

2010

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Original Publication Citation

McMillan, B. A., & Day, F. P. (2010). Micro-environment and plant assemblage structure on Virginia's barrier island "pimple" dunes. *Northeastern Naturalist*, 17(3), 473-492. <https://doi.org/10.1656/045.017.0308>

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Micro-environment and Plant Assemblage Structure on Virginia's Barrier Island "Pimple" Dunes

Brett A. McMillan^{1,*} and Frank P. Day²

Abstract - "Pimple" dunes are small, rounded coastal dunes that form along major dune ridges of the barrier islands along the Eastern Shore of Virginia. Although most pimple dunes are small structures ranging between 10 and 20 m in diameter, they have distinct plant assemblages that replicate the upland ecotones of their barrier islands. We examined the relationship between microenvironment, edaphic factors, and plant assemblage structure on pimple dunes. Water availability was an obvious major ecological driver, but we also tested other environmental factors that may correlate with plant assemblage structure. We found distinct assemblage types that segregated themselves by habitat type: marsh, shrub thicket, and dry summit. Freshwater availability was important in delineating vegetation differences, both among transects and among species. However, soil nutrients, such as ammonium, potassium, magnesium, and boron, were also spatially correlated with plant assemblage structure. We hypothesize that interactions between water and other environmental factors (e.g., the accumulation of nutrients in the marsh after they are leached from the dune summits) are important determinants of plant species distribution and abundance, and suggest that more attention be given to micronutrients in future phytosociological studies of barrier islands.

Introduction

Plant assemblages of barrier islands and coastal dunes were among the first research subjects of modern ecologists, and understanding the environmental influences on plant assemblage structure on dunes remains a basic research goal of plant ecology (e.g., Cowles 1899, Hayden et al. 1995, Kearney 1904). Olsson-Seffer (1909) identified several groups of abiotic factors influencing plant assemblage structure on dunes: "atmospheric, hydrodynamic, edaphic, topographic, and historical." Studying plant-environment interactions on dunes relates directly to community- and ecosystem-level functioning and has practical uses for ecosystem monitoring and restoration in coastal systems (Ehrenfeld 1990, Hayden et al. 1995).

On barrier islands and coastal dunes, hydrodynamic factors, especially freshwater availability, are usually the most important ecological drivers shaping assemblages (Ehrenfeld 1990). On the barrier islands of the Virginia Coast Reserve (VCR), depth to mean freshwater table is considered by researchers to be largely responsible for creating the differences

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between freshwater marsh, shrub thickets, and xeric dunes (Hayden et al. 1991, 1995).

Researchers have studied “pimple” dunes of Virginia’s barrier islands as geomorphological oddities for years (Cross 1964, Dietz 1945, Melton 1935, Rich 1934). The main dunes of the barrier island are typically laid down in longitudinal rows by significant weather events, whereas pimples are circular to slightly ovate and flat-topped (Fig. 1; Anthonsen et al. 1996, Cross 1964). There have been no conclusive studies about their formation, despite a few hypotheses being posited (e.g., Cross 1964). We assume that they arise from sand being deposited around pioneer plants, but the mechanism for how that sand can be deposited in concentric circles is not clear. Pimple dunes are typically 0.5–2 m taller than the elevation of the surrounding marsh, and their diameters range from 5–25 m (Fig. 1).

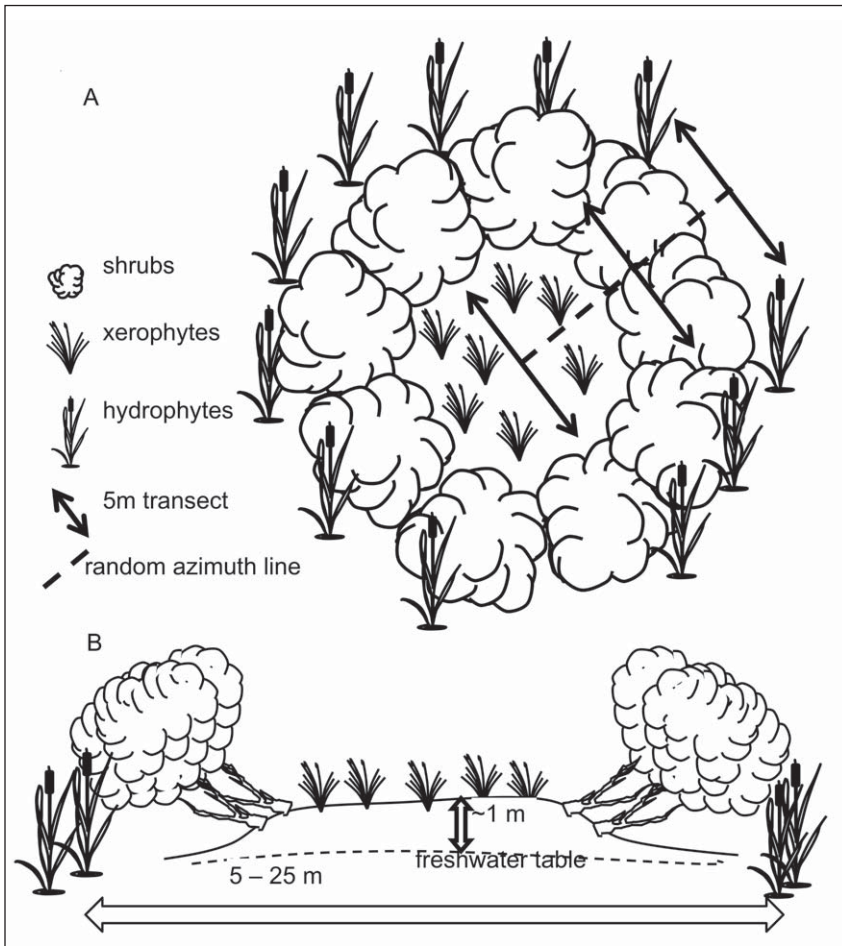


Figure 1. Structural diagram of a pimple dune: A. Overhead view; B. Cross-section.

The ecology of pimple dunes is not as well characterized as their geology, but there have been some preliminary studies of their plant assemblages. During the early years of research at the VCR Long-Term Ecological Research (LTER) site, Hayden et al. (1995) noted that pimple dunes had clearly delineated concentric zones that were readily distinguished by plant assemblages, i.e., marsh graminoids, *Morella cerifera* (L.) Small (Wax Myrtle) thickets, *Iva frutescens* L. (Marsh Elder) thickets, conifers, xeric forbs, and graminoids. Similar assemblages occur along the inland elevation/water gradients of the islands in much wider (100s of meters instead of 1–3 m) bands that follow the lines of the main dunes.

