1992

A Vegetational Analysis of Interdunal Swale Communities of False Cape State Park, Currituck Spit, Virginia

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College of William & Mary - Arts & Sciences

A VEGETATIONAL ANALYSIS OF INTERDUNAL SWALE COMMUNITIES OF FALSE CAPE STATE PARK, CURRITUCK SPIT, VIRGINIA

A Thesis

Presented to

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Of the Requirement for the Degree of

Master of Arts

by

Heather A. Jones

1992

APPROVAL SHEET

This thesis is submitted in partial fulfillment of the requirements for the degree of

Master of Arts

Heather A. Jones

Approved December 4, 1992

Gene M. Silberhorn, Ph.D.

Stewart A. Ware, Ph.D.

Martin C. Mathes, Ph.D.

TABLE OF CONTENTS

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Thank you to J. Christopher Ludwig of Natural Heritage for his interest and materials, and special thanks to the workers at False Cape State Park and Back Bay National Wildlife Refuge.

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The purpose of this study was to analyze the vegetation of interdunal swale communities of False Cape State Park (FCSP), which is located south of Virginia Beach on Currituck Spit. These swale areas are important habitats for rare species in the state, and this study describes the plant community composition of the selected sites, and provides some explanation as to why these and other species are found there.

Swale sites were selected using aerial photographs. Three 100m transects were laid out in each site in the direction of dune formation, and sampling of vegetation was done every 5m using a meter square. Diversity indices were calculated for each sample site at each time. This data was subjected to statistical testing to compare sites with each other and each site over time. Prevalence indices were calculated for each species for each sampling time at each site. These data were compared for twelve signature species for each site at each time.

There appears to be a significant difference between one site and the five based on diversity. This site was consistently less diverse, and it is suggested that the high soil moisture in that site contributes to the lower diversity found therein. There is no significant difference in overall diversity by time for any site.

Prevalence indices indicate a strong dominance by *Andropogon virginicus* in each site, with various other species becoming more or less influential in the flora over the summer.

Soil samples were collected and analyzed for nutrients. These data were compared based on sampling site and collection location within the site. Results suggest no significant difference in soil nutrients by site, but a highly significant difference by sampling location. Dune face soils are higher in potassium, and lower in all other tested nutrients than the swale soils.

The effect of various selecting factors on the flora is discussed, as well as the effect of disturbance by feral hogs. Appendices describe the distribution of all species, and how the community composition of FCSP swales compares to others in the U.S. and worldwide.

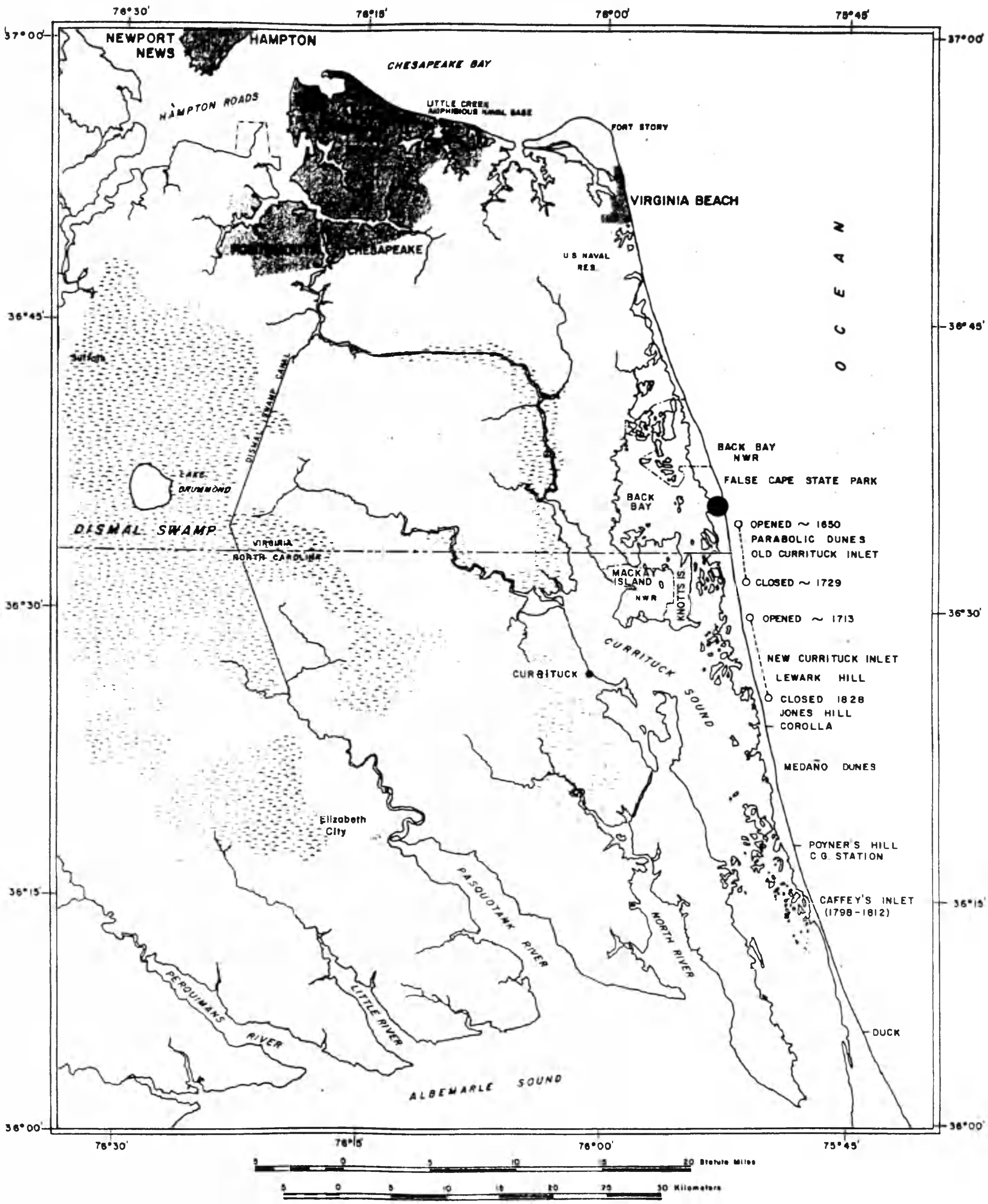
A VEGETATIONAL ANALYSIS OF INTERDUNAL SWALE COMMUNITIES OF FALSE CAPE STATE PARK, CURRITUCK SPIT, VIRGINIA

INTRODUCTION

False Cape State Park (FCSP) is a 1749 hectare property managed by the Division of State Parks, Virginia Department of Conservation and Recreation (Ludwig, 1990). It is located directly south of Back Bay National Wildlife Refuge on Currituck Spit, a long, narrow barrier spit which runs from Virginia Beach down into North Carolina (Figure 1). The nature and history of this spit have a profound influence on the plant communities of False Cape. Once dominated by maritime forest, intensive logging and grazing in the late 1800's and early 1900's led to large-scale destabilization of the FCSP dune fields. The result was massive erosion and sand movement which caused the inhabitants to leave the area in the 1920's (Ludwig, 1990). A hurricane in 1933 reduced most of the remaining vegetated area to bare sand. Sand fencing along the coast in 1935 has resulted in primary dune formation, and the slow rebuilding of the Park's topography. The sand, free of vegetation, was shaped by the prevailing winds into medano dunes, and then into the parabolic dunes found today (Hennigar, 1977). As the layers of loose sand were blown away, the surface between dunes slowly neared the water table. Eventually, the top layer of sand in these depressions was too wet and heavy to be easily moved, and these interdunal areas, or swales, became stabilized (Hennigar, 1977). Parabolic dune

Figure 1: Map of False Cape State Park area, southeastern Virginia.

From Hennigar, 1977.


76°30'
76°15'
76°00'
75°45'
37°00'
36°45'
36°30'
36°15'
36°00'
NEWPORT NEWS
HAMPTON
CHESAPEAKE BAY
HAMPTON ROADS
LITTLE CREEK AMPHIBIOUS NAVAL BASE
FORT STORY
VIRGINIA BEACH
PORTSMOUTH
CHESAPEAKE
U S NAVAL RES.
OCEAN
Suffolk
DISMAL SWAMP CANAL
LAKE DRUMMOND
DISMAL SWAMP
VIRGINIA
NORTH CAROLINA
BACK BAY NWR
FALSE CAPE STATE PARK
BACK BAY
OPENED ~ 1650
PARABOLIC DUNES
OLD CURRITUCK INLET
MACKAY ISLAND NWR
KNOTTS IS
CLOSED ~ 1729
OPENED ~ 1713
NEW CURRITUCK INLET
LEWARK HILL
CLOSED 1828
JONES HILL
COROLLA
CURRITUCK
CURRITUCK SOUND
MEDAÑO DUNES
Elizabeth City
POYNER'S HILL C.G. STATION
CAFFEY'S INLET (1798-1812)
PASQUOTANK RIVER
NORTH RIVER
PERQUIMANS RIVER
LITTLE RIVER
ALBEMARLE SOUND
DUCK
20 Statute Miles
30 Kilometers

swales in England may be 50-60 meters across at their widest point (Ranwell, 1959). The largest swale sites at FCSP appear to be much wider than the English sites, but measurements of their width were not made in this study. Once stabilized, these swales provided ample area for seed germination, and a unique swale community had its beginnings.

Today, the dunes are fairly stable, due mostly to the influence of grasses and shrubs, and many are still roughly parabolic. Swales within these dunes differ in their size and shape, as well as average soil moisture. Some swales flood and remain flooded long after a heavy storm, due to the sheer volume of rainwater and some maritime overwash, while others drain quickly. This is evidenced by the effects of Hurricane Bob (August, 1991). Stochastic events are important to the hydrology of the swale system, and cannot be overlooked (James Perry, pers. comm.).

There are also variations of habitat within each swale. Secondary ridges, built up during the continuing process of dune migration, provide drier, sandier microhabitats. These areas have vegetation which differs from the surrounding lower swale area. In contrast, the rootings of feral hogs create "digs"--patches of varying width and depth, most being approximately one meter across and twenty to thirty centimeters deep (pers. obs.)--which are moister and more sheltered than the surrounding swale.

Disturbance of the natural swale plant communities comes in three forms. First, trails and roads have been built and are maintained in the Park. Trail building involves dragging a weighted board with an all-terrain vehicle to crush vegetation and clear the soil. Sites were selected for this project such that this activity has not been a factor. Roads require occasional grading, and frequent mowing in the grassier areas of the Park (crossroads, educational center, ranger housing area, etc.). These activities have not been factors in this project, since the sites sampled here were spared these impacts.

The second form of disturbance, the aforementioned feral hogs, have had effects on the distribution of plants in the Park. These inhabitants of the Park and nearby Back Bay National Wildlife Refuge are large, black, tusked descendants of domestic pigs which escaped in the 19th and early 20th centuries (Hennigar, 1977). In digging for edible roots and rhizomes, these hogs create large dig areas which are utilized by plants such as *Xyris sp., Scirpus americana, Drosera rotundifolia* and *Drosera intermedia*, which are not good competitors in the drier, less protected areas of the swale. Thus, based on personal observation, a high number of pig digs roughly correlates to a higher species diversity per swale.

The third form of disturbance was due to an experiment in waterfowl management in which the Department of Game and Inland Fisheries planted wheat in one of the swales to attract ducks and geese. The plowing necessary for such an undertaking disrupted that portion of the swale. This site has remained fallow for two and a half years, and its sampling as part of site 3 in this study provides some insight into the natural colonization process of swale plant species.

