechtites hieracifolia (EREC)[4]	–	+	–	–	-	–	–	–
Fimbristylis caroliniana (FMBR)[3]	+	-	+	+	–	–	–	–
Heterotheca subaxillaris (HTRO)[4]	+	+	+	+	+	+	+	+
Hydrocotyle bonariensis (HYDR)[5]	–	+	–	–	+	+	+	+
Ilex vomitoria (ILEX)[7]	+	+	+	+	–	–	–	–
Iva imbricata (IVA)		+	+	+	+	+	+	+
Juncus roemerianus (JUNC)[2]	+	+	+	+	–	–	–	–
Linaria floridana (LINA)[4]	–	+	–	–		+	–	–
Muhlenbergia capillaris (MULY)[3]	–	–	-	+	–	–	–	–
Oenothera humifusa (OENO)	–	+	+	+	–	+	–	+
Panicum amarum (PANA)	-	–	–	–	–	–	–	+
Panicum virgatum (PANC)[3]	+	–	–	–	–	–	–	–
Paronychia erecta (PARO)[5]	+	+	+	+	–	+	–	+
Pinus elliottii (PINU)[7]	-	+	–	–	–	–	–	–
Polgonella polygama (POLP)[5]	–	–	–	+	–	–	–	–
Polypremum procumbens (POLY)[1]	+	+	+	–		–	–	–
Schizachyrium maritimum (SCHZ)[3]	+	+	+	+	+	+	+	+
Smilax bona-nox (SMBA)[5]		+	–	+	–	–	–	–
Spartina patens (SPRT)	+	+	+	+	–	+	+	–
Stipulicida setacea (STIP)[4]		+	+	–	–	+	–	–
Strophostyles helvola (STRO)[4]	-	–	–	-	–	-	+	+
Uniola paniculata (UNIO)[3]	+	+	+	+	+	+	+	+
Total	17	24	20	25	5	13	8	11

A "+" indicates that the species was designated as an indicator in the determination of a vegetation type. Species life forms (see text) are indicated by subscript after species name: 1 = lichen, 2 = C_3 perennial grass, 3 = C_4 perennial grass, 4 = C_3 annual forb, 5 = C_4 perennial forb, 6 = C_4 annual forb, 7 = woody plant

visions revealed four dune subtypes (Figure 3); *i.e.*, established dunes, developing dunes, disturbed dunes, and low dunes. Indicator species and cover of the dominant species of these subtypes in Autumn 1989 are shown in Tables 1 and 4 and a comparison is made with the classifications of WOODHOUSE (1982), DOING (1985) and MORENO-CASASOLA and ESPEJEL (1986) in Table 3. The characteristics of these four subtypes are described below.

Established Dunes

This was the largest vegetation subtype. It and developing dunes differed from the disturbed and low dunes due to high cover of *Uniola paniculata*. Maximum topographic development of the dune system was found to be associated with this subtype. Established dunes were distinguished from developing dunes by high cover of *Schizachyrium maritimum* and *Heterotheca subaxillaris*.

Table 2. *Species composition (% cover) of vegetation types identified using TWINSPAN of permanent plots in Autumn 1989. + = species present at <0.01% cover overall. Species with cover percentages underlined are those identified as indicator species for their respective groups. This list is comprised of indicator species and the five species (shown by *) in each vegetation type with the highest mean percentage cover.*