We studied the relationships between plant assemblage composition and microhabitat conditions to understand the environmental drivers that create these tightly packed habitat zones. There have been many studies of the synergistic effects between water table, soil, landscape, and biota on plant assemblage composition, but there is no unified theory of plant species-environment interactions as yet (Bazzaz 1996, Curtis and McIntosh 1951, Frego and Carleton 1995, Gauch 1982, Olsson-Seffer 1909, Palmer 2010, Peet and Loucks 1977, Peet et al. 1988, Pielou 1984). Our goals were to verify that water was indeed the most important ecological driver shaping assemblages on the dunes and to describe what other factors might be at play. We studied pimple dunes because they represent simplified models of the inland ecosystem of the island, with sharply divided plant assemblages.

We had three hypotheses: First, we expected that water availability would be the most important factor determining assemblage structure on pimple dunes. Second, we expected that soil variables other than water might influence the distribution of plant species. Third, we expected that species distributions may also be related to geomorphological features of the dune system. In all three cases, we hoped to get both a broad view of species' distributions as well as a finer view of how species with similar habitat preferences partitioned themselves among microhabitats.

Field-site Description

We conducted this study on the pimple dunes of Hog Island, Northampton County, VA. Approximately 30 to 40 dunes on Hog Island lie along a north-south line in the oldest interior swale marsh between two dune ridges that formed in 1871 and 1955, respectively, with most pimple dunes positioned closer to the 1955 ridge. We chose 17 pimples for our study based on access to this line. The northwest and southeast corners of the study were 37.454°N, 75.670°W and 37.446°N, 75.667°W (WGS84 datum), respectively. We surveyed and marked permanent transects for annual floristic surveys across the dunes during summer of 2003.

Methods

Floristic surveys

We designed our floristic sampling methods to begin to understand the influence of the unique geomorphology of the dune system on vegetation patterns. To maintain a constant elevation across the pimple dunes, we surveyed plants using line transects instead of two-dimensional survey plots. On each dune, there were three 5-m transects stratified among the three assemblage zones: summit, shrubs, and marsh. Therefore, 51 transects (3 transects x 17 dunes) were laid out in total.

We defined assemblage types based on the growth habit of plant species growing in them and on the amount of time that the types were routinely inundated with water. Dry, sandy interiors with graminoids and forbs, but few woody plants were defined as the *summit*. Sloping, dry to moist zones with woody shrubs (mostly *M. cerifera*) were defined as *shrub*. The areas within ≈ 2 m of the outer edge of the shrub canopy that were dominated by marsh graminoids were defined as *marsh*.

The boundaries between assemblages were readily apparent and easily distinguishable from both the growth habit of the plant species (e.g., graminoids vs. woody plants) and their topographic setting (e.g., swale vs. dune slope). Besides these large-scale differences, however, it was difficult to see clearly defined patterns of individual species distributions, either in relation to each other or to microhabitat. *Morella cerifera* was the only species found on every dune, but most species were found in more than one assemblage type. It was not apparent how habitat conditions other than elevation and water availability varied between transects, if at all. Moreover, there was overlap in the elevations, slopes, etc. between shrub and summit transects on different pimples.

We conducted floristic surveys in June and July of 2003, 2004, and 2006 (logistical issues prevented a complete survey in 2005). We flagged the endpoints of each transect and recorded coordinates for them so that the same area could be measured each year. We made a collection of all plant species encountered, and identified species using three floras for the region (Gleason and Cronquist 1991, Radford et al. 1968, Weakley 2008). Each plant species encountered was given an a priori habit-preference designation to label them in ordination results: xerophytic, mesophytic, or hydrophytic. We based these designations on the floras and field observations of the habitat type where each species was usually encountered, but we had no preconceptions about the edaphic or other microhabitat preferences of individual plant species. Vouchers of all species recorded are deposited at the Old Dominion University Herbarium.

Water availability

We measured the depth to the water table along each survey transect using a soil auger to bore monitoring holes. The holes more or less remained

open for the duration of the study, and could be re-checked with minimal re-augering. Water levels were checked at each monitoring hole twice every summer of 2003, 2004, and 2006 to determine the average range.

Soil variables

We measured a variety of soil properties. During the summers of 2005 and 2006, three soil cores collected at the middle and ends of each line transect were mixed together (≈ 100 g total) to produce a composite soil sample. Sub-samples of the composite samples were extracted with 2N KCl solution, and extracts were tested for ammonium and nitrate/nitrite concentration with a Lachat colorimetric autoanalyzer at the Environmental Science Department of the University of Virginia. Another set of subsamples was sent for analysis at the Virginia Tech soil-testing laboratory. Each soil sample was tested for pH, cation-exchange capacity (CEC), and nutrient concentrations (P, K, Ca, Mg, Zn, Mn, Cu, Fe, and B). Organic matter was determined by mass loss on ignition. Full descriptions of the chemical analyses are provided in Mullins and Heckendorn (2005). Stratified samples collected during the initial excavation of the water-table bore hole revealed that pimple dunes are made of a well-sorted sand with little horizon development, and we therefore did not use particle size as a factor. The thickness of the organic soil horizon was measured at the bore holes.

Geomorphological features

We recorded physiographic variables for each transect. The elevation of each transect above the mineral substrate was determined using a surveying transit. We used the change in elevation and a plumb-bob inclinometer to measure the percent slope of the ground within 1 m on either side of the transect. We organized each of the three transects on each dune along a radius line from the center of the dune to its periphery. This radius had a random azimuth, so that we could investigate the influence of aspect on plant assemblage and environmental conditions. Since aspect/azimuth is recorded in degrees, a circular measurement, we converted it to two linear variables, eastness and northness, using the sine and cosine of the azimuth, respectively.

Statistical analyses

For the purpose of summarizing most environmental variables, we calculated the mean \pm 1 S.D. per assemblage type and tested for differences between assemblages using parametric tests, i.e., ANOVA and ANCOVA. Based on our first two hypotheses, it was important to account for the effect of water-table depth on edaphic characteristics. We therefore tested for assemblage effects (marsh vs. shrub vs. summit) on mean levels of soil nutrients and other edaphic variables using mean water-table position as a covariate in a one-way ANCOVA. We did not include dune identity as a factor or block in the model since doing so reduced the residual degrees of freedom too low for water-table position to be included as a covariate.