The true value of FCSP, with all of its microhabitats and variable moisture levels and site ages, is its location. The Park is located geographically in the ecotone between the northern and southern coastal floras. Thus, in the maritime forest we see *Tillandsia usneoides* near its northernmost limit (the northernmost limit is believed to be in Seashore State Park, about 20 miles to the north), and along the roads and in swales we see *Hudsonia tomentosa* near its southernmost (Gene Silberhorn, pers. comm.). Other plants have a wider distribution, but many are more northern or southern in their biogeographic distribution (Appendix B). This location provides an excellent opportunity to look at the competitive interactions between these species. This area is also one of the last largely undisturbed areas of its type in coastal Virginia. Its geographical and political location make it very difficult to reach by land or boat--one needs to hike in through the Back Bay Wildlife Refuge or up from North Carolina, or dock at False Cape Landing and hike. This isolation has been a boon to the natural systems in the Park, as the wear caused by a large visitorship has not been a factor here. Thus we have a unique area at False Cape--a large, intact coastal ecosystem in the ecotone between northern and southern dune systems and floras.

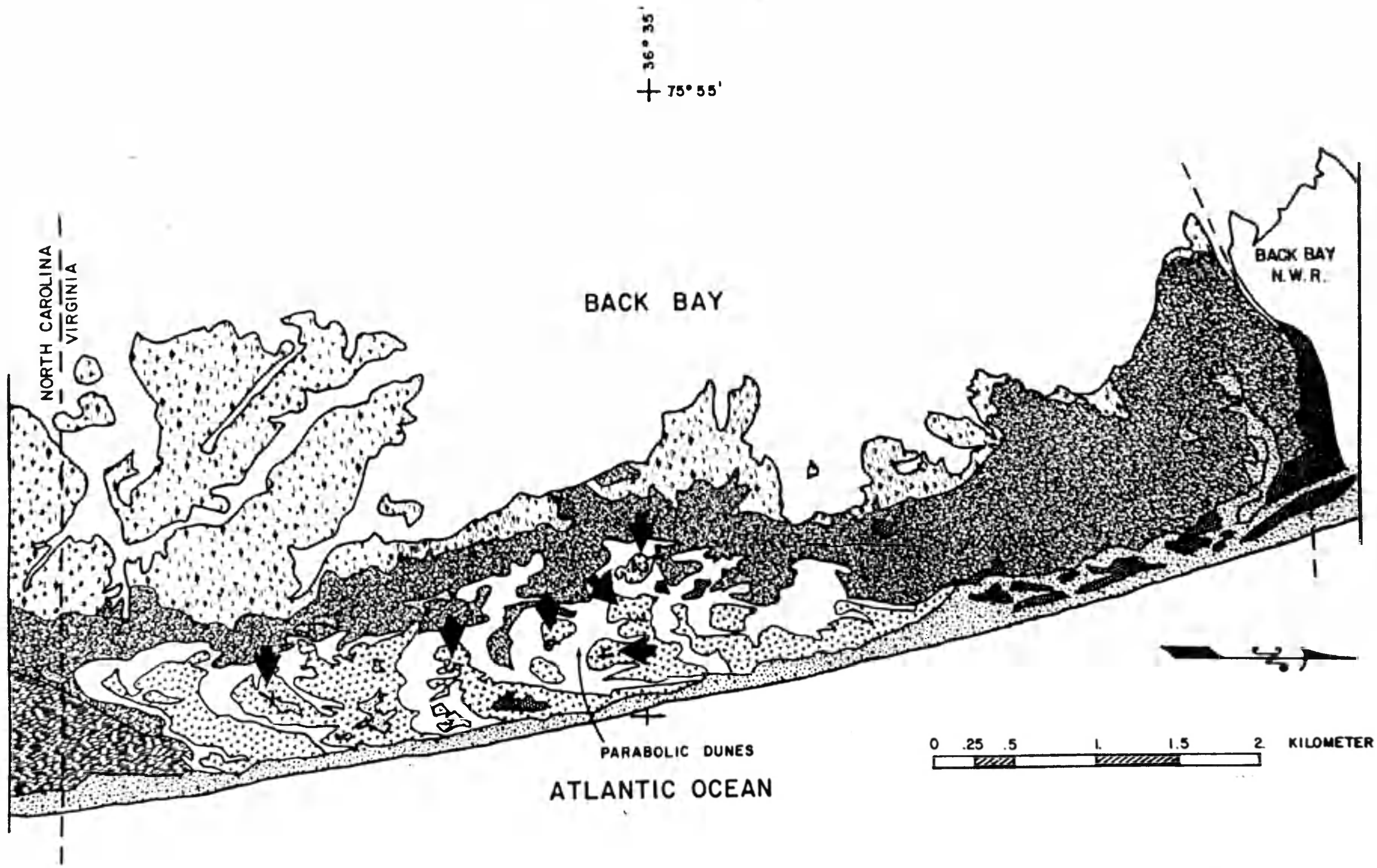
The objective of this study was to sample the plant communities of various swale areas of FCSP and determine the vegetational differences between them at any given time, and within them over the course of the summer. I therefore describe the vegetation of each of six swale sites based on dominance and importance, noting changes through the season, and provide some explanation of the factors responsible for the vegetational differences between and within these swales. Finally, I seek to place the FCSP sites in the context of other vegetational and floristic studies by comparing their vegetation with that of other swale sites around the world.

MATERIALS AND METHODS

Sites for this study were chosen via aerial photographs of the Park provided by the City of Virginia Beach. The photographs, taken in March, 1986, show major topographical features of the Park, including parabolic dunes. Seven of these dunes were located by this method, and trips to the selected sites were made to ensure suitability. To be suitable for this study, a swale had to be wide enough to fit three parallel 100-meter transects across it, and had to be dominated by herbaceous vegetation. Seven sites were initially selected, but site 1 was later eliminated, leaving six workable sites numbered 2 - 7 (Figure 2).

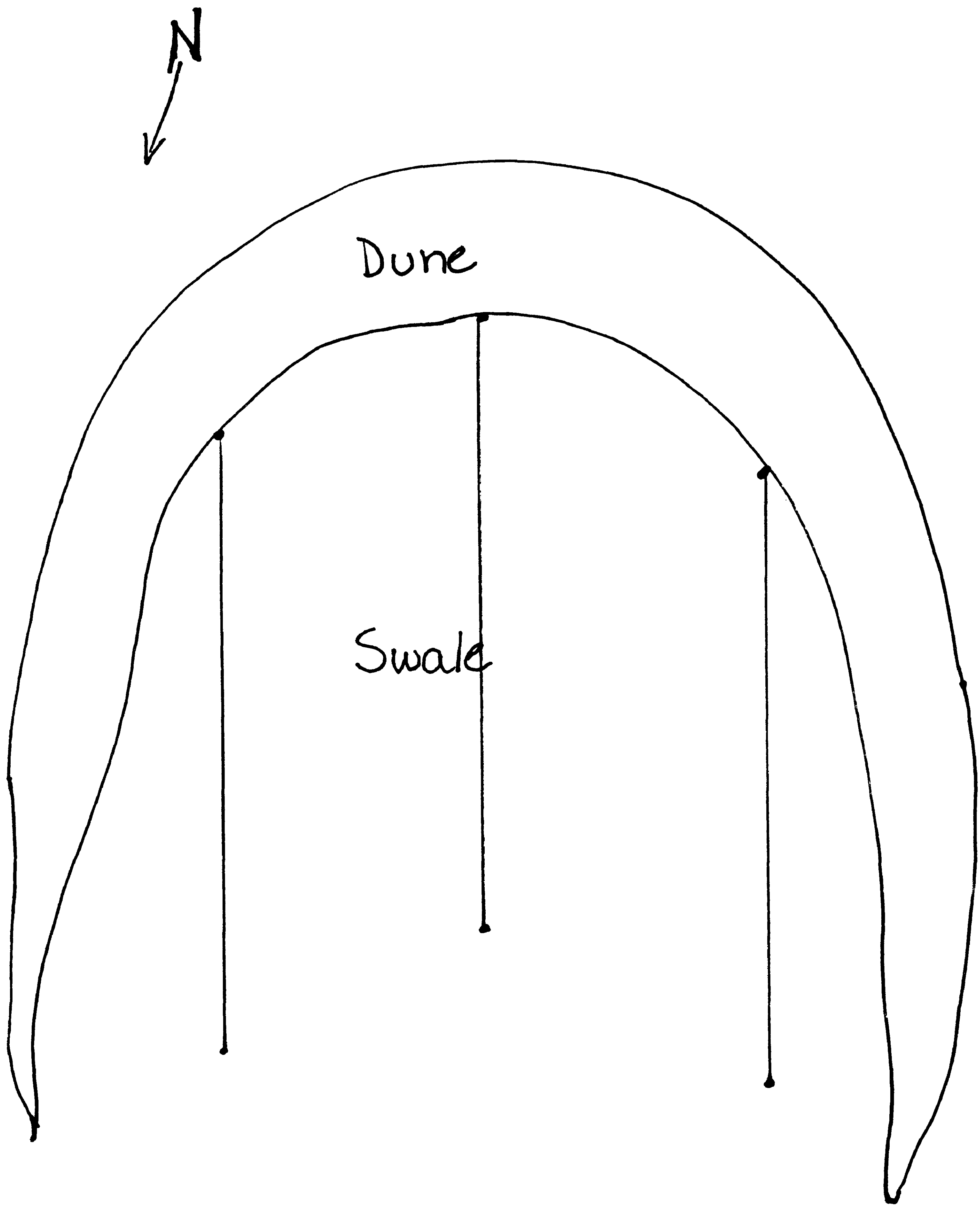
Once sites were selected, set-up and sampling of the sites was begun. Set-up required the placement of three transects in each site (Figure 3). Each transect ran from the base of the parabolic dune towards the rear of the swale, and was 100 meters long, or to the foot of the next dune if the swale was particularly short. Bearing of the transects was based on the direction of dune formation; thus the first five sites bear 20 degrees from magnetic North, and the southernmost bears 280 degrees from North. Fluorescent pink surveyor's flags were placed every ten meters along the transect for easy location during subsequent visits. Relative elevations were measured at each flag by use of a hand-held

Figure 2: Locations of study sites within False Cape State Park.



1975 FALSE CAPE VEGETATION MAP

Figure 3: Set-up of transects in each study site.


N
Dune
Swale

level and portable stadia rod. These elevations were recorded for future reference.

Sampling was done every five meters along the transect using a meter square constructed of 1" PVC pipe. The flags at each ten meters were used as guides for this sampling, and the samples taken at 5, 15, 25, etc. meters required the placement of a temporary flag between the two permanent flags at each sample time. The meter square was laid on the ground at each flag such that the flag was in the center of the square and the sides of the square ran parallel to the transect line. Percentage of bare ground (no cover) was estimated by sight and recorded for each quadrat. Each species was then assessed for its contribution (in percentage) to the vegetation in the quadrat. Soil moisture and pH were also measured for each plot with an electronic soil tester. This procedure was repeated at each site on each of four visits: one each calendar month from late May to mid-September.

At the end of the season, permanent stakes of 2" X 2" X 5′ salt-treated pine were driven to a depth of two feet at the beginning and end of each transect line. The top portion of each stake was painted green for easy identification later, and all semi-permanent flags were removed from between these stakes. Soil samples for nutrient analysis were collected from seven locations in each swale: one from the dune face, one from an "average" location along each transect, and one from a "low" location along each transect. The "averageness" and "lowness" of the sample locations was based purely on the perception of the sampler, as soil samples were not necessarily taken from sampled plots. The 42 total samples were taken using a garden trowel and plastic self-closing bags, and were subsequently sent to the agronomy lab at Virginia Polytechnic Institute for pH and nutrient analysis. Relative elevations of all sample sites were also rechecked using the portable surveying kit during clean-up.