	Vegetation Type						
					Swales		
Species	Strand	Wooded Dunes	Back Slopes	Dunes	Dry	Wet	Marsh
Cakile constricta	3.58*	–	–	0.04	–	–	–
Chamaesyce ammannioides	–	–	0.04	0.32	–	–	–
Chrysopsis godfreyi	–	0.02	1.09	0.09	0.23	–	–
C. godfreyi f. *viridis*	–	3.62*	0.67	1.24*	0.19	–	–
Conradina canescens	–	8.05*	0.15	–	–	3.42	–
Dicanthelium sabulorum	–	0.87	0.63	+	5.74*	1.09	–
Distichlis spicata	–	–		–	–	0.04	5.55*
Fimbristylis caroliniana	–	–	–	0.02	0.56	0.02	0.78
Heterotheca subaxillaris	–	–	1.40*	3.15*	0.07	–	–
Hydrocotyle bonariensis	0.04*	–	0.28	1.30*	0.16	0.01	0.47
Ilex vomitoria	–	1.68	0.50	–	8.74*	29.20*	+
Iva imbricata	+*	–	+	0.54	–	–	–
Juncus roemerianus		–	0.16	–	1.02	4.01	74.40*
Mikania scandens	–	–	–	–	0.50	0.20	1.91*
Muhlenbergia capillaris	–	0.11	–	–	–	16.40*	+
Myrica cerifera	–	–	–	0.08	–	4.76*	–
Oenothera humifusa	+*	+	0.08	0.35	0.01	–	–
Panicum virgatum	–	–	0.02	–	2.44*	1.19	0.31
Paronychia erecta	–	0.22	1.60*	0.29	0.89	0.06	–
Polygonella polygama	–	3.94*	0.29	–	–	0.44	–
Polypremum procumbens	–	0.41	2.37*	0.02	1.94	–	–
Quercus geminata	–	15.06*	0.02	–	–	1.05	–
Quercus myrtifolia	–	3.40	–	–	–	–	–
Samolus parviflorus	–	–	–	–	–	–	0.49
Schizachyrium maritimum	–	4.54*	5.67*	2.89*	6.77*	1.30	–
Smilax auriculata	–	0.85	–	–	0.01	5.06*	–
Smilax bona-nox	–	1.21	0.29	0.01	1.28	4.91*	0.02
Spartina patens	–	–	0.08	0.80	13.67*	1.92	5.13*
Strophostyles helvola	–	–	–	0.13	0.11	–	0.99*
Uniola paniculata	0.11*	0.65	3.20*	7.31*	0.42	0.01	–
Mean no. species per plot	1.9	8.9	10.0	5.6	19.1	14.7	6.1

Table 3. *Comparison of the classification of barrier island vegetation types between this study and three previous studies. The comparisons were made on the basis of floral and geomorphological similarities.*

	Previous Studies		
This Study	WOODHOUSE (1982)	DOING (1985)	MORENO-CASASOLA & ESPEJEL (1986)
Strand	Pioneer	Ephemeral tidemark	Embryo
Wooded dunes	Scrub/Forested	Stabilized	Fixed
Back slopes	Back slopes	Sheltered	Sheltered
Dunes	Intermediate	Central fore-dunes	Foredunes, blowouts, active, fixed
Established	Active	Central fore-dunes	Active
Developing	Live	Embryonic	Embryo
Disturbed	Deflation plains	n/a	Blowouts
Low	Flats	n/a	Foredune
Dry swales	Swales	n/a	Humid swales
Wet swales	Swales	n/a	Wet swales
Marsh	Marsh	Marsh	Marsh

Developing Dunes

A vegetation subtype present towards the front of the island close to or just behind the strand vegetation. Developing dunes were intermediate in composition and species richness between established dunes and strand.

Disturbed Dunes

This was a subtype that showed extensive seasonal variation. It contained low amounts of *Uniola paniculata* along with the presence of *Hydrocotyle bonariensis* and *Iva imbricata*. These dunes were most frequently found in areas disturbed by humans.

Low Dunes

This subtype was represented by only a few plots in which *Hydrocotyle bonariensis* and *Heterotheca subaxillaris* had a higher cover than in the plots classified as disturbed dunes. The origin of low dunes may either be as revegetating disturbed dunes or developing dunes to the north of the established dune type.