In a separate set of ANOVAs, however, in which pimple-dune identity was included with assemblage in a full-factorial model, only three variables exhibited a significant assemblage effect: potassium, potassium saturation, and ammonium concentrations (see Results). We used repeated-measures ANOVA to test for an assemblage effect on water table level and ANOVA to test for differences in geomorphological variables; as with the edaphic variable tests, we did not include a dune effect in the model.

To summarize the distribution of plant species among the assemblage types, we calculated the annual mean species abundance along each transect. If possible, we used ANOVA to determine if species distributions were influenced by the assemblage type. However, many species were not common enough to use ANOVA to test whether assemblage type was significantly related to their distribution. For the same reason, we could not examine the influence of water-table level on most species distributions using ANCOVA or linear regression. We therefore chose an alternate statistical method for analyzing species distributions and environmental variables.

We primarily designed this study for analysis by ordination methods, because typical parametric tests are not robust for data sets with many zeroes, nor do they have the ability to evaluate relationships between all species and environmental gradients simultaneously (McCune and Mefford 1999, Pausas and Austin 2001, ter Braak 1986). Moreover, the primary goal of ordination methods is to collapse a multivariate data set into fewer variables so that patterns are more easily discernable (Palmer 2010).

Canonical correspondence analysis (CCA) is an ordination method expressly designed to relate assemblage composition (i.e., combinations of species abundances) to environmental factors (Kent and Ballard 1988, Kourtev et al. 1998). The test creates regression relationships between all variables in the species and environmental matrices. Those regression relationships in turn are used in different combinations to produce mutually orthogonal axes that explain a portion of the total variation between transects or species (Gauch 1982, Kent and Ballard 1988). By convention, the axes are ordered by the percentage of variation in the data that they explain; typically, the amount of variation explained by each successive axis decreases rapidly, so only the first two or three axes are usually examined for patterns (McCune and Mefford 1999, Palmer 2010).

Plotting species or transects along a CCA axis creates a spatial representation of statistical similarity or relatedness. For example, in an ordination of transects, each transect is assigned a coordinate on the first axis, based on both relative proportions of species and environmental variables. The numeric distances between specific plant assemblages are measures of similarity or relatedness between them. Assemblages farthest apart on the axis are the most different. For that same axis, each environmental factor and species also has a coordinate that can be thought of as a vector and represents the relative contribution of that factor or species to the explanatory value of the axis. Often, there will be groups of sample units (transects, in this example),

whose connection may be surmised from the factors or species important to the axis. Although the second axis was created using the same environmental and species data as the first axis, it represents different combinations of those data and is not correlated with the first. To tease out differences among groups on the first axis, they may be plotted in a two-dimensional space using the second axis.

We used two post-hoc tests from the CCAs to test our hypotheses. Monte-Carlo resampling tests determine whether axes significantly described linear, non-random relationships within the data matrices—i.e., whether CCA-derived patterns and associations are significantly different from random ones (McCune and Mefford 1999). We also used Pearson's correlation coefficients (r), which determine the percent contribution each variable made towards the solution of each axis.

We ran CCA analyses in two different matrix configurations: 1) with mean values of species abundances in each transect and mean values of environmental characteristics in each transect and 2) with matrices transposed so that we tested the average species cover per transect against the mean value of environmental variables per species. To create this species-environmental factors matrix, we calculated mean values of each environmental variable from all transects in which a particular species occurred. The conventional way to use CCA in studies like this one is with the first configuration (Palmer 2010), but we wanted to see if rearranging the matrices to focus on species would reveal different patterns. Examining the analyses of the transect matrix is still pertinent, however, because our field observations could not discern differences in seemingly similar transects that were home to different assemblage types. For example, there was variation within the range of ca. 75 cm where the transition from shrub to summit assemblages started, around the same as the range in pimple dune heights: 30–150 cm.

Results

Ordination overview

The transect matrix CCA and species matrix CCA explained 31% and 32%, respectively, of variation in the data with the first three axes of their solutions (Table 1 and Figs. 2, 3). Each of the first three axes in both ordinations explained 9–12% of variation in the data. In both ordination solutions, relationships between variables and patterns were not random (Monte-Carlo, $P < 0.05$ for all).

Assemblages: Water availability

Assemblage types had significantly different water levels (repeated-measures ANOVA: $F_{2, 29} = 72$, $P < 0.001$; Table 2). Water-table position and its direct correlate, elevation, were the two most important factors explaining variation in plant species composition among transects (Pearson's $r = 0.9$ for the first axis in the transect CCA; Table 1). In the ordination, the tight groupings formed by marsh transects indicated that they varied least among

Table 1. Pearson's correlation coefficients (r) for the five most important variables in the first three axes of each CCA solution.

Transects					
Axis 1: 12%		Axis 2: 10%		Axis 3: 9%	
Variable	r	Variable	r	Variable	r
Elevation	0.906	Mg	-0.434	P	-0.795
Water table	-0.901	CEC	-0.406	MgSat	0.694
O horizon	-0.784	Ca	-0.306	OM	0.646
CEC	-0.540	Salinity	-0.304	Fe	0.621
B	-0.534	OM	-0.295	Zn	-0.597

Species					
Axis 1: 12%		Axis 2: 11%		Axis 3: 9%	
Variable	r	Variable	r	Variable	r
K	0.567	NH ₄	0.536	Fe	-0.380
KSat	0.552	O horizon	0.522	OM	-0.345
MgSat	-0.536	Water table	0.451	Mn	-0.305
O horizon	0.486	Elevation	-0.447	Slope	0.268
CEC	0.432	Mn	-0.379	NO _x	0.237