After data collection was complete, vegetation data was analyzed to set up a prevalence index (P_i) for each species at each site for each sampling time. First, mean cover was calculated by adding all cover values for that species at that sampling date, and dividing by the total number of plots recorded on that date. Next, relative frequency was calculated by counting the total number of plots that species was present in on the sampling date, and dividing by the sum of frequencies for all species at that site on that date. Then, an importance value (I.V.) for each species was then calculated by Minitab for each species at each site for each sampling date, giving a total of four I.V.'s for each species at each site. Each I.V. was then divided by the sum of all I.V.'s per site per date, yielding a prevalence value (P_i) for each species. These P_i's were then used to find the diversity index (D.I.) for each site at each sampling date. The diversity index equation is : D.I. = - sum (P_i log P_i). Again, Minitab was used to calculate the P_i, log P_i, P_i log P_i, and the resulting D.I. Minitab was also employed to rank the species by their I.V. for each site at each sampling time, with the most important species given the rank of 1, the second most important ranked 2, etc.

Analysis of diversity index variance was computed on the SPSS-X statistical package using the Friedman two-way test. This test was chosen because it is nonparametric, and the diversity indices themselves neither represent equal sample sizes nor are homoskedastic; thus parametric analyses of variance (ANOVA's) would not be appropriate. However, a oneway ANOVA was also run on the diversity indices to compare sites with each other merely to get *a posteriori* Tukey-based subsets for a deeper analysis of the significance indicated by the Friedman test. Tukey's Honestly Significant Difference test was chosen because of its moderate nature. D.I.'s were grouped in two ways: by site to show any differences between D.I.'s based on site, and by time of sampling to show differences in D.I.'s based on time. The null hypotheses for the site tests was H_0: there is no significant difference between diversity indices based on the site of sampling. The null hypothesis for the time tests was H_0: there is no significant difference between diversity indices based on the time of sampling. A confidence of 95% was chosen for significance ($p=.05$) of difference between groups.

Nutrient and pH analysis of soil samples were obtained from the agronomy lab at the Virginia Polytechnic Institute. These results came in the form of a printout which listed the pH for each sample as well as the ppm phosphorous, potassium, calcium, and magnesium, as well as the ppm of the trace elements zinc and manganese. Soil data was analyzed via oneway ANOVA's run on SPSS-X. Data were grouped in two ways to show two different types of contrasts. First, data was grouped by original site number in order to determine significant differences in soil properties between the study sites. ANOVA's were then run separately for pH, phosphorous, potassium, calcium, and magnesium data in order to show between site variance for these properties. *A priori* comparisons between site data sets were tested as follows: Site 4 vs. Site 7; Site 2 vs. Site 3; Site 2 vs. Site 5; Site 6 vs. Site 7; and Site 5 vs. Site 6. These contrasts were meant to find any significant difference in the soils due to which sites the samples came from. The Tukey's Honestly Significant Difference *a posteriori* test was also used on the data to find any significant difference between sites that was not considered in the creation of the *a priori* tests. Tukey's test was chosen because of its moderate nature.

Soil data was also grouped according to sampling location for analysis. Group 1 consisted of data from dune face samples, Group 2 from "average" samples, and Group 3 from "low" samples. ANOVA's were run on these groups for pH and the minerals mentioned above in order to find within site soil variation due to the location at which the sample was taken. The *a priori* contrast tested was between the "normal" and "low" samples, because these were not likely to be found to be significantly different. The Tukey's test was also employed to find significant differences, if they exist, between the dune face samples and the other two groups.

RESULTS

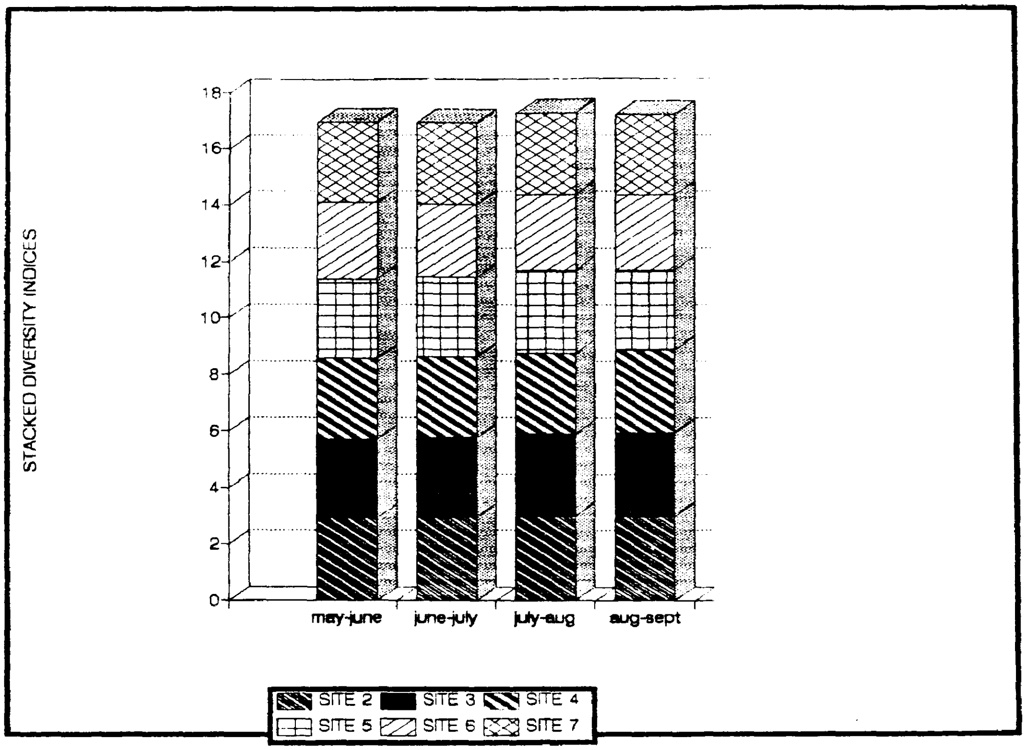
Vegetation

The diversity indices for each sample site at each sample time can be seen in Appendix C. The results of the Friedman two-way test of diversity data by time showed no overall significant change in diversity (as measured by the D.I.'s) over time at the 95% confidence level (p=.1447), and the null hypothesis cannot be rejected. This can be seen graphically in Figure 4, which shows the diversity indices for each site stacked as a bar representing overall diversity for each given time. There is a slight trend upwards over the summer, but the test indicates that this is not statistically significant.

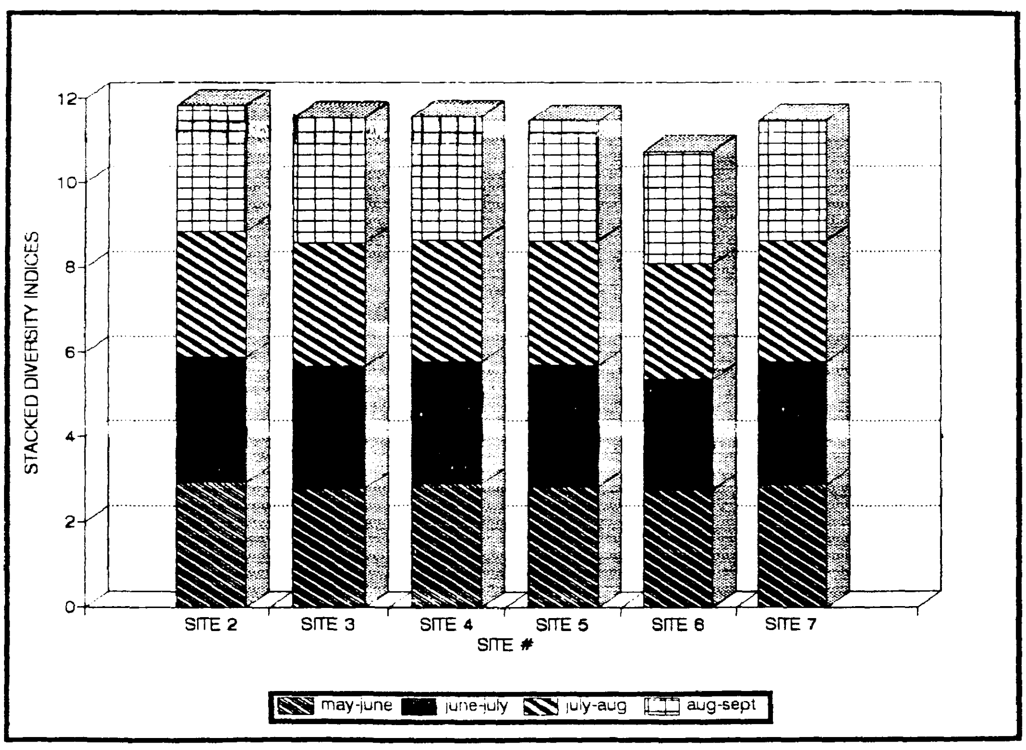
The results of the Friedman two-way test of the data by site showed a very significant difference between the sites (p=.0117*), thus voiding the null hypothesis. The subsequent oneway ANOVA and Tukey test showed that sites 2,3,4,5, and 7 were, statistically speaking, part of the same subset. Site 6 was found to be significantly different from the other sites, based on vegetation diversity, and was not included in the same statistical set. This can be seen graphically in Figure 5, which shows the diversity indices for each time stacked as a bar representing overall diversity for each site. Site 6 has a distinctly smaller bar than the other sites. Thus it can be assumed that there was lower overall species diversity in that site over the summer. Figure 6 shows the change in D.I. for each site over time. Note that there is no

Figure 4: Stacked diversity indices (D.I.'s) by time.

Figure 5: Stacked diversity indices (D.I.'s) by site.

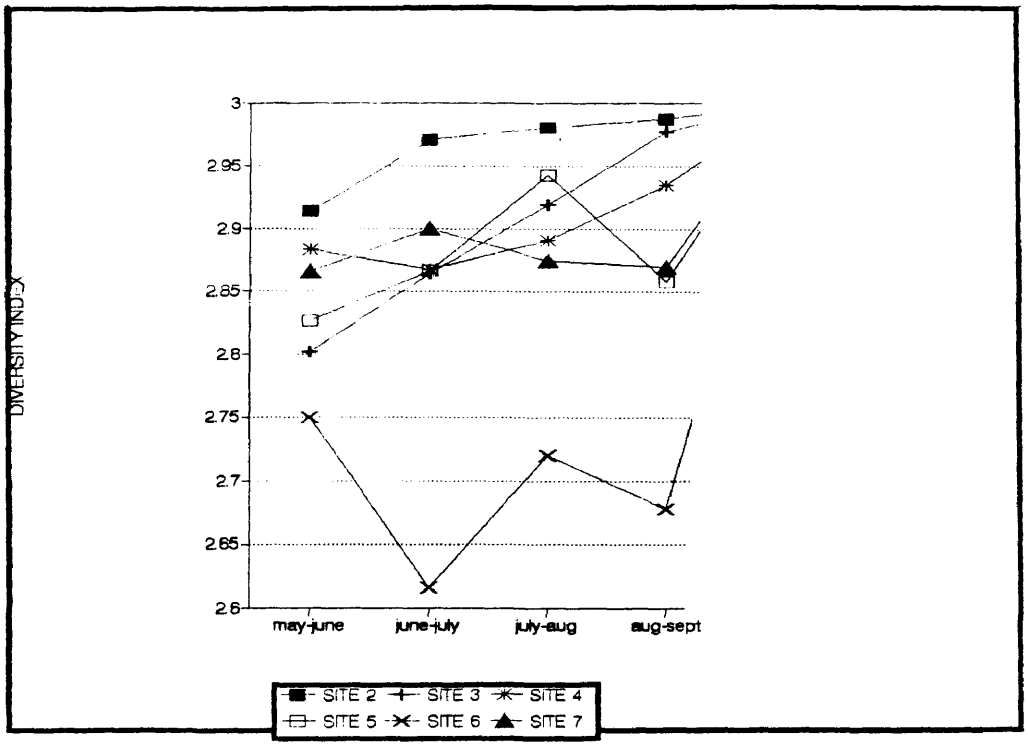


STACKED DIVERSITY INDICES
18
16
14
12
10
8
6
4
2
0
may-june
june-july
july-aug
aug-sept
SITE 2
SITE 3
SITE 4
SITE 5
SITE 6
SITE 7



STACKED DIVERSITY INDICES
12
10
8
6
4
2
0
SITE 2
SITE 3
SITE 4
SITE 5
SITE 6
SITE 7
SITE #
may-june
june-july
july-aug
aug-sept

Figure 6: Change in diversity indices over time by site.