Indicator Species

The 8 C_4 perennial grass indicator species (Table 1) were more than would be expected by chance drawing from the pool of 323 species on Perdido Key (chi-square = 5.99, P < 0.025 at 1 df). Similarly, the 4 C_4 perennial grass species identified as indicators for the dune classification (Table 1) were more than would be expected by chance (chi-square = 3.84, P = 0.05 at 1 df). On a seasonal basis, the 5 C_4 perennial grass species identified in the Autumn 1989 classification and the 6 indicator species of this type identified for Autumn 1990 were also more than would be expected by chance (chi-square = 6.88 with P < 0.025, and chi-square = 4.27 with P < 0.05, respectively). The occurrence of other life form categories was not significantly different from a random expectation given the species pool.

Seasonal Changes

The seven general vegetation types were consistently present in the classifications from each season (Figure 2). The primary division of plots was always between the wet (marsh and dry and wet swales) and dry (dune, back slope, wooded dune, and strand) vegetation types. This principal division of plots was keyed into the presence of indicator species *Juncus roemerianus* and *Spar-*

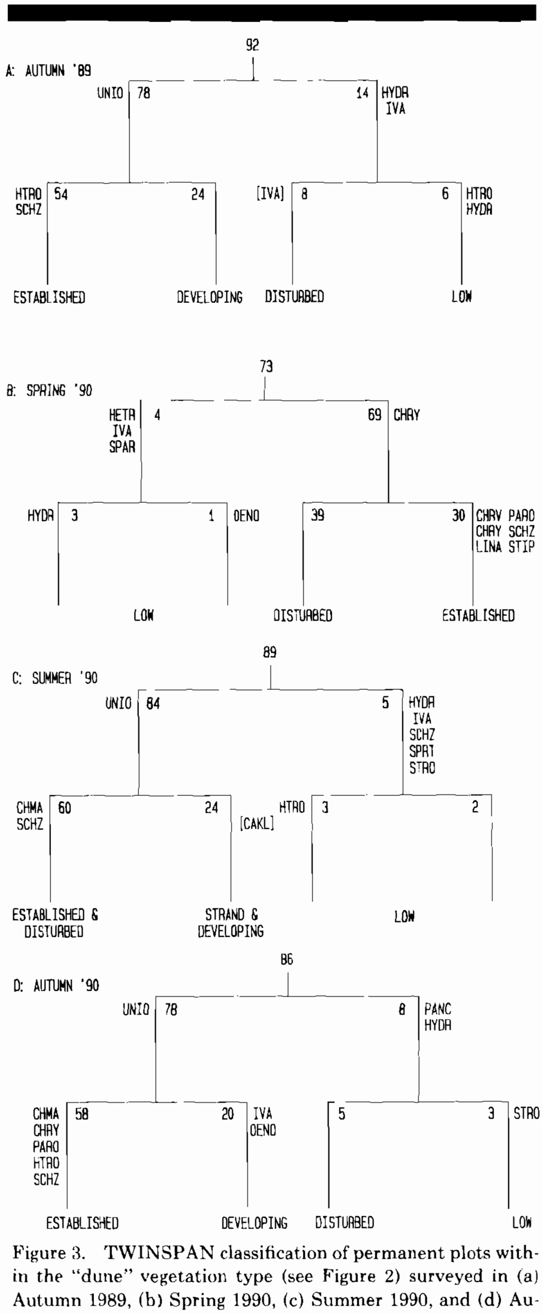

Figure 3. TWINSPAN classification of permanent plots within the "dune" vegetation type (see Figure 2) surveyed in (a) Autumn 1989, (b) Spring 1990, (c) Summer 1990, and (d) Autumn 1990. Indicator species associated with each division are shown (codes as in Table 1). The number of permanent plots associated with each division are also shown. Vegetation types are named based on environmental characteristics of the plots comprising a vegetation type (see text).