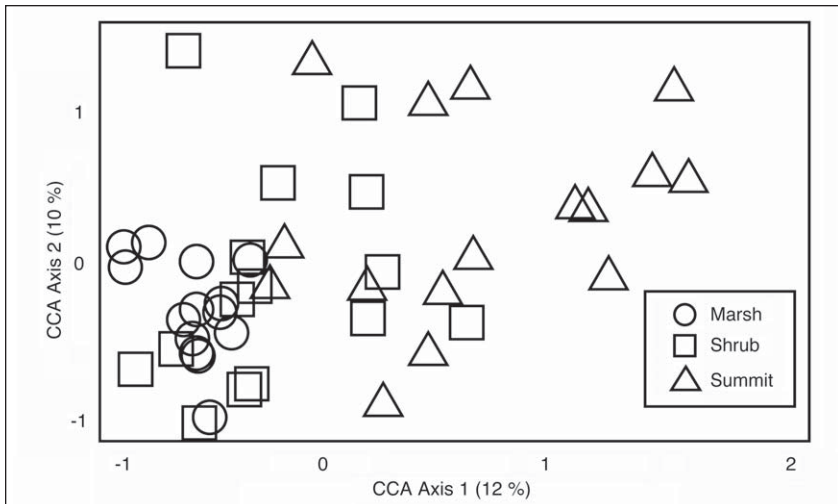


Figure 2. Canonical correspondence analysis ordination of transects based on environmental factors. Symbols represent transects; shapes indicate assemblage type. In this and following figures, percentages listed on axes refer to the percentage of variation explained. The percentages are cumulative and can be added to determine the total percent of variation explained by both axes. The proximity of transect symbols to each other on the two axes represents their similarity to each other based on the environmental factors and species that occurred there. For example, the relatively tight clustering of circles in the lower left indicates that marsh assemblages were more similar in species composition and/or conditions than shrub and summit assemblages, whose coordinates are more variable. Furthermore, the spacing of most assemblages from marsh to shrub to summit along the first axis reflects the high importance of water and elevation to Axis 1 (Table 1) and therefore represents a moisture gradient between assemblages.

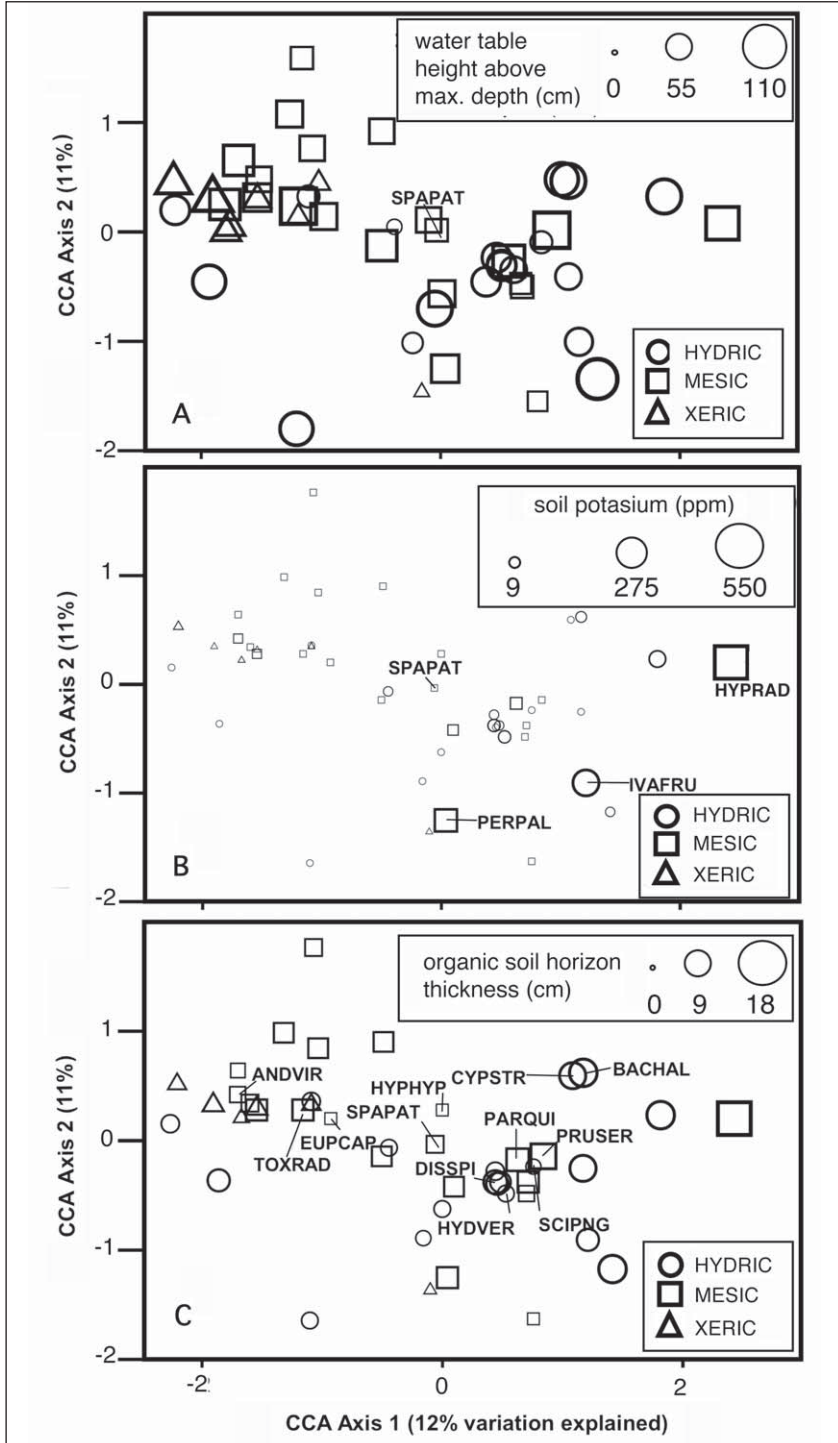
the three assemblage types in terms of water availability, environmental variables, and species composition (CCA; Fig. 2).

Assemblages: Soil variables

Although water availability was the most important factor associated with the differences among plant assemblage types, some soil properties were important as well. Concentrations of six soil elements: B, Cu, Fe, Mn, P, and Zn, differed significantly among assemblage types (ANCOVA, for all tests: $F_{2,46} \geq 7.8$, $P \leq 0.001$; Table 2); B, Ca, and Mg were associated with water table depth (ANCOVA, for all tests: $F_{1,46} \geq 5.0$; $P \leq 0.03$; Table 2). B, P, and Zn occurred in highest concentration in marsh transects, whereas Cu was lowest in marsh habitat (Tukey's: $P < 0.01$ for all). There was little NH_4^+ or NO_3^- and no discernable pattern in nitrogen distribution among assemblage types, but NH_4^+ , along with K and K base saturation, did exhibit a significant difference in distribution among pimple dunes (Table 2). In terms of these three variables, most dunes formed a single homogenous group, with two to five dunes having significantly higher mean concentrations for NH_4^+ , K, and K base saturation (Tukey's: $P < 0.05$ for all comparisons).