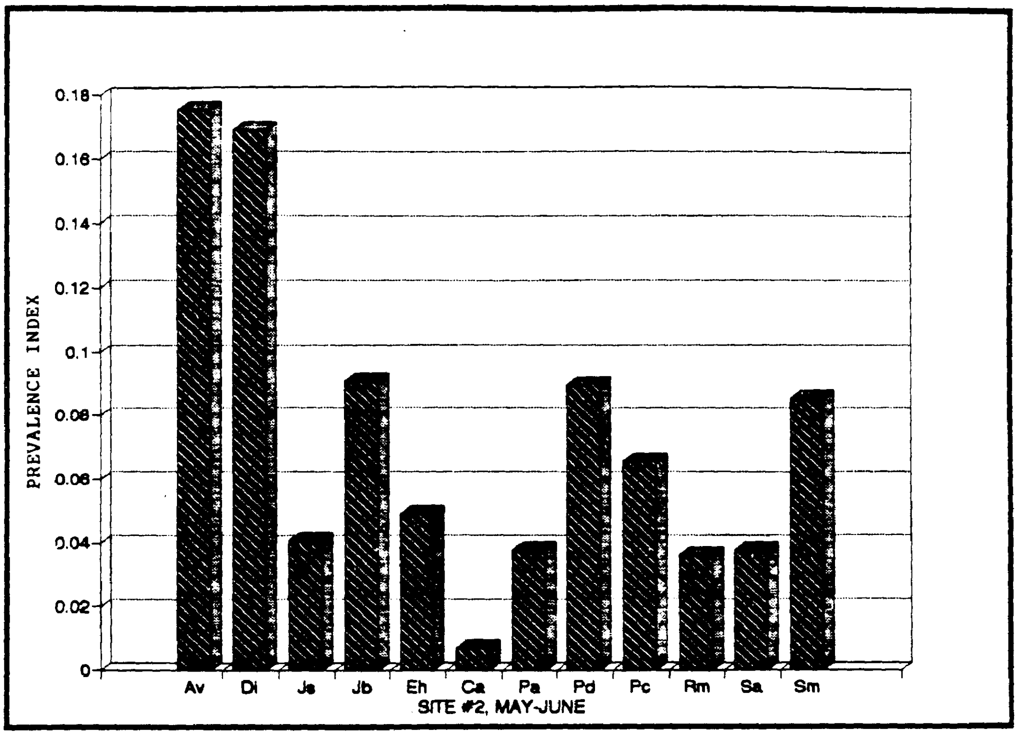
DIVERSITY INDEX
3
2.95
2.9
2.85
2.8
2.75
2.7
2.65
2.6
may-june
june-july
july-aug
aug-sept
SITE 2
SITE 3
SITE 4
SITE 5
SITE 6
SITE 7

particular pattern of diversity change apparent. This lack of pattern is somewhat odd, as one might expect the species diversity to peak in June or July, and then lower in the later part of the summer (Perry, pers. comm.). Note also that sites 2,3,4,5, and 7 are all clustered toward the top of the figure, whereas site 6 lags at the bottom. This, too, suggests that the other sites are similar in their species richness, whereas site 6 is less diverse.

In order to show the overall differences in species composition between sites, a group of twelve species was selected for graphing. The species which ranked 1 through 10 by prevalence index for each sampling time at each site were recorded. From that group, twelve species ranked 1 through 10 in at least three sites over the course of the study, and were present at least once in all of the sites. These species were considered, subjectively, to be the twelve signature swale species, and their relative abundance (based on P_i) in each site show important differences between sites based on community structure. The species are : *Andropogon virginicus* (Av), *Drosera intermedia* (Di), *Juncus scirpoides* (Js), *Juncus biflorum* (Jb), *Eupatorium hyssopifolium* (Eh), *Centella asiatica* (Ca), *Panicum amarum* (Pa), *Panicum dichotomiflorum* (Pd), *Polystichum commune* (Pc), *Rhexia mariana* (Rm), *Scirpus americanus* (Sa), and *Solidago microcephala* (Sm). The graphs in Figures 7 through 18 show the overall prevalence of the twelve swale signature species for each site. Each bar represents the prevalence index (P_i) for a species in the given

Figure 7: Prevalence indices for twelve signature swale species in site 2, May-July.

Figure 8: Prevalence indices for twelve signature swale species in site 2, July-September.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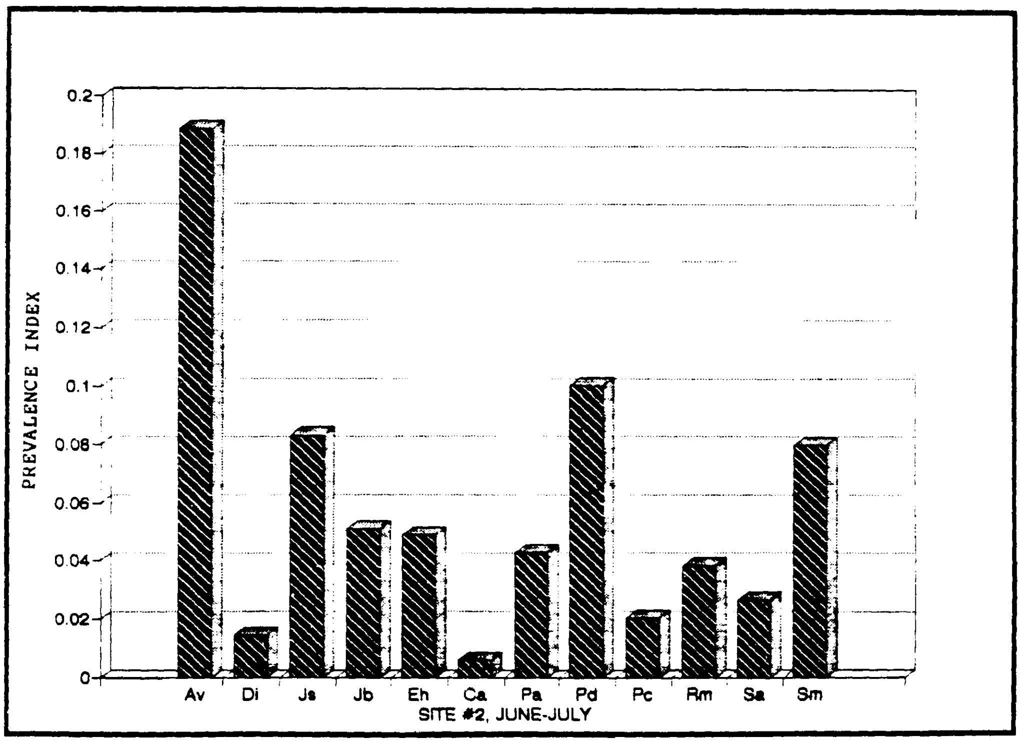
0.12
0.1
0.08
0.06
0.04
0.02
0
Av
Di
Js
Jb
Eh
Ca
Pa
Pd
Pc
Rm
Sa
Sm
SITE #2, MAY-JUNE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0.08
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0.04
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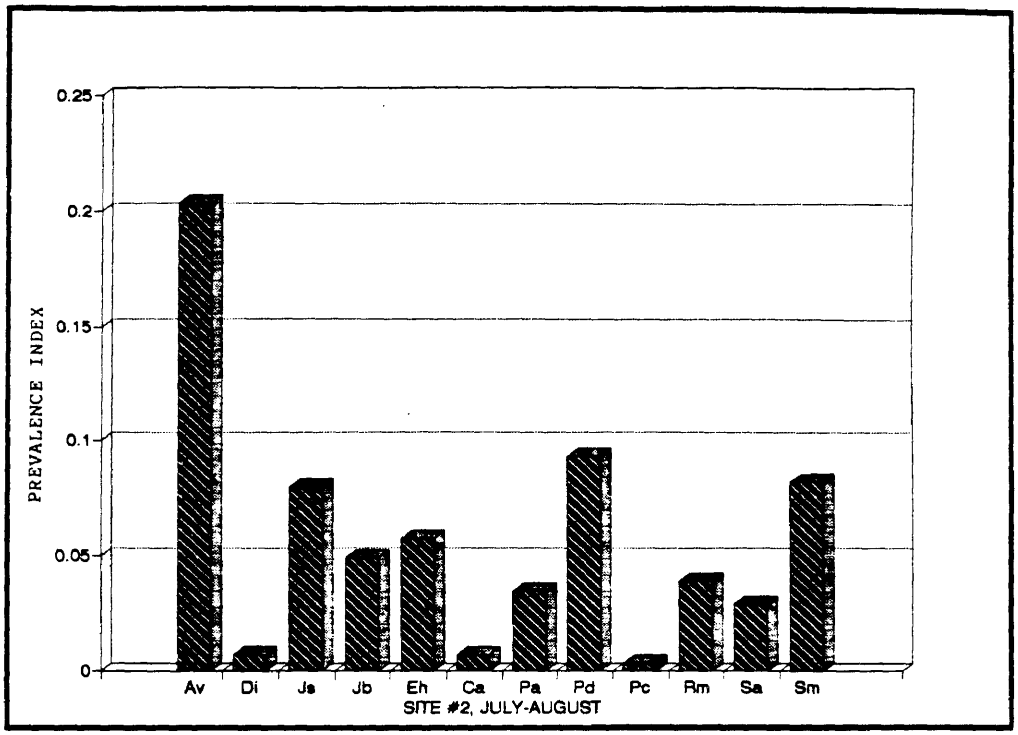
Sa
Sm
SITE #2, JUNE-JULY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PREVALENCE INDEX
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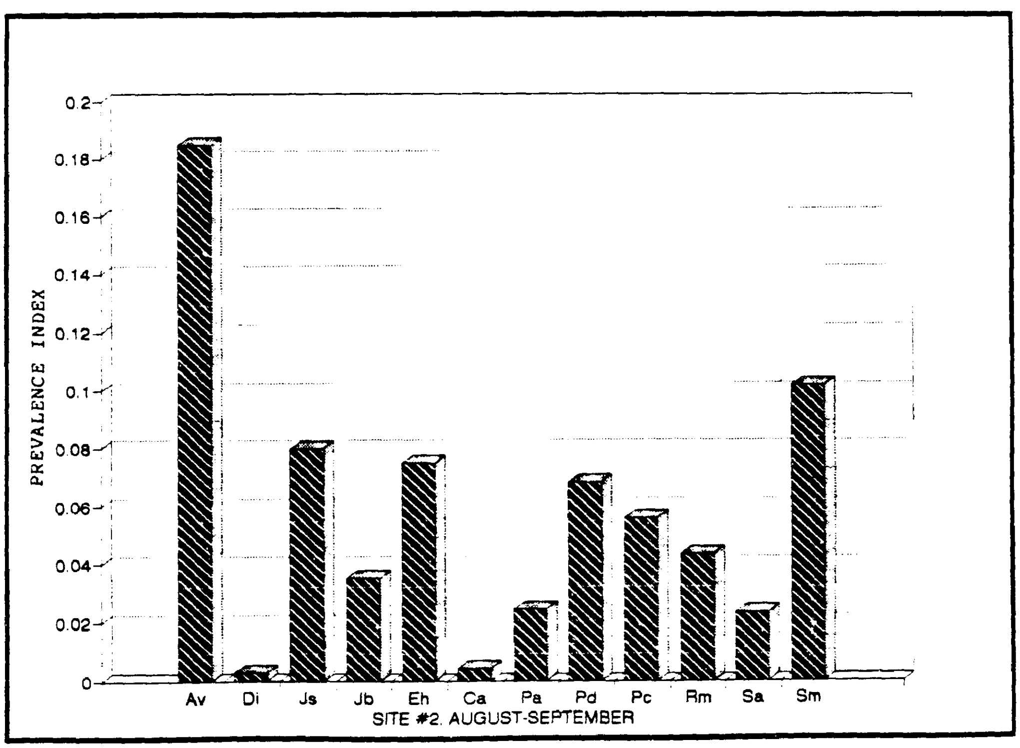
Sm
SITE #2, JULY-AUGUST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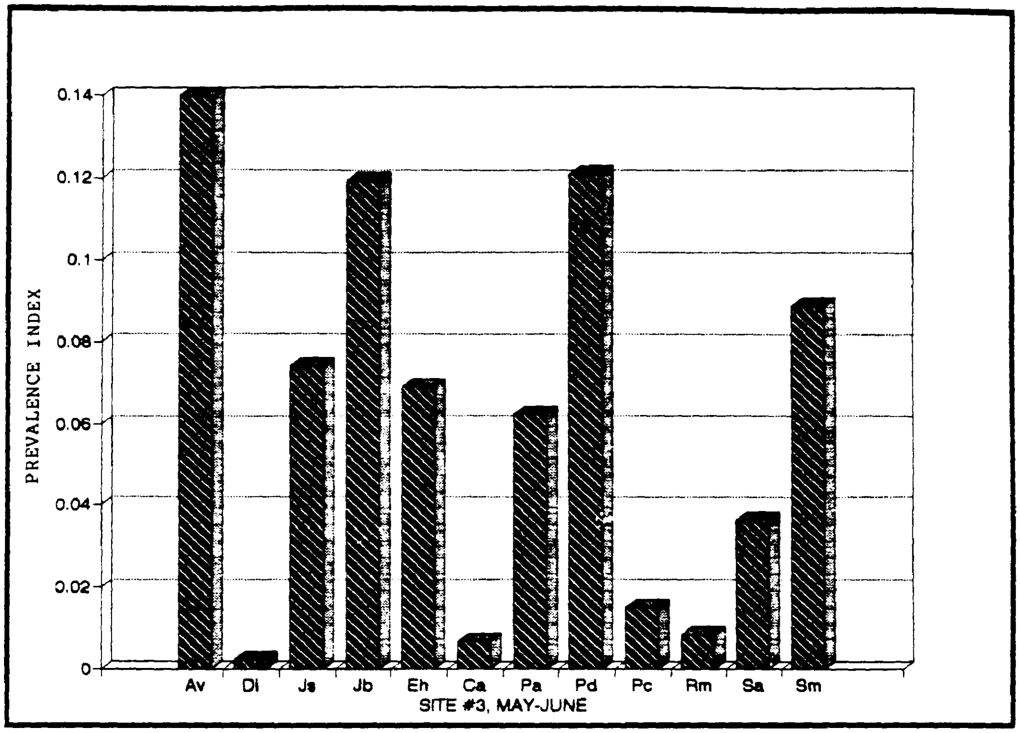
0.08
0.06
0.04
0.02
0
PREVALENCE INDEX
Av
Di
Js
Jb
Eh
Ca
Pa
Pd
Pc
Rm
Sa
Sm
SITE #2. AUGUST-SEPTEMBER