Table 4. *Species composition (% cover) of "dune" subtypes identified using TWINSPAN of permanent plots in Autumn 1989. + = species present at <0.01% cover overall. Species with cover percentages underlined are those identified as indicator species for their respective groups. This list is comprised of the five species (shown by *) in each dune subtype with the highest mean percentage cover.*

	Dune Subgroup			
Species	Established	Developing	Disturbed	Low
Cakile constricta	+	0.09*	–	0.20
Chamaesyce ammonnioides	0.37	0.06	0.20	0.95
Chrysopsis godfreyi f. *viridis*	1.14*	–	–	–
Conzya canadensis ssp. *pusila*	0.24	·	0.38*	–
Heterotheca subaxillaris	4.94*	0.05*	+	3.70*
Hydrocotyle bonariensis	0.39	–	1.49*	14.38*
Iva imbricata	0.25	0.26*	0.53*	4.30*
Oenothera humifusa	0.38	0.41*	0.04	0.20
Paronychia erecta	0.47*	0.01	0.16	0.05
Schizachyrium maritimum	3.67*	0.05	1.15*	9.57*
Spartina patens	0.01	–	–	12.23*
Uniola paniculata	10.37*	4.31*	1.00*	0.12
Mean no. species per plot	6.5	3.0	4.0	9.7

tina patens in the marsh and swale plots and *Uniola paniculata* and *Heterotheca subaxillaris* in the dune/back slope/wooded dune/strand plots (Table 2). At the second level of division (Figure 2), the two swale types always separated from the marsh plots independent of the season, however the indicator species associated with this division varied. *J. roemerianus* and *Ilex vomitoria* were indicators in three and two seasons, respectively (Figure 2). The second level of division was not consistent through the seasons for the dune/back slope/wooded dune/strand plots except for the two Autumn classifications which were the same. In a similar manner, the indicator species associated with these divisions were not consistent through the seasons. Only three species consistently indicated specific vegetation types; *Dicanthelium sabulorum* was an indicator for back slopes, *Conradina canescens* was an indicator species for wooded dunes, and *Cakile constricta* was an indicator for the strand. The summer 1990 classification (Figure 2c) was least like the other three seasonal classifications placing strand plots along the gradient between dry swales and dunes. The two most similar classifications were the autumn samples in which the same pattern of branching is apparent in the dendrogram (Figure 2a and b) even though the indicator species were not entirely the same (Table 1).

The vegetation of the dune subtypes showed more variation between seasons than did the general vegetation types. The two autumn classifications recognized the same subtypes with the same relationship to each other (Figure 3a and d). There was also a high degree of indicator species similarity between these two seasonal classifications: *Uniola paniculata, Heterotheca subaxillaris* and *Schizachyrium maritimum* were indicators of established dunes in both autumn classifications. Developing dunes were not present as a subtype in the Spring 1990 classification as they were identifiable at a higher level in the general classification (Figure 2b). In Summer 1990 the established and disturbed dunes were not distinct from each other, and developing dunes were in a group with strand vegetation plots. The four to six plots identified as low dunes were a distinct subtype in all seasons, although the relationship with the other subtypes varied seasonally (Figure 3).

The percentage of permanent plots assigned to the each of the vegetation types and dune subtypes reflected the changing character of the vegetation through the sampling period (Table 5). A relatively constant percentage of plots were assigned to the seven general vegetation types with the most consistent percentage assignment (lowest range) being for the marsh plots (4.8 to 6.2%); strand, and wet and dry swales also had a fairly constant proportion of the surveyed plots assigned to these vegetation types (Table 5). Dunes and back slopes were the most variable with the percentage of plots being assigned to these vegetation types varying by 8.1 and 10.4% respec-

Table 5. *Summary of percentage assignment of permanent plots to vegetation types in Autumn 1989, Spring 1990, Summer 1990 and Autumn 1990.*

Vegetation Type	Autumn 1989	Spring 1990	Summer 1990[a]	Autumn 1990	Range[b]
Strand	4.5	6.2	7.1	6.9	2.6
Wooded dunes	7.8	12.9	8.2	10.1	5.1
Back slopes	19.7	13.5	20.2	23.9	10.4
Dunes	51.7	56.7	48.6	45.7	8.1
Established	30.3	16.9	32.8	30.8	13.9
Disturbed	4.5	21.9	[c]	2.7	19.2
Developing	13.5	15.7	13.1	10.6	5.1
Low	3.4	2.2	2.7	1.6	1.8
Dry swales	3.9	1.1	3.3	3.2	2.8
Wet swales	6.2	3.4	6.0	5.3	2.8
Marsh	6.2	6.2	6.0	4.8	1.4