Table 2. Mean environmental conditions in pimple dunes by assemblage type (± 1 SD). CEC = cation exchange capacity; meq = milliequivalents; OM = organic matter measured as loss on combustion; Water = water table position relative to the marsh soil mineral horizon. For all variables except water, the effect of assemblage type was tested with ANCOVA, using average water-table position as covariate. Water-table position was tested with repeated measures ANOVA. Italics = water-table position effect, $F_{1,46} \geq 5.0$, $P < 0.03$; bold = significant assemblage effect, $F_{2,46} \geq 12.5$, $P < 0.001$; letters indicate significantly different groupings determined by Tukey's post-hoc test, $P < 0.05$. For assemblage effect with water table, $F_{2,29} = 72$, $P < 0.001$. Asterisks indicate a significant pimple effect in an alternate ANOVA testing for pimple and assemblage effects with interactions, $F_{16,46} \geq 5000$, $P < 0.01$.

	Marsh	Shrub	Summit	Total
B (ppm)	<i>0.6 ± 0.2^a</i>	<i>0.3 ± 0.3^b</i>	<i>0.14 ± 0.1^c</i>	0.34 ± 0.3
Ca (ppm)	224 ± 32	151 ± 110	91 ± 36	154 ± 87
Cu (ppm)	<i>0.16 ± 0.05^a</i>	<i>0.1 ± 0.01^b</i>	<i>0.1 ± 0.02^b</i>	0.12 ± 0.04
Fe (ppm)	85 ± 20	134 ± 56	86 ± 35	102 ± 46
K (ppm)*	62 ± 103	88 ± 186	20 ± 11	57 ± 124
Mg (ppm)	<i>111 ± 20</i>	<i>108 ± 64</i>	<i>51 ± 27</i>	90 ± 50
Mn (ppm)	2 ± 0.5	2 ± 1	2 ± 1	2 ± 1
NH_4 (ppm)*	94 ± 131	143 ± 255	90 ± 107	109 ± 175
NO_x (ppm)	6 ± 12	10 ± 10	22 ± 23	13 ± 17
P (ppm)	<i>25 ± 6^a</i>	<i>11 ± 7^b</i>	<i>14 ± 5^b</i>	16 ± 8
Zn (ppm)	<i>1.7 ± 0.5^a</i>	<i>1 ± 0.2^b</i>	<i>1 ± 0.3^b</i>	1 ± 0.5
CEC (meq/100g)	<i>2.2 ± 0.4^a</i>	<i>1.9 ± 1.1^b</i>	<i>0.9 ± 0.4^c</i>	1.6 ± 0.9
Ca_{sat} (%)	52 ± 4	41 ± 11	50 ± 11	47 ± 10
K_{sat} (%)*	6 ± 7	7 ± 11	6 ± 3	6 ± 7
Mg_{sat} (%)	42 ± 4	52 ± 9	44 ± 12	46 ± 9
OM (%)	0.9 ± 0.3	2.4 ± 1.3	1.1 ± 0.8	1.5 ± 1.1
Organic Horizon (cm)	<i>9.8 ± 4.0^a</i>	<i>7.9 ± 4.0^a</i>	<i>3.0 ± 3.0^b</i>	6.8 ± 4.6
Water (cm)	<i>11 ± 7^a</i>	<i>-17 ± 17^b</i>	<i>-51 ± 25^c</i>	-19 ± 31
Elevation (cm)	<i>22 ± 9^a</i>	<i>54 ± 19^b</i>	<i>84 ± 32^c</i>	54 ± 33 ^a



Species: Distribution among assemblages

The most abundant plant species exhibited measurable differences in distribution among assemblage types, but most species did not restrict themselves to assemblages that corresponded to their a priori habitat preference designations (ANOVA: $P < 0.05$; Table 3). *Morella cerifera* was the species with the highest amount of cover regardless of assemblage type, with shrub zones having the most cover and summit transects the least (Tukey's: $P < 0.0001$; Table 3).

A large number of species were perennial graminoids. For example, *Distichlis spicata* (L.) Greene (Saltgrass) was common in the marsh only (Tukey's: $P < 0.0001$; Table 3). Cover of *Spartina patens* (Aiton) Muhl. (Saltmeadow Cordgrass), a C4 marsh grass, however was not significantly different between marsh and summit plots (Tukey's: $P < 0.01$; Table 3). There were a few abundant perennial forbs as well, such as *Polygonum hydropiperoides* Michx. (Waterpepper, Swamp Smartweed), which were more abundant in the marsh and shrubs than in summit transects (Tukey's: $P < 0.01$; Table 3).

Species: Water availability

Although water availability was the best predictor of differences between assemblages, it was only one among many factors that were associated with variation in the distribution and abundances of individual plant species (Pearson's $r = 0.4$ for the second axis in the species CCA; Table 1). Moreover, there was not as much variation in average water availability per species as per transect assemblage type (Figure 3, cf. Table 2). Half of the factors that were more important in the ordination (i.e., magnesium base saturation, organic horizon thickness, cation exchange capacity; Table 1)

Figure 3 (opposite page). Canonical correspondence analysis ordination of species based on environmental factors with overlays of environmental variables: A. water availability overlay; B. soil potassium overlay; C. organic horizon depth overlay. In this figure and Figure 4, symbols represent species, their shapes represent a priori habitat preference, and their size represents the mean value of the particular variable across the transects in which it was encountered. In the case of water, the variable is height of the water table above the maximum depth, i.e., the bigger the symbol, the wetter the plot. Each plot presents the same similarity data; i.e., species are in the same place in each plot. The only difference between A, B, and C is that relative amounts of a particular environmental variable are presented on top of the ordination data, hence the term "overlays". Species abbreviations are the same in this and Figure 4. ANDVIR = *Andropogon virginicus*; BACHAL = *Baccharis halimifolia*; CYPSTR = *Cyperus strigosus*; DISSPI = *Distichlis spicata*; EUPCAP = *Eupatorium capillifolium* (Lam.) Small (Dogfennel); HYDVER = *Hydrocotyle verticellata* Thunberg (Whorled Marsh Pennywort); HYPHYP = *Hypericum hypericoides*; HYPRAD = *Hypochaeris radicata*; IVAFRU = *Iva frutescens*; PARQUI = *Parthenocissus quinquefolia*; PERPAL = *Persea palustris*; PRUSER = *Prunus serotina*; SCIPNG = *Scirpus pungens*; SPAPAT = *Spartina patens*; TOXRAD = *Toxicodendron radicans* P. Mill (Poison Ivy).

did have a significant correlation with water in the parametric tests of assemblages (Table 2).