Figure 9: Prevalence indices for twelve signature swale species in site 3, May-July.

Figure 10: Prevalence indices for twelve signature swale species in site 3, July-September.



PREVALENCE INDEX
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0.12
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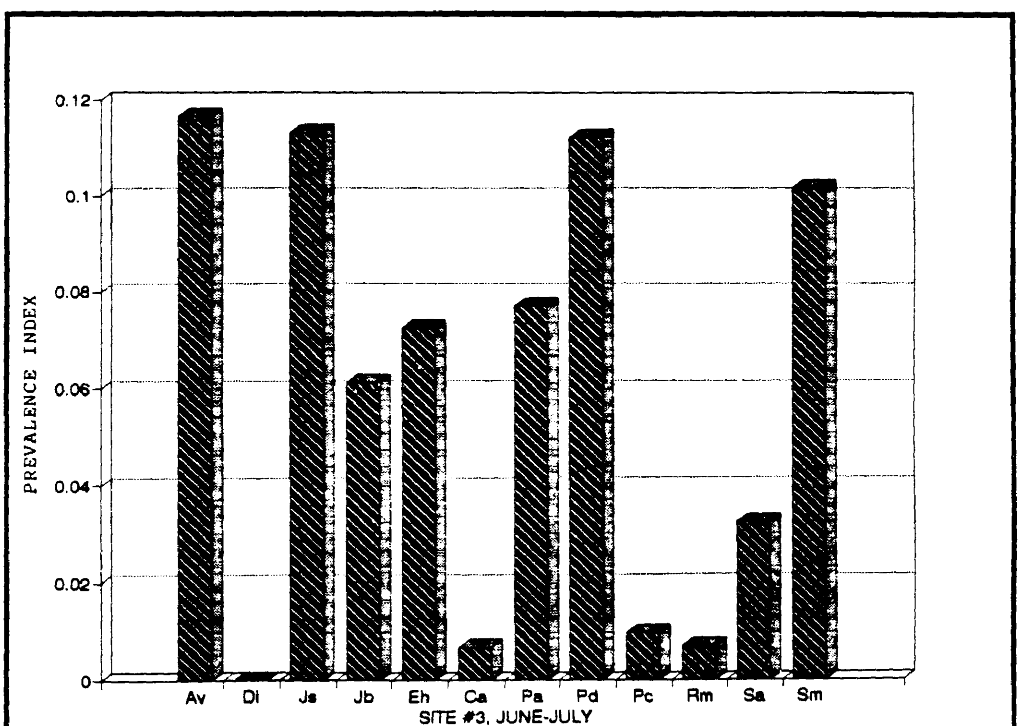
0.06
0.04
0.02
0
Av Di Js Jb Eh Ca Pa Pd Pc Rm Sa Sm
SITE #3, MAY-JUNE



PREVALENCE INDEX
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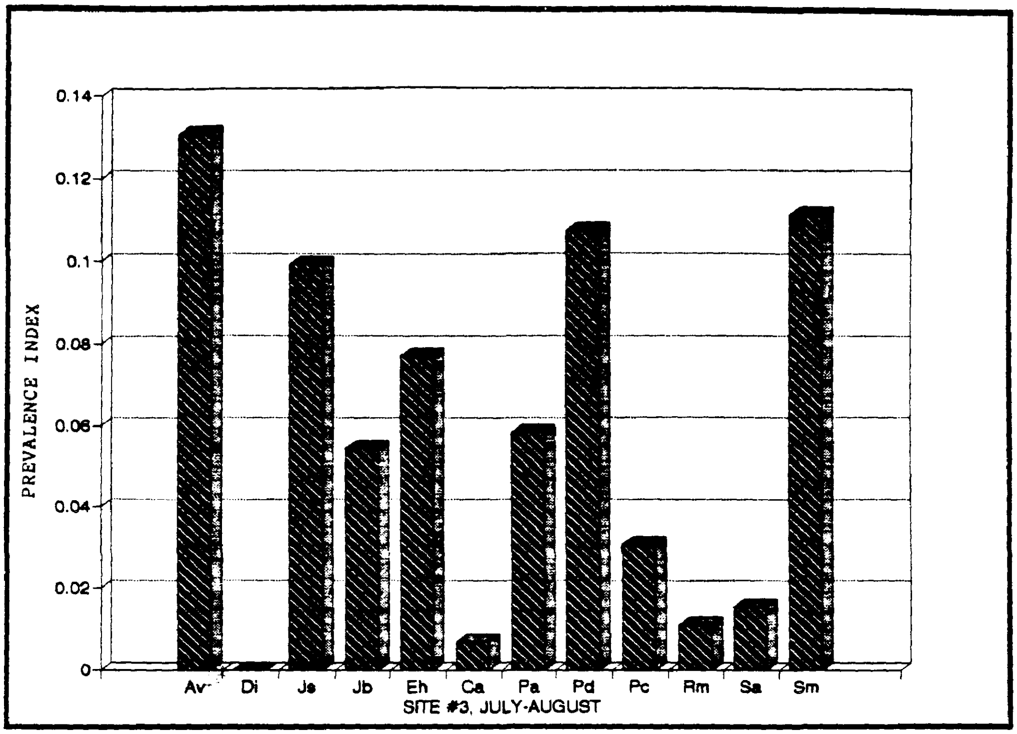
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Av
Di
Js
Jb
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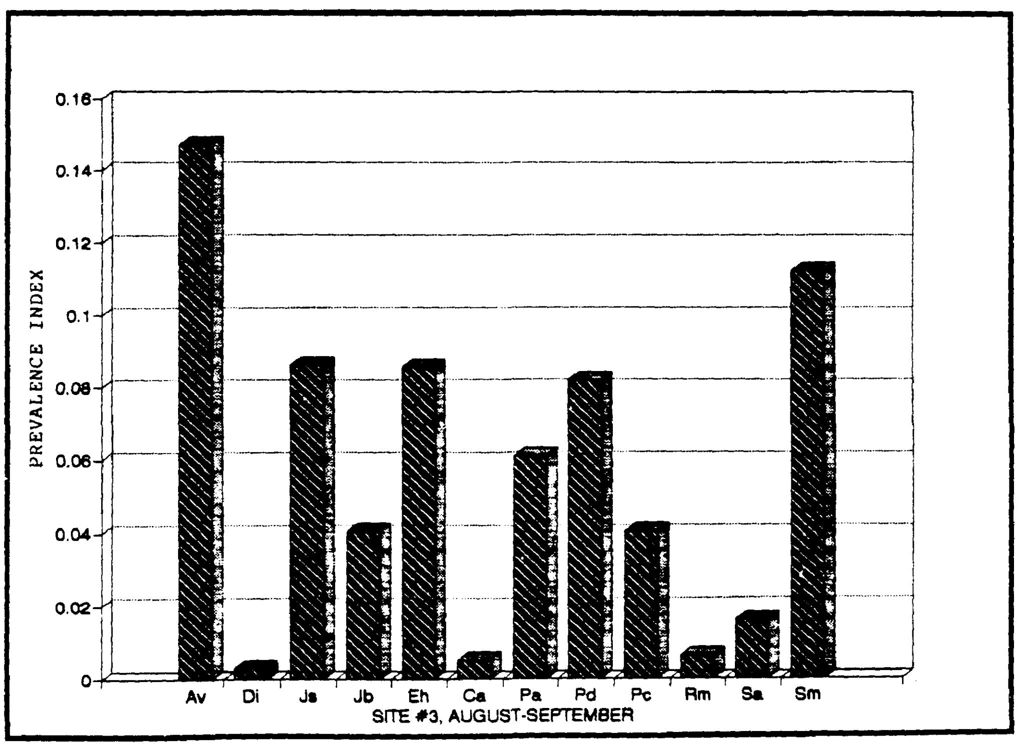
Ca
Pa
Pd
Pc
Rm
Sa
Sm
SITE #3, JULY-AUGUST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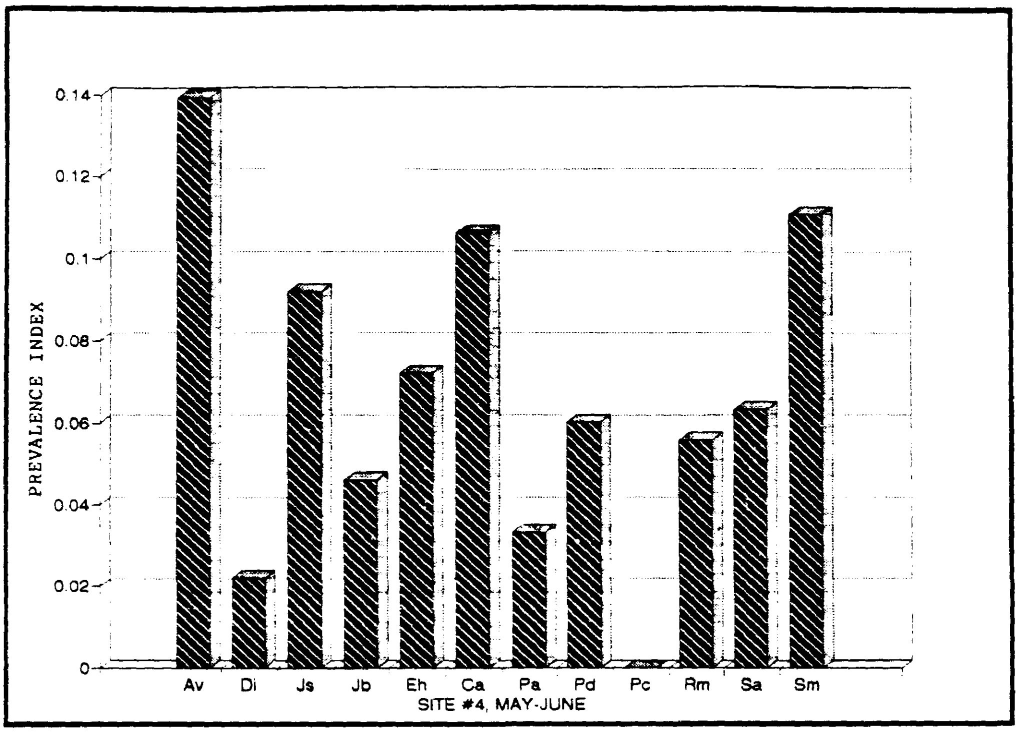
0.08
0.06
0.04
0.02
0
Av
Di
Js
Jb
Eh
Ca
Pa
Pd
Pc
Rm
Sa
Sm
SITE #3, AUGUST-SEPTEMBER