[a]A single plot classified as a revegetating blowout in Summer 1990 not included
[b]Range is the value of the highest minus lowest percentage assignment value for a vegetation type
[c]Disturbed and established dune subtypes were in the same category in Summer 1990

tively (Table 5). By far the greatest range in plot assignment was in the established and disturbed dune subtypes. This was in part because, in Summer 1990, these two dune subtypes were not discernable from each other thus increasing the number of plots assigned to the joint subtype.

As with the percentage of plots assigned to each vegetation type, the faithfulness of an individual plot to a vegetation type allows for quantification of seasonal variation in the classification scheme. In this context, faithfulness refers to the percentage of plots that were, for example, assigned to the strand vegetation type in Autumn 1989 that were also assigned to this vegetation type in the Spring 1990 classification (Table 6). Plots assigned to the wooded dune, dune, wet swales and marsh vegetation types showed the highest level of faithfulness through the period of the study. The other vegetation types and dune subtypes showed considerable seasonal variation. For example, 100% of the plots assigned to dry swales in spring 1990 were also assigned to this vegetation type in the following summer, yet there were no plots that were assigned to this vegetation type throughout the duration of the study. The level of faithfulness between the two autumn classifi-

Table 6. *Faithfulness[a] (%) of individual permanent plots to the vegetation types identified using TWINSPAN (Figures 2 and 3).*

Vegetation Type	Time Period[b]				
	AU89–SP90	SP90–SU90	SU90–AU90	AU89–AU90	All Times
Strand	38	27	23	38	25
Wooded dunes	100	65	100	93	86
Back slopes	51	67	95	83	43
Dunes	67	79	87	82	56
Established	33	53	83	80	20
Disturbed	25	85	3	25	13
Developing	58	46	50	50	29
Low	50	75	40	33	33
Dry swales	14	100	33	43	0
Wet swales	55	100	91	91	55
Marsh	100	100	82	82	82

[a]Faithfulness was calculated as the percentage of plots assigned to a vegetation type in one sample that were also assigned to the same vegetation type in the later season
[b]Time periods considered were: AU89–SP90, Autumn 1989 to Spring 1990; SP90–SU90, Spring 1990 to Summer 1990; SU90–AU90, Summer 1990 to Autumn 1990; AU89–AU90, Autumn 1989 to Autumn 1990; and All Times where faithfulness was calculated as the percentage of plots assigned to a vegetation type in Autumn 1989 that remained in the same vegetation type in all subsequent seasons

cations was generally high; only strand, dry swales, and disturbed and low dunes were less than 50%, reflecting again the seasonal nature of the differences between the classifications.

DISCUSSION

The general classification of permanent plots (Figure 2) allowed the recognition of seven vegetation types that were seasonally stable; *i.e.* strand, wooded dunes, back slopes, dunes, wet and dry swales, and marsh. Similar vegetation types have been recognized by other authors working in different dune systems (Table 3). The distribution of the vegetation types on the barrier island (Figure 4) as a series of zones parallel to the coast is similar to the pattern reported from other local studies (*e.g.* ELEUTERIUS, 1979; BURKHALTER, 1987; JOHNSON and BARBOUR, 1990) and barrier island vegetation worldwide (DOING, 1985): strand vegetation was limited to the extreme front edge of the barrier island within 24 m of mean high water (MHW); dune vegetation occurred between 24 and 180 m; back slope vegetation was on the lagoon side of dunes 84+ m back from MHW; wooded dunes occurred from 280+ m back from MHW; marsh vegetation was on the margin of lagoons towards the back of the island; wet swales were on the higher margins of marshes; and dry swales occurred around wet swales and in low depressions throughout (GIBSON and LOONEY, 1990). These vegetation types were recognizable during any of the three seasons of data collection. It is at this general level that most classifications of dune vegetation are made, *e.g.* MORENO-CASASOLA and ESPEJEL (1986), CASTILLO *et al.* (1991). This scale of resolution is equivalent to the "formation level" used by DORP *et al.* (1985) in an interpretation of aerial photographs of dunes in The Netherlands. DORP *et al.* (1985) similarly observed that changes at the smaller "community level" were too fast for successful and repeated vegetation mapping. These seven "stable" vegetation types correspond to persistent differences in the soil; COUSENS (1988) showed that the soil of areas on Perdido Key that would be classified as strand or dune vegetation had a pH of 6.5 whereas wooded dunes had a soil pH of 4.9. Marshes were intermediate with a soil pH of 5.7. Increasing acidity with increased vegetation development on barrier islands has been reported from other barrier islands (EHRENFELD, 1990). Average soil moisture content varied on Perdido Key from 1.0 to 3.28% in COUSENS' (1988) study, with marshes forming a contrast at 61.9%.