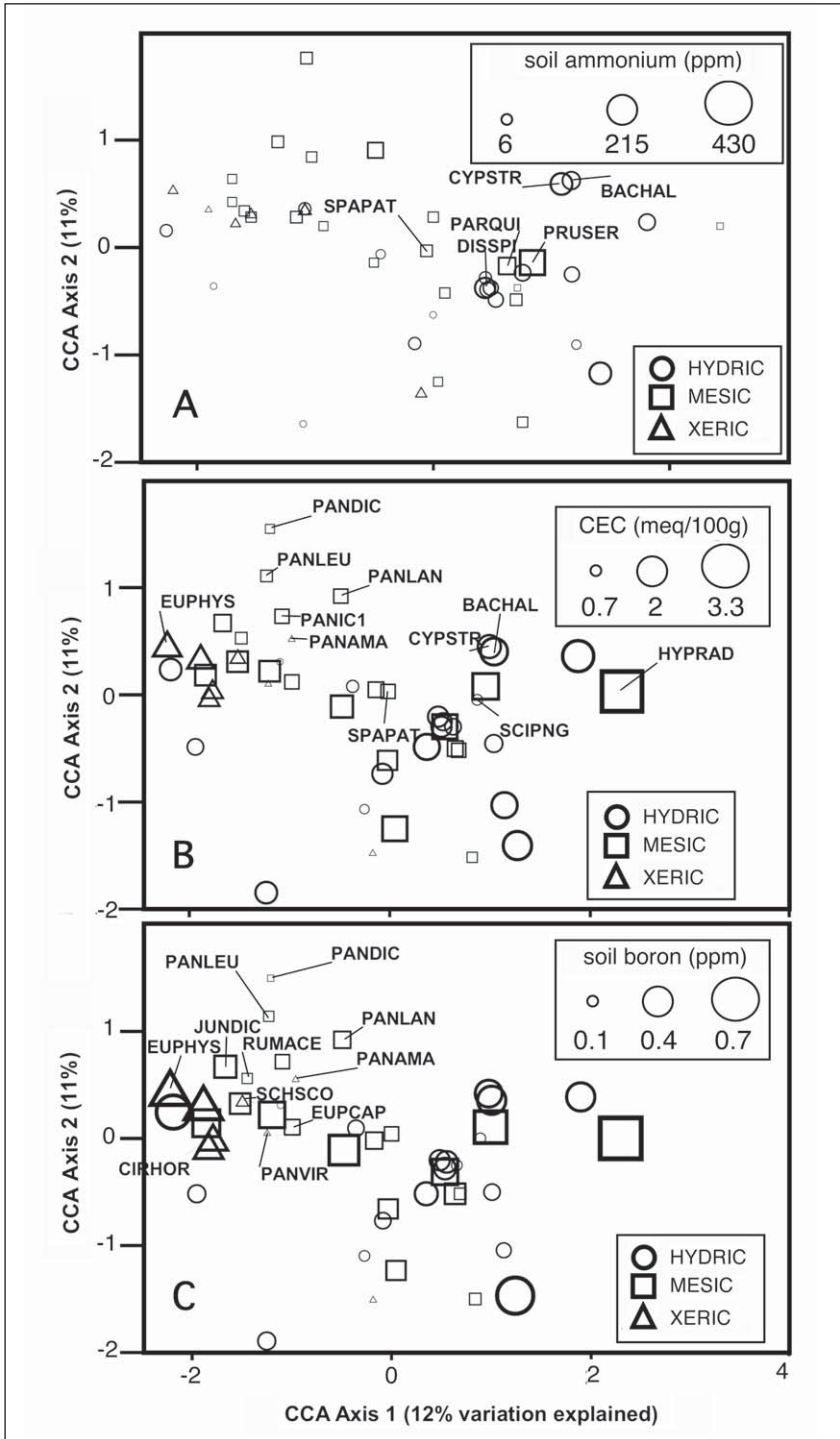
Species: Soil variables

Soil conditions were the best predictors of individual species' distributions; the most important factors were potassium and potassium base saturation, magnesium base saturation, depth of organic horizon, cation exchange capacity, and soil ammonium (CCA; Figs. 3, 4). The distributions of *Iva frutescens* L. (Jesuit's Bark), *Persea palustris* (Raf.) Sarg. (Swamp Bay), and *Hypochaeris radicata* L. (Hairy Cat's Ear) were all influenced

Table 3. Mean percent cover per year, per transect, based on habitat type (± 1 SD) for the 20 species with highest average percent cover. Numbers in parentheses by habitat type are total number of species encountered across five years. Key to superscripts: habit—F = forb, G = graminoid, L = liana (i.e., woody vine), S = shrub, T = tree, and V = herbaceous vine; I = introduced, NI = both native and non-native sub-species/genotypes. All herbaceous species are perennial, and all species are native except as designated. Lowercase letters indicate significantly different groups based on habitat (ANOVA: $F_{2,426} \geq 3.1$, $P < 0.05$; Tukey's: $P < 0.01$). Asterisks indicates insufficient data for parametric tests.

Species	Marsh (27)	Shrub (22)	Summit (37)
<i>Morella cerifera</i> ST	59 \pm 43b	100 \pm 20a	67 \pm 45b
<i>Spartina patens</i> ^G	14 \pm 23a	0.2 \pm 1.2b	8 \pm 22a
<i>Polygonum hydropiperoides</i> ^F	17 \pm 29a	11 \pm 24a	4 \pm 14b
<i>Mikania scandens</i> ^V	3 \pm 12a	1 \pm 8b	0.5 \pm 1.7c
<i>Parthenocissus quinquefolia</i> ^L	1 \pm 7a	11 \pm 24b	2 \pm 10a
<i>Schoenoplectus pungens</i> ^G	14 \pm 30a	0.02 \pm 0.17b	0.2 \pm 0.9b
<i>Juncus dichotomus</i> ^G	0.04 \pm 0.27	0.09 \pm 0.62	4 \pm 12
<i>Festuca rubra</i> ^{GN1}	-	4 \pm 12a	5 \pm 12b
<i>Ammophila breviligulata</i> ^G	-	-	1 \pm 5
<i>Schizachyrium scoparium</i> ^G	-	-	4 \pm 11b
<i>Rubus argutus</i> ^S	0.04 \pm 0.23a	0.2 \pm 0.7ab	10 \pm 19b
<i>Panicum amarum</i> ^G	-	-	0.9 \pm 5
<i>Baccharis halimifolia</i> ST	3 \pm 10a	1 \pm 6.5b	0.4 \pm 2.7c
<i>Rumex acetosella</i> ^{F1}	-	-	5 \pm 15
<i>Galium</i> spp. ^{F*}	1 \pm 3	1 \pm 3	-
<i>Eupatorium capillifolium</i> ^{F*}	-	-	1 \pm 7
<i>Dichanthelium sphaerocarpon</i> ^{G*}	-	1 \pm 2	1 \pm 3
<i>Phyla lanceolata</i> ^F	0.7 \pm 3a	0.06 \pm 0.42b	-
<i>Eupatorium hyssopifolium</i> ^{F*}	-	-	2 \pm 8
<i>Hydrocotyle verticellata</i> ^F	1 \pm 8a	2 \pm 9a	0.03 \pm 0.14b