Figure 11: Prevalence indices for twelve signature swale species in site 4, May-July.

Figure 12: Prevalence indices for twelve signature swale species in site 4, July-September.


PREVALENCE INDEX
0.14
0.12
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0.08
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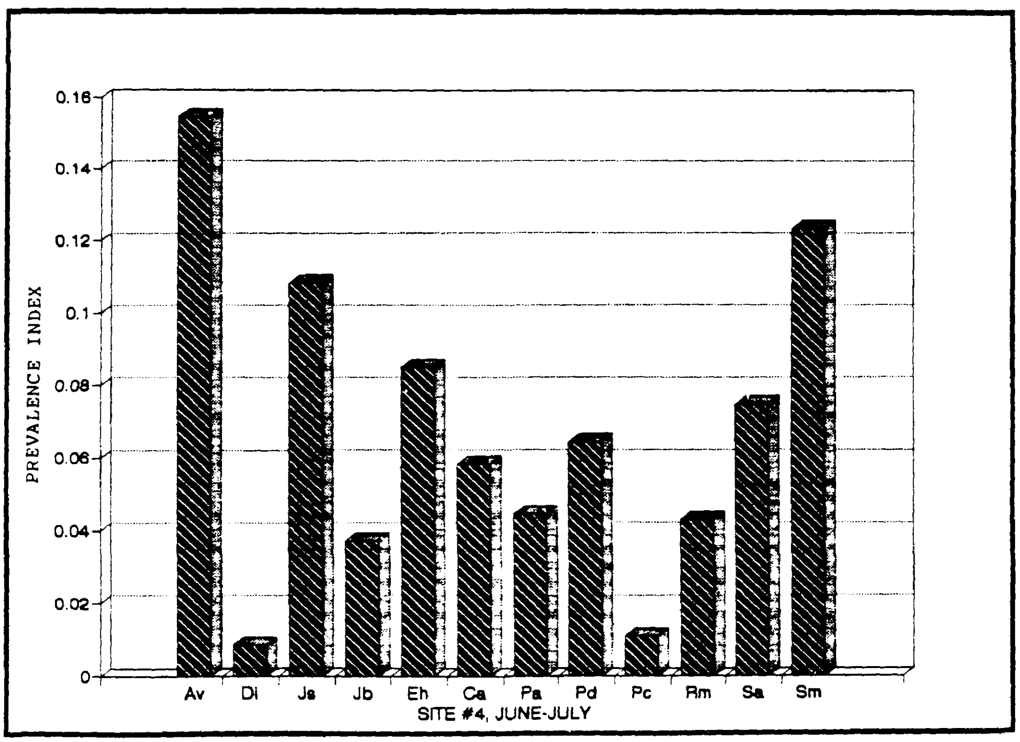
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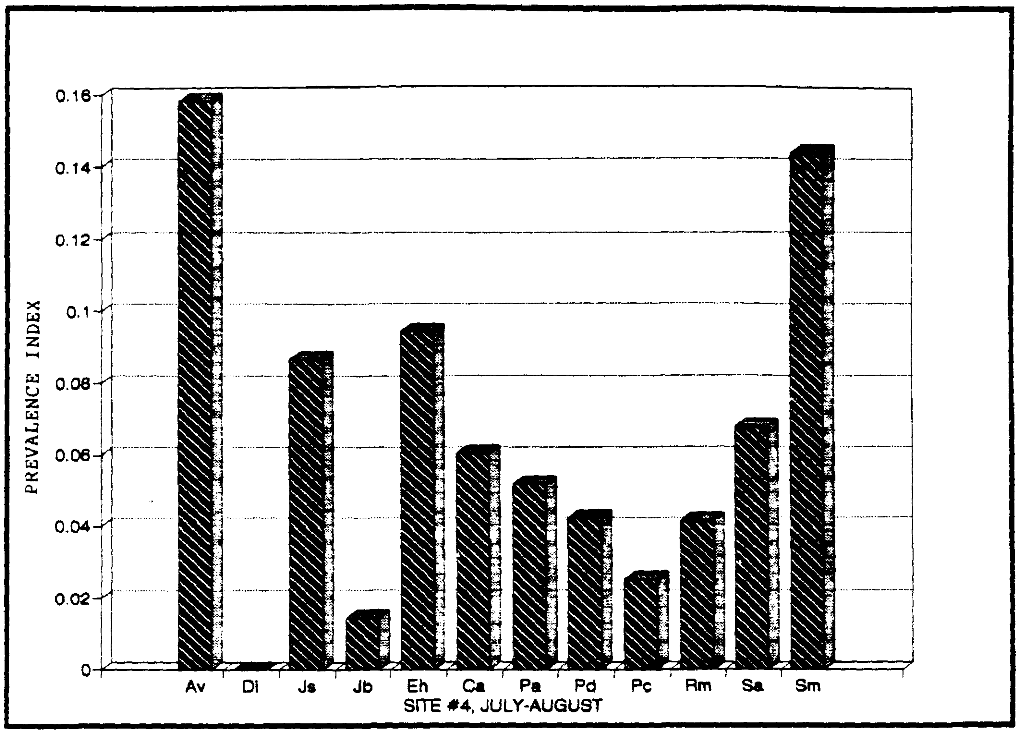
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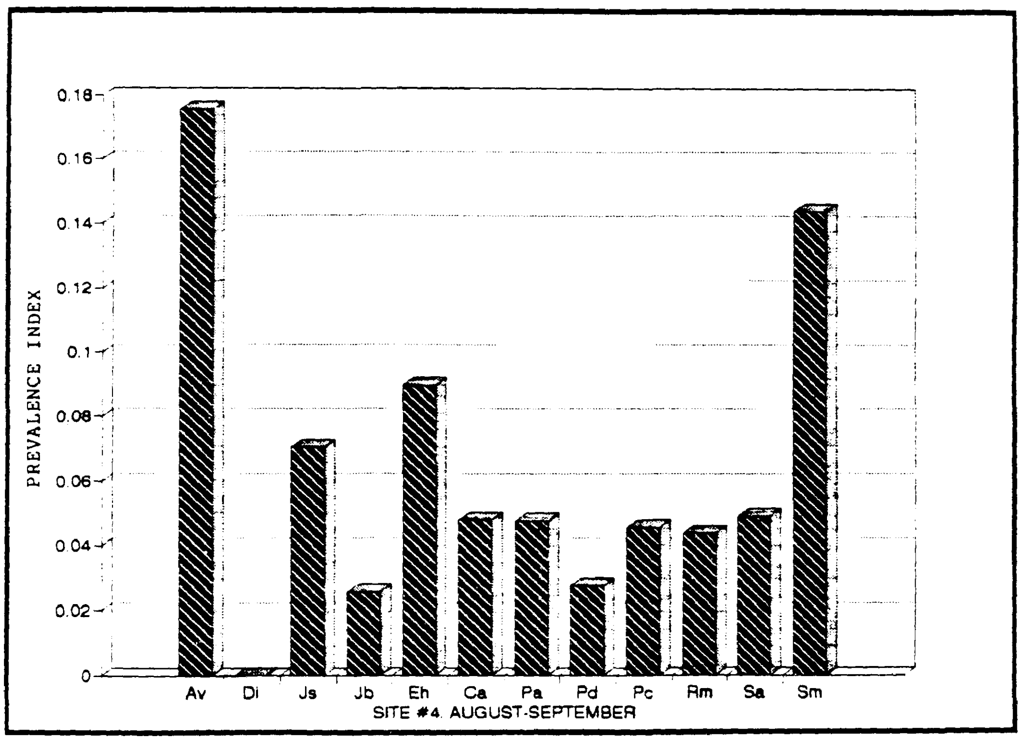
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Pa
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Rm
Sa
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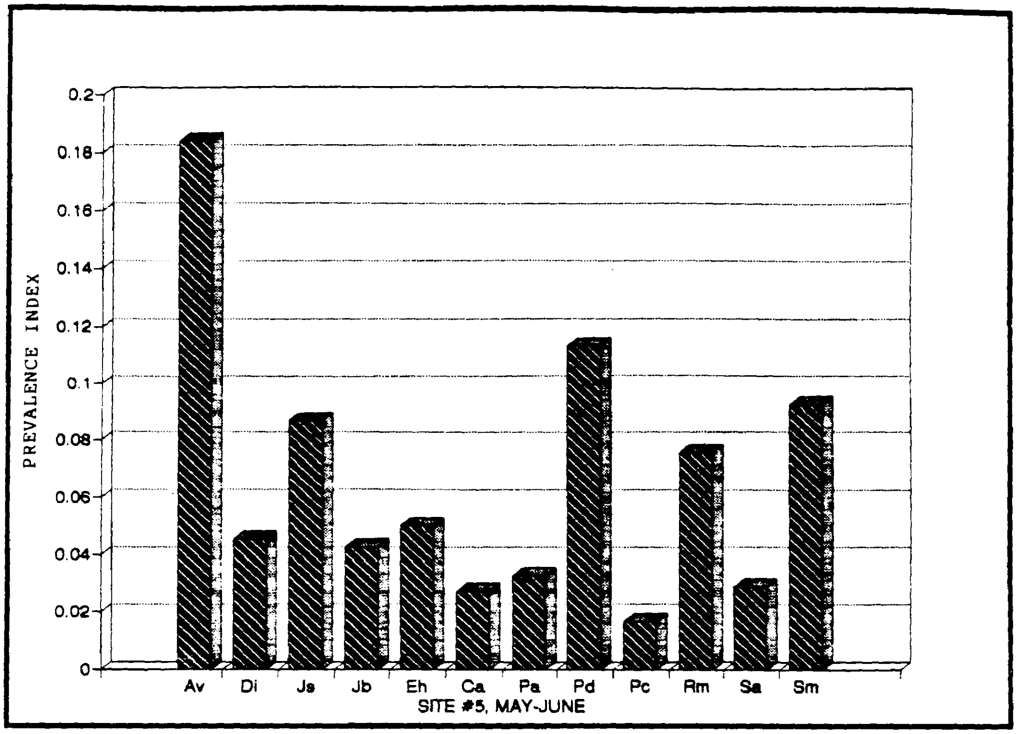
Figure 13: Prevalence indices for twelve signature swale species in site 5, May-July.