More C_4 perennial grasses were identified as indicator species than would have been expected by random drawing from the species pool. These species, *e.g. Uniola paniculata, Spartina patens, Schizachyrium mortimum,* are also the dominant species in several of the vegetation types. EHRENFELD (1990) notes that the competitive interactions between barrier island species place a premium on space acquisition and retention, and the ability to tolerate mobile sand and salt spray. This is likely the reason that perennial grasses and common barrier island species form the basis of the classification scheme identified in this study. MORENO-CASASOLA (1988) similarly noted that sand-binding plant species with rhizomatous growth forms characterized dunes of the southeastern U.S.A. north of Mexico.

Of the seven vegetation types, the marshes and wooded dunes stayed easily recognizable throughout the seasons with minimal variation. Plots assigned to one of these two vegetation types had a greater than 82% chance (one exception at 65%) of remaining in the vegetation type during a subsequent survey (Table 6). The dominance of the perennial *Juncus roemerianus* in constantly waterlogged conditions in the marsh, and the preponderance of woody perennials that exhibit few short-term changes in cover in the wooded dunes account for the relative stability of these vegetation types. Nevertheless, there were seasonal differences in the identity of herbaceous indicator species associated with these two vegetation types, *e.g. Polygonella polygama* was an indicator of wooded dunes only in Autumn, 1990.

Classifications at the general level identified in this study (Figure 2) are useful for understanding fairly coarse changes in coastal vegetation. Long-term changes in vegetation are best addressed at this level (*e.g.* VAN DER MAAREL *et al.*, 1985; CORONA *et al.*, 1988). However, there is an increasing interest in the dynamics of dune vegetation, especially from a management perspective (DE RAEVE, 1989). To better understand the effects of the various recreational pressures to which many dune systems are subject, there is a need for finer scale classification of dune vegetation types. This study shows that as this finer level of resolution is approached as in the recognition of the dune subtypes (Figure 3, Table 4), so the effects of seasonal variation become more pronounced. Four main dune subtypes were recog-