Figure 4 (opposite page). CCA of species based on environmental factors: A. ammonium overlay; B. cation exchange capacity overlay; C. boron overlay. CIRHOR = *Cirsium horridulum* Michx. (Yellow Thistle); EUPHYS = *Eupatorium hyssopifolium* L. (Hyssoleaf Thoroughwort); JUNDIC = *Juncus dichotomus* Eill. (Forked Rush); PANAMA = *Panicum amarum*; PANDIC = *Panicum dichotomum* (L.) Gould (Cypress Panicgrass); PANIC1 = *Panicum* sp.; PANLAN = *Panicum lanuginosum* Eill. (Tapered Panicgrass); PANLEU = *Panicum leucothrix* Nash (Rough Panicgrass); PANVIR = *Panicum virgatum*; RUMACE = *Rumex acetosella* L. (Common Sheepsorrel); SCHSCO = *Schizachyrium scoparium*. (for other species abbreviations, see Fig. 3).



by soil potassium and potassium base saturation—the two most important variables in the species ordination and two of three variables that were significantly different among individual dunes (Pearson's $r > 0.5$ for both variables relative to the first CCA axis, Tukey's: $P < 0.05$; Tables 1 and 3, Fig. 4). These species were only encountered on one or two dunes that coincidentally were among the few dunes exhibiting higher soil potassium.

Most species did not form cohesive groups in the ordination based on our a priori habitat preference designations. A group of hydric and mesic species including *Cyperus strigosus* L. (Strawcolored Flatsedge), *Distichlis spicata*, *Parthenocissus quinquefolia* (L.) Planch. (Virginia Creeper), and *Prunus serotina* Ehrh. (Black Cherry) shared particularly thick organic horizons (CCA, Pearson's $r = 0.5$; Fig. 3c). Other mesic and hydric species not in this group, e.g., *Hypericum hypericoides* (L.) Crantz (St. Andrew's Cross), *Typha latifolia* L. (Cattail), *Ptilimnium capillaceum* (Michx.) Raf. (Herbwilliam/Bishopweed), and *Andropogon virginicus* L. (Bluestem), were associated with relatively thinner soil organic horizons. There was a similar pattern between species associations and soil ammonium (Fig. 4a). All of the grass species in the genus *Panicum* were grouped in the same area of the species ordination (Fig. 4a), despite being both mesic and xeric. They appeared to have similar affinities for environmental variables, notably magnesium base saturation.

There was a relatively tight group of xerophytes in the species ordination. This group tended to be found in soil with relatively high cation exchange capacity, with the exceptions of *Panicum amarum* Elliot (Bitter Panicgrass), *P. virgatum* L. (Switchgrass), and *Schizachyrium scoparium* (Michx.) Nash (Little Bluestem) (Fig. 4b). There was a similar pattern with B, which, although of relatively minor importance in the species ordination, was one of the top factors discriminating transects in the transect ordination (Fig. 4c).

Spartina patens, the grass found in both marsh and dune summits, had scores close to zero on the first three axes of the CCA. Being near the origin of the ordination means that *S. patens* was intermediate in most of its habitat preferences relative to other species.

Species: Geomorphological features

Of the geomorphological features used to describe species distributions in the ordination, only elevation had a major impact (Table 1). The influence of elevation, as measured by CCA, was nearly equal and opposite that of the water table (Table 2; Pearson's $r = -0.47$ and -0.45 , respectively, for the second axis; hydric species tended to associate with water availability and xeric species with elevation. We performed a linear regression analysis of the effect of elevation on water table and found the relationship to be strong ($R^2 = 0.8$, $P < 0.0001$). We therefore considered elevation a strong analog to water table.

Discussion

We found that distance to the water table was the best predictor of plant assemblage on pimple dunes. It was not, however, the best predictor of species found within any given assemblage, but rather one of several variables. The factors most strongly associated with plant species distribution were soil nutrients. Physiographic features such as slope and aspect were not important.

Influence of water

As we hypothesized, water availability was the most important factor determining assemblage type, based on both the direct results of the ordinations and water being a significant covariate in many of the ANCOVAs. This finding agrees with the long-held hypothesis about the importance of the relative positions of the freshwater table and soil surface as an ecological driver on the barrier islands (Hayden et al. 1995). Although water availability is directly important for meeting the transpiration requirements of plants and soil biota, it may also influence a host of other environmental factors that could influence assemblage structure.

Most of the other variables that were significantly different between assemblage types in the ANCOVA tests were also significant covariates with water availability (Tables 1 and 3). Most of the important variables describing transect variation in the ordination were also among those that covaried with water availability, but CCA is designed to be robust in dealing with correlated variables (Palmer 2010). Furthermore, water was not the most important variable in the species ordination, and it was difficult to see a pattern of influence between water and species (Fig. 3a). We concluded that the influences of other environmental factors were not simply proxies for water availability, with the exception of elevation. Our results suggest that edaphic variables, especially mineral nutrient concentrations in the soil, are potential secondary determinants of assemblage type. The nature of biogeochemical cycles on barrier islands and the interactions between the water table and soil nutrients lend support to this conclusion.

Influence of soil variables

According to our ANCOVA results, many soil properties differed significantly among assemblage types and were the most important variables (besides water) in the ordinations of transects and plant species. These findings support our second hypothesis with two concessions. First, most of these variables were significantly correlated with water table and may more or less be proxies for the effect of water. Second, this study was designed to describe patterns and cannot show causation directly. Nevertheless, there have been several studies supporting the influence of various soil nutrients on vegetation structure in dunes (e.g., Gorham 1958; Hester and Mendelsohn 1990; Jones 1972, 1975; Lammerts et al. 1999, 2001). Our evidence is

correlational; we can only point out that some nutrients, e.g., K, are linked to species distributions, and cannot conclude that those nutrients determine species distributions. Our findings combined with previous studies led us to re-examine our second hypothesis that soil conditions also shape assemblage structure and suggest a modification. We propose that, on a broad scale, the *interactions* of soil nutrients and soil organic matter with the water table are an important determinant of species distributions. In other words, it is not simply water availability that is important, but also how water affects the availability of soil nutrients. We base the assumption that it is nutrients affecting plant distribution, not vice versa, on our own observations and the results of the studies we present below, but we acknowledge that only experimentation could determine which is actually the case.