Figure 14: Prevalence indices for twelve signature swale species in site 5, July-September.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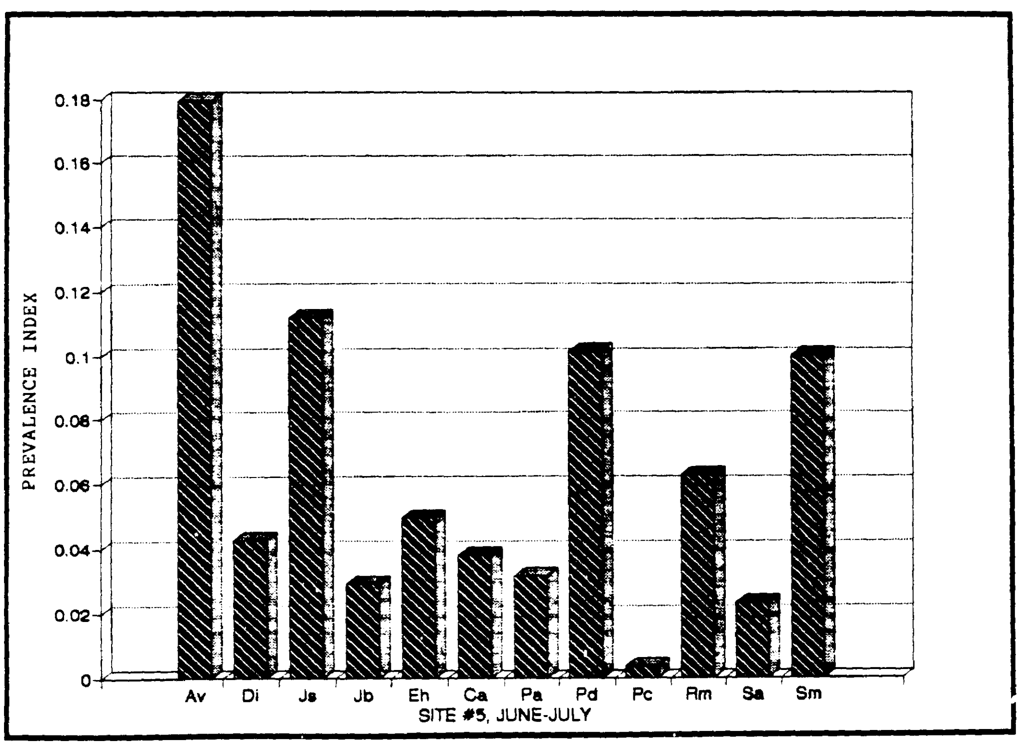
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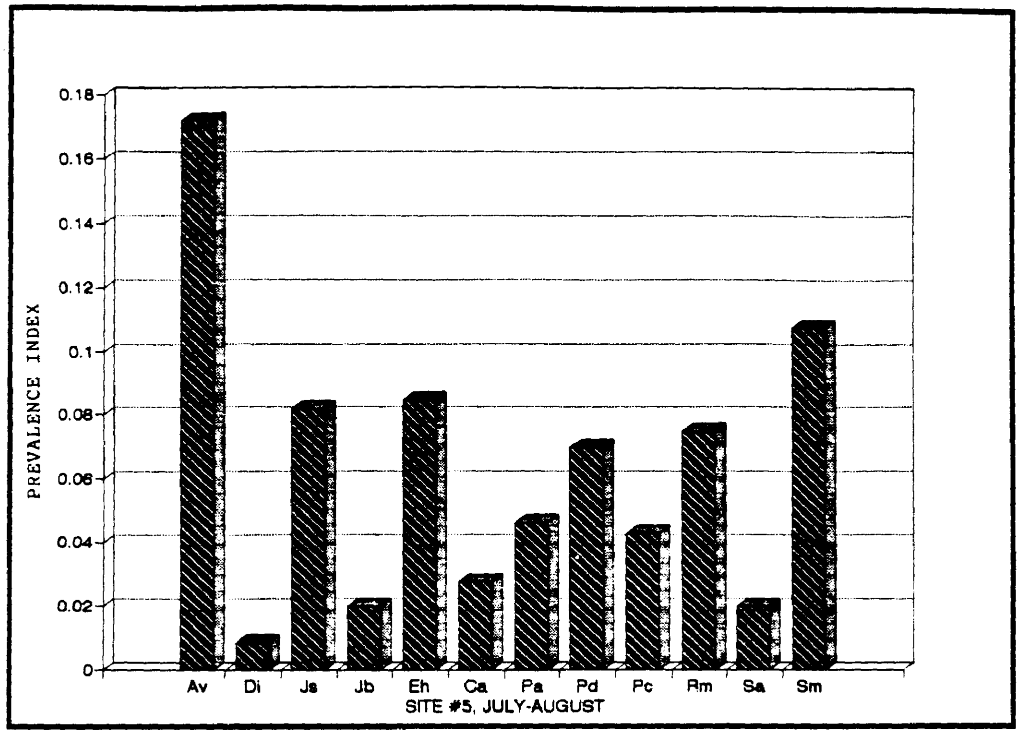

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Rm
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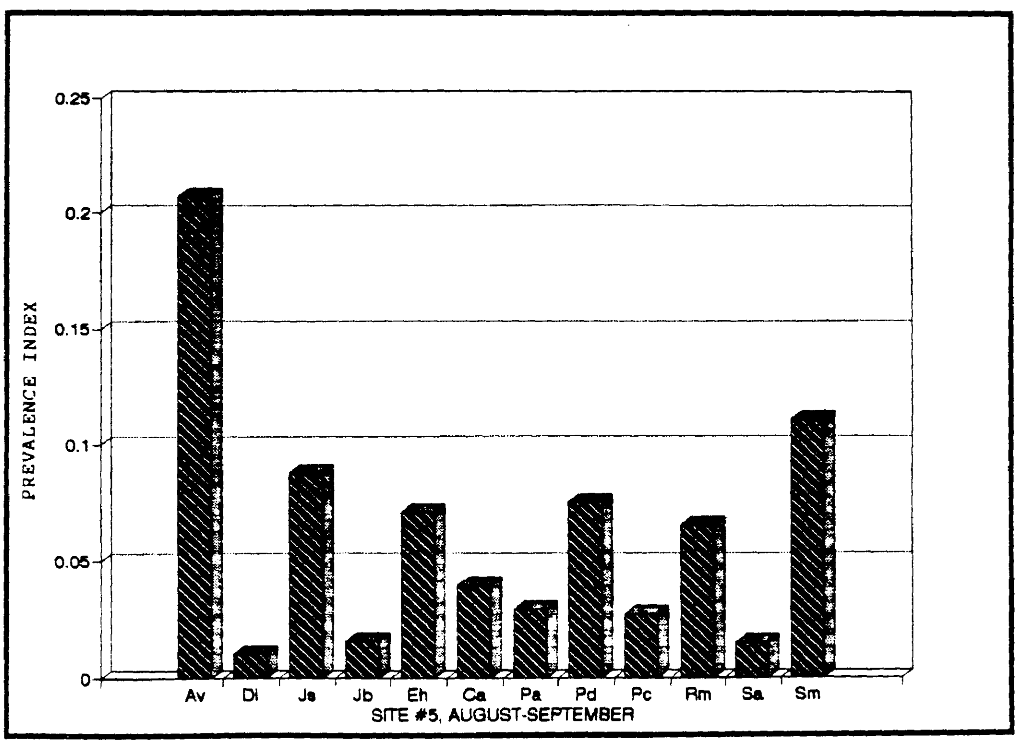
SITE #5, JULY-AUGUST



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Sa
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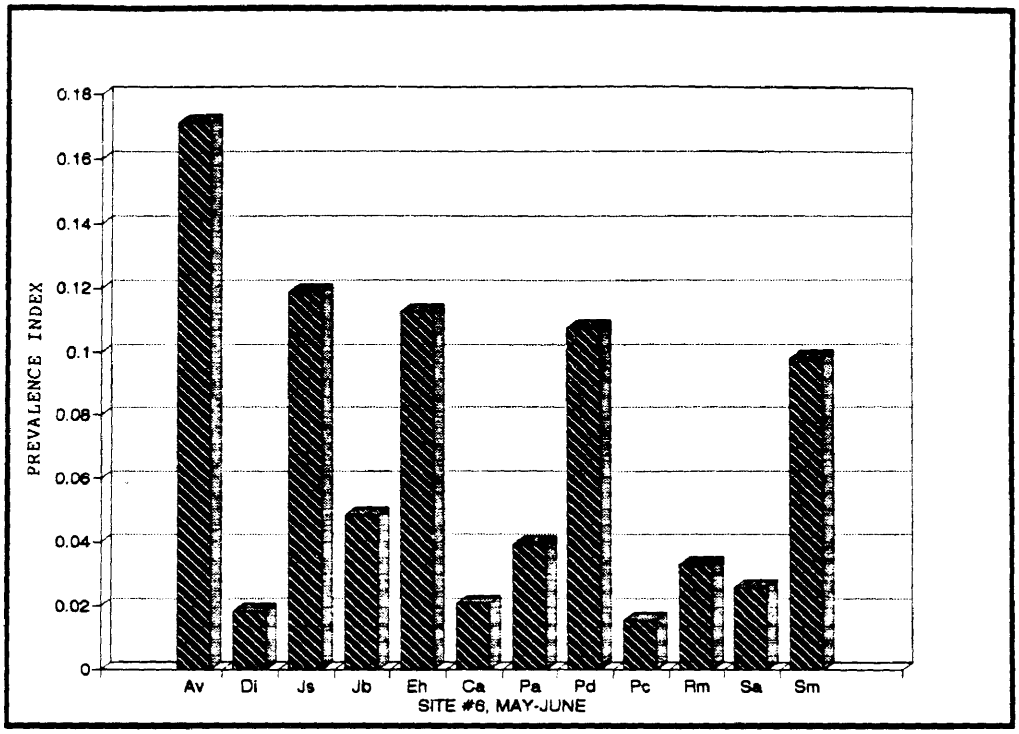
SITE #5, AUGUST-SEPTEMBER

Figure 15: Prevalence indices for twelve signature swale species in site 6, May-July.