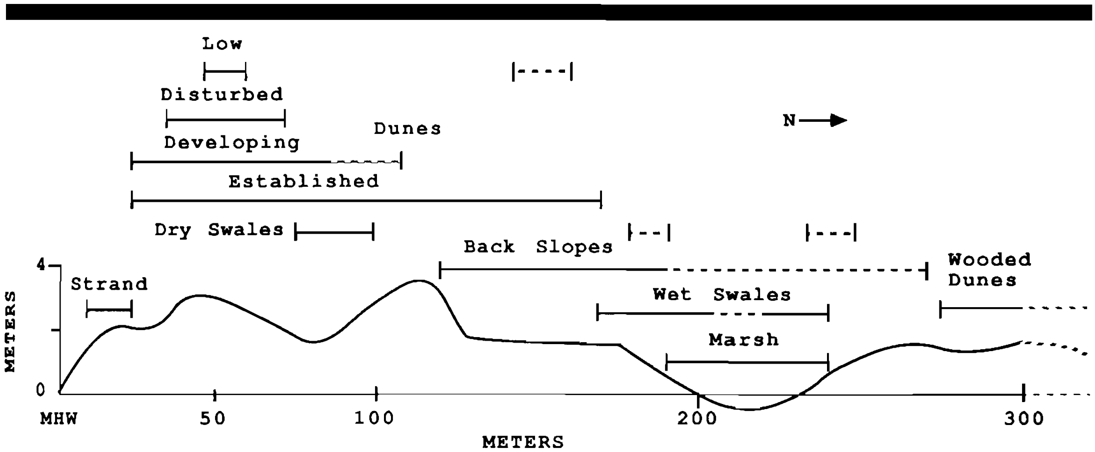

Figure 4. Schematic profiles of the eastern 11 km of Perdido Key showing the distribution of vegetation types (minimum and maximum distances from MHW). The profile is shown extending to 300 m although >75% of this portion of the island is <180 m (see Figure 1).

nized in this study (established, disturbed, developing, and low dunes), but the assignment of plots to each of these vegetation types varied seasonally, as did the relationship between the vegetation types and the indicator species associated with each of them. For example, *Iva imbricata* was an indicator species for low dunes in Spring and Summer 1990, and for developing dunes in Autumn, 1990. The reasons for these seasonal changes are related to the seasonal phenology of the species on the barrier island (COUSENS, 1988; CORDAZZO and SEELIGER, 1988). Seasonal growth patterns can affect the spatial pattern of dune species, the spatial relationship of one species to another, and hence local species associations and community types (VAN TOOREN *et al.*, 1983; GIBSON, 1988). Local changes in the ground water regime have also been shown to alter the spatial and temporal relationship between dune species (VAN DER LAAN, 1979). In addition, there can be associated seasonal differences in the soil fauna (*e.g.* GHABBOUR *et al.*, 1987).

Surprisingly, there are few comparable studies emphasizing the importance of seasonal variation in classification of plant communities. FORAN (1986) classified arid grassland sites in Australia and observed a dominating influence of season over grazing. In a south Wales dune system, WILLIAMS and RANDERSON (1989) used TWINSPAN and DECORANA, an ordination procedure, to show the seasonal movement of vegetation stands in relation to repeated trampling. Trampling was shown to eliminate dicotyledonous species and reduce the seasonal development of communities on north-facing dune slopes. Without a knowledge of the seasonal variation in community development an understanding of the effect of that particular recreational pressure would not have been possible.

COUSENS (1988) suggested that a "whole island" perspective is appropriate for the management and conservation of the Gulf Islands National Seashore (GINS) portion of Perdido Key (Figure 1). The management plan for the GINS includes a program to evaluate the effects of beach renourishment on the natural plant communities to assist in policy decisions regarding the feasibility of recurring renourishment (GULF ISLANDS NATIONAL SEASHORE, 1990, 1991). Of particular concern is the preservation of the natural dune systems. This involves both an identification and recognition of the various vegetation types on the barrier island as well as an assessment of their temporal stability. The need to incorporate this type of habitat management has been recognized elsewhere both in Florida (DAVIS, 1975) and internationally (*e.g.* OLSON and VAN DER MAAREL, 1989; WANDERS, 1989). Clearly, as a better understanding of coastal plant communities is sought for management purposes so the seasonal variation in plant communities and the consequent different classifications that can result are going to become increasingly important.

ACKNOWLEDGEMENTS

This project was supported by funds from the United States Department of the Interior through the National Park Service (Cooperative Agreement Number CA-5320-9-8001). Thanks are due to Diana Athnos, Michelle Misner, and Debbie Stein Looney for assistance in the field, Amelie Blyth and James Burkhalter for assistance with the identification of plant specimens, and James P. Morgan, Gregory Stone and Carl Zimmerman for discussions on the geomorphology and management of Perdido Key. This is ICER Publication Number 91-6.