The interaction of weather, water, and soil nutrients on barrier islands affects the availability and bioavailability of those nutrients and should therefore affect the distribution of plants. Elements such as phosphorus, boron, magnesium, and potassium often enter the ecosystem by being deposited from salt spray (Boyce 1954, Bricker 1993). The uneven distributions of mineral nutrients could be artifacts of deposition events, such as storms. Once in the ecosystem, many nutrients are easily leached from sandy summits and can accumulate in the marsh or anywhere with abundant organic matter (Bardgett et al. 2001, Boyce 1954, Bricker 1993, Brooks and DeWalt 1976, Westman 1983, Willis and Yemm 1961). This process supports our second hypothesis that soil chemistry is likely to influence the creation of assemblage zones on pimple dunes as well as the distribution of individual species.

Differences in availability of magnesium and calcium have been implicated in dominance shifts and growth responses in dune species, some of which are congeneric or identical to those found on the pimple dunes (Clayton 1972, Hester and Mendelsohn 1990, Khedr and Lovett-Doust 2000, Willis and Yemm 1961). For example, fertilization of dunes with macronutrients (N, P, K) and micronutrients (Ca and Mg, if severely limited) elicited a shift in dominance from a beach-colonizing grass (*Ammophila* sp.) to a generalist grass with higher nutrient requirements (*Festuca rubra* L. [Red Fescue]) (Clayton 1972, Gorham 1958). Magnesium and calcium-related alkalinity is important to growth of endangered basiphilous swale species in the Netherlands; one of those species, *Samoilus valerandi* L. (Seaside Brookweed), is also a member of the Hog Island marsh flora, albeit uncommon (Bekker et al. 1999, Lammerts et al. 2001, Willis 1963). Finally, mineral cations, especially calcium, often form complexes with soil organic matter, which is typically highest in wet soils with low decomposition rates, and may become more or less bioavailable depending on the nature of the complexes (Khedr and Lovett-Doust 2000). This characteristic of the cations could help explain the importance of organic layer thickness in the ordinations.

Potassium is generally considered unlikely to be limited in a coastal system, but it does leach freely and forms complexes with organic matter (Gorham 1958, Jones 1975, Lammerts, et al. 1999). It could have a potential role to play in the toxicity of reduced species of iron and manganese in anoxic marshes (Jones 1972, Willis 1963). It has been shown to influence growth in some dune species, especially when input is limited by lack of salt spray, which is the case for dunes in the sheltered interior of the island (Boyce 1954, Clayton 1972, Gorham 1958, Hester and Mendelsohn 1990, Jones 1975, Willis and Yemm 1961, Willis 1963). High levels of potassium were only associated with a few species in the ordination (Fig. 3b), which suggests that it is indeed limiting and that some species may have a high demand for it. Lastly, potassium was one of the few soil variables important in the species ordination that did not co-vary with water, suggesting that its putative effect on species' distributions may be independent of interaction with the water table.

Ammonium may be another soil nutrient that influences species distributions independent of water. Like potassium, ammonium did not significantly co-vary with water, and both variables varied significantly among pimples (Table 2). Unlike potassium, the species that were associated with it were not all uncommon (Table 3, Fig. 4a). Furthermore, the species associated with higher ammonium concentrations occurred in all three habitat types (Fig. 4a). This result suggests that ammonium has a patchy distribution that in turn influences the distribution of a subset of species that may have a higher nitrogen demand.

Hyperaccumulation of micronutrients in the freshwater marsh, such as boron, could explain the dominance of many salt-tolerant species there. Boron is toxic to most plants in amounts only ten times that of optimal fertilizing concentrations (Brooks and DeWall 1976). Rozema et al. (1992) demonstrated that six graminoid and forb halophyte species (including a species of *Spartina*) were generally more tolerant of high levels of boron than glycophytes, probably as an adaptation to the relatively high concentration of boron in seawater. Although swales between dunes on Hog Island are essentially freshwater marshes, many of the dominant hydrophytes are salt tolerant or even facultatively halophytic, e.g., *S. patens* and *D. spicata*, as are some uncommon species, e.g., *Typha angustifolia* L. (Narrowleaf Cattail) (Boyce 1954, Kearney 1904, Radford et al. 1968, Rozema et al. 1992).

Influence of geomorphological features

The geomorphological variables other than elevation, slope, and aspect (divided here into eastern and northern exposure), are essentially proxies for other factors such as wind exposure and insolation. They have been shown to influence plant assemblages on dunes (Willis and Yemm 1961); however, the lack of importance of these factors in the ordinations suggests that pimples are too protected from exposure to prevailing winds or salt spray for them to make a difference. Thus, our third hypothesis was not supported (Olsson-Seffer 1909).

Summary

As hypothesized, freshwater availability was an important factor delineating changes in plant assemblages. Only a few species on the island, most notably *S. patens*, demonstrate an ability to grow well in both wet and dry areas. Although freshwater is a driving force behind the ecology of the islands, our findings suggest that there are some recurring patterns with nutrients and their distribution that can potentially explain assemblage structure and species distribution on the pimple dunes. Species that can survive both inundated and saline conditions, i.e., halophytic hydrophytes or vice versa, may be at a competitive advantage for life in the swale marsh, despite it being a freshwater system. Many of the woody mesic species were associated with high CEC or soil organic matter, suggesting that they needed relatively “rich” soils. Summit assemblages generally comprised species that can withstand low nutrient retention, although some xeric species were associated with high CEC soils or other nutrients. Therefore, water table, organic matter, and nutrient availability in general are associated with differences among assemblages, whereas differences in individual nutrient concentrations are associated with species composition within assemblages.

Acknowledgments

Financial support was provided by subcontract 5-26173 through the University of Virginia’s National Science Foundation LTER grant (NSF 0080381). Many thanks are due the staff at the VCR LTER, my undergraduate assistants, and colleagues who volunteered their time on the Islands. Drs. T. Crist, R. Colwell, and N. Gotelli provided support for their statistical programs. Dr. R.D. Bray helped with species identifications, oversaw the reposition of the plant voucher collection, and offered editorial advice, as did S. Derosier.

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