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□ RÉSUMÉ □

La végétation de 224 parcelles de 5 m × 2 m, localisées sur 13 transects à travers l'extrême Est de l'île de Perdido Key (Florida) a été classée en utilisant une analyse d'espèces ("two-way indicator"). La variation saisonnière de la végétation a été évaluée à partirde données collectées à l'automne 1989, aux printemps, été et automne 1990. On a pu reconnaître 7 types généraux de végétation pour ces quatre saisons. La plus importante variation a lieu sur et entre les parcelles de type "végétation de dune". Par opposition, les parcelles des dunes boisées et des marais ont eté intersaisonnièrement plus stables. Quatre sous-types de végétation dunaire ont été identifiés: dunes établies, perturbées, en accrétion et dunes basses. Mais ces sous-types n'ont pas toujours pu être significativement reconnus sur les parcelles et variaient entre les saisons. Les deux classifications d'automne se ressemblaient, celles d'été et de printemps ou d'automne comparées entre elles étaient plus dissemblables. A la lumière de la conservation et de l'aménagement de la végétation littorale, on discute de la possibilité de développer pour une île barrière, une classification consistante intégrant les variations saisonnières.—*Catherine Bousquet-Bressolier, Géomorphologie E.P.H.E., Montrouge, France.*

□ ZUSAMMENFASSUNG □

Die Vegetation auf 224 Dauerflächen von 5 × 2 m Größe auf 13 Querprofilen am Ostende des Perdido Key, Florida, wurde aufgrund einer Analyse der Arten klassifiziert. Die saisonalen Veränderungen wurden festgestellt durch Erhebung im Herbst 1989 sowie Frühjahr, Sommer und Herbst 1990. Verschiedene allgemeine Vegetationstypen konnten innerhalb der 4 Jahreszeiten erkannt werden, wobei die größten Variationen innerhalb der Flächen der Dünen-vegetation auftraten. Im Gegensatz dazu zeigten Testflächen in bewaldeten Dünen und auf Marschen stabile Verhältnisse innerhalb der Jahreszeiten. Es wurden 4 Sub-Typen für die Dünenvegetation festgestellt: Diejenigen der gut ausgebildeten Düne, der gestörten, der initialen und der niedrigen Dünen. Allerdings gab es zu allen Jahreszeiten erhebliche Veränderungen der Vegetation auf den dazugehörigen Testflächen. Insgesamt ähnelten sich die beiden Herbstzustände stärker als die des Frühjahrs und des Sommers, und auch deren Unterschied zum Herbstzustand. Die Probleme in der Entwicklung einer schlüssigen Klassifikation der Vegetation auf Nehrungsinseln, welche auch die saisonalen Veränderungen einschließen, werden vor dem Aspekt des Schutzes und des Management der Küstenvegetation diskutiet.—*Dieter Kelletat, Essen, Germany.*

□ RESUMEN □

Por medio del Análisis Indicador de Especies de Doble Entrada, se clasificó la vegetación de 224 puntos permanentes de 5 m × 2 m situados sobre 13 transectas que cruzan las islas sobre el extremo este de Perdido Key.

La variación estacional en la clasificación de la vegetación se estableció utilizando datos colectados en el otoño de 1989, y la primavera, verano y otoño de 1990. Siete tipos generales de vegetación fueron reconocidos a través de las cuatro estaciones de recolección de datos, presentándose la mayor variación en el tipo de vegetación de los médanos, dentro y entre los puntos. En contraste, los puntos dentro de los médanos y los tipos de vegetación de la marisma eran los más estables entre estaciones. Se identificaron cuatro subtipos de vegetación tipo en los médanos: los establecidos, los perturbados, en desarrollo y en los médanos bajos. Sin embargo, estos subtipos, poseían una baja asignación permanente y entre estaciones varió. Las dos clasificaciones de otoño eran similares entre sí, que lo que lo eran las clasificaciones de primavera con la de verano o con las de otoño. Los problemas en el desarrollo de una clasificación consistente, en la vegetación de las barreras de islas, que pueden incorporar variaciones estacionales se han discutido a la luz de la conservación y manejo de la vegetación costera.—*Néstor W. Lanfredi, CIC-UNLP, La Plata, Argentina.*