Figure 16: Prevalence indices for twelve signature swale species in site 6, July-September.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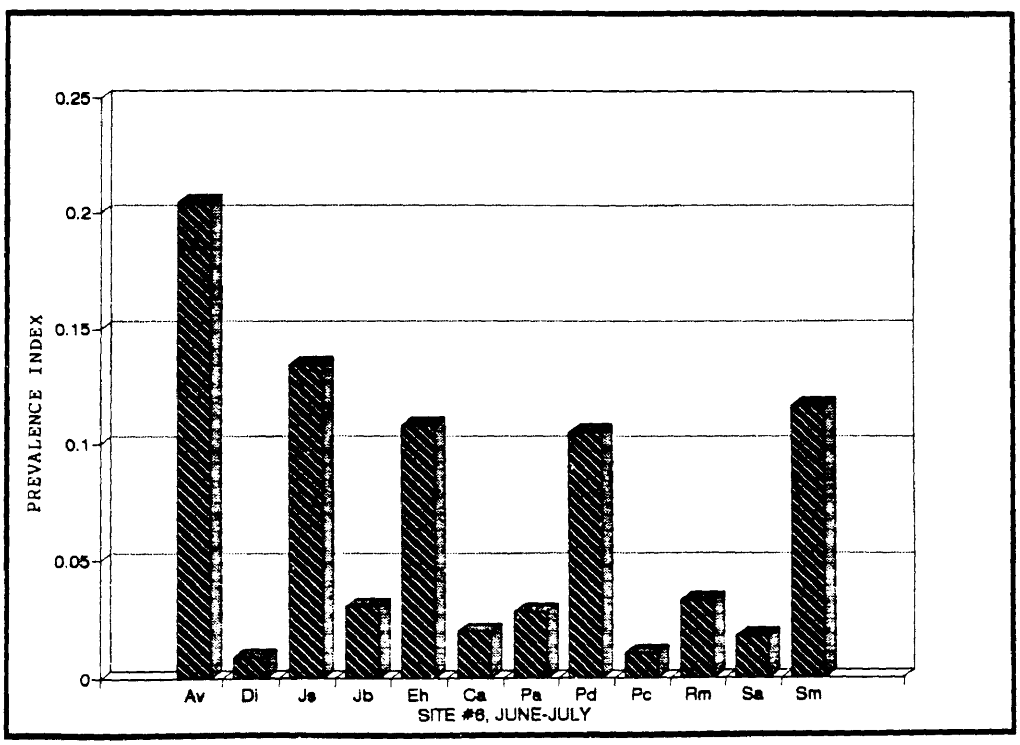
SITE #6, MAY-JUNE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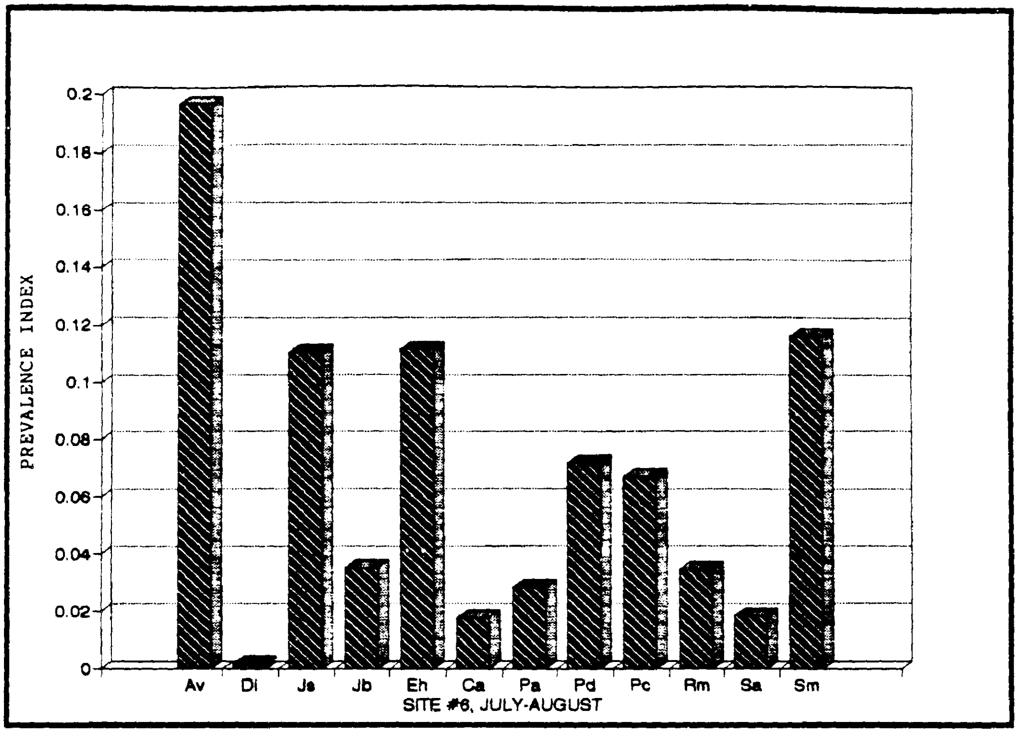
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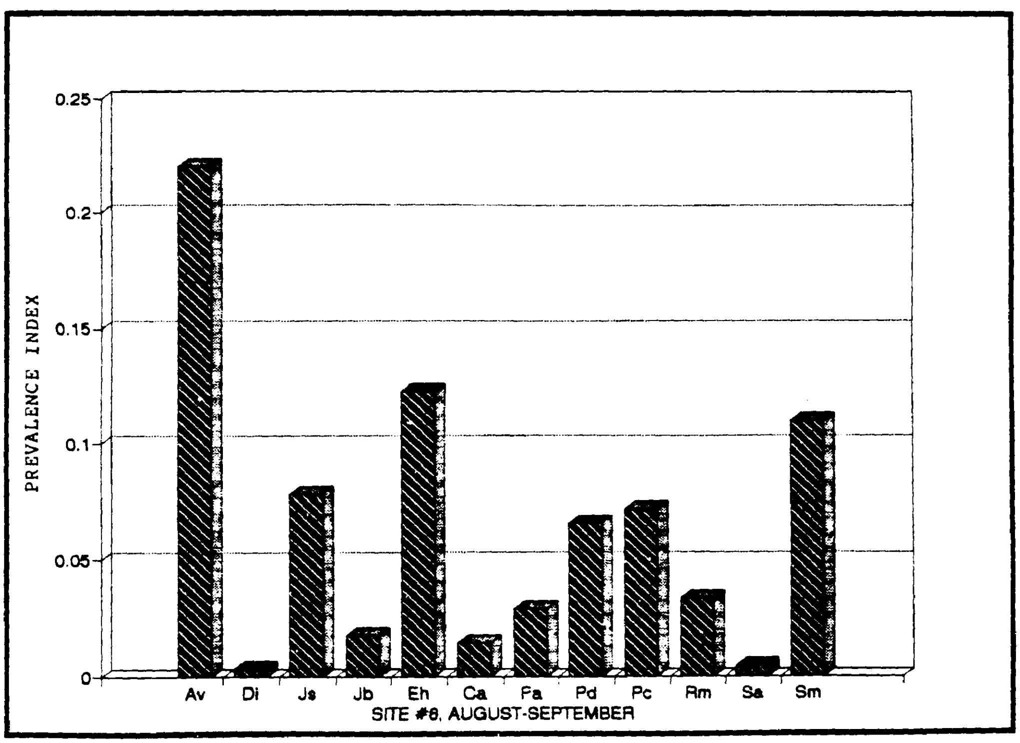
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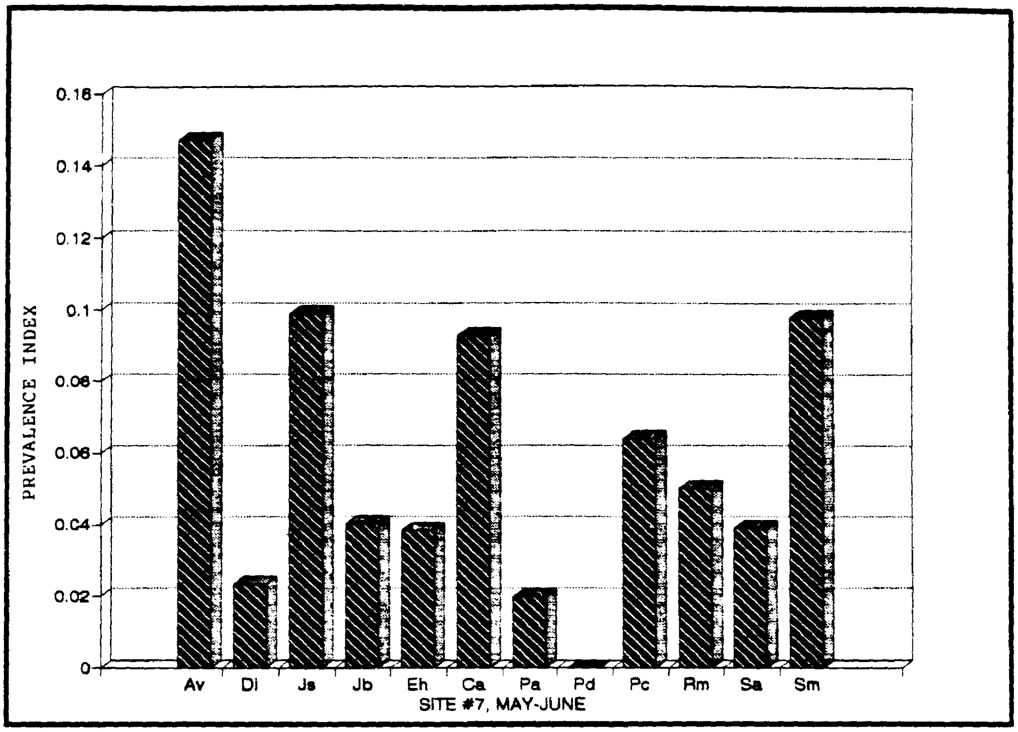
Pc
Rm
Sa
Sm
SITE #6, AUGUST-SEPTEMBER

Figure 17: Prevalence indices for twelve signature swale species in site 7, May-July.

Figure 18: Prevalence indices for twelve signature swale species in site 7, July-September.



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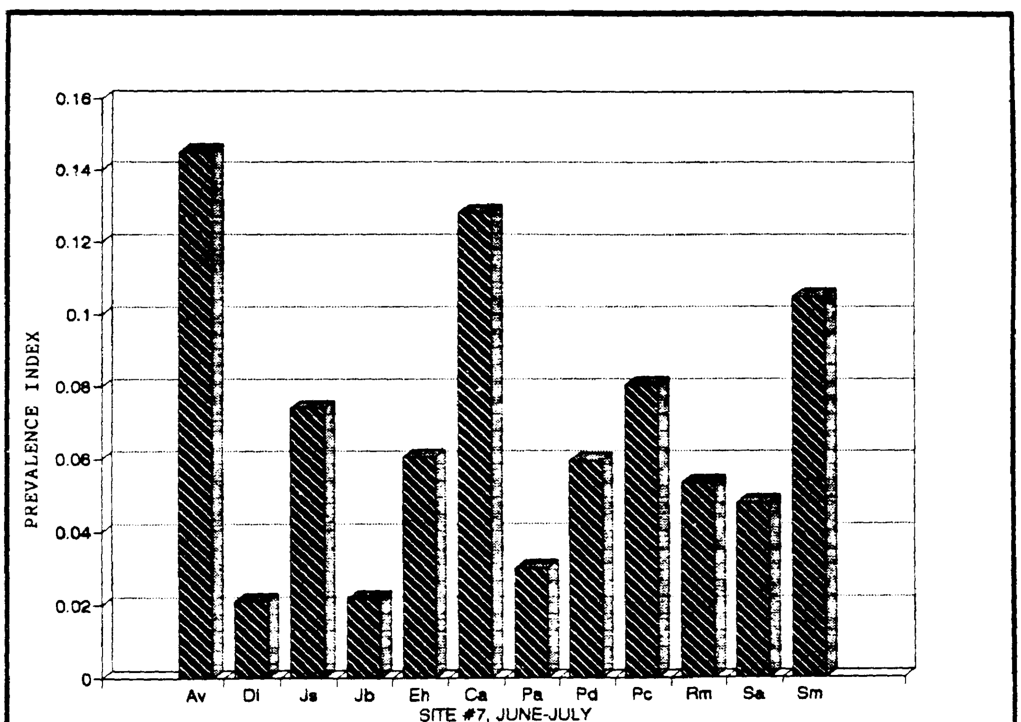
SITE #7, MAY-JUNE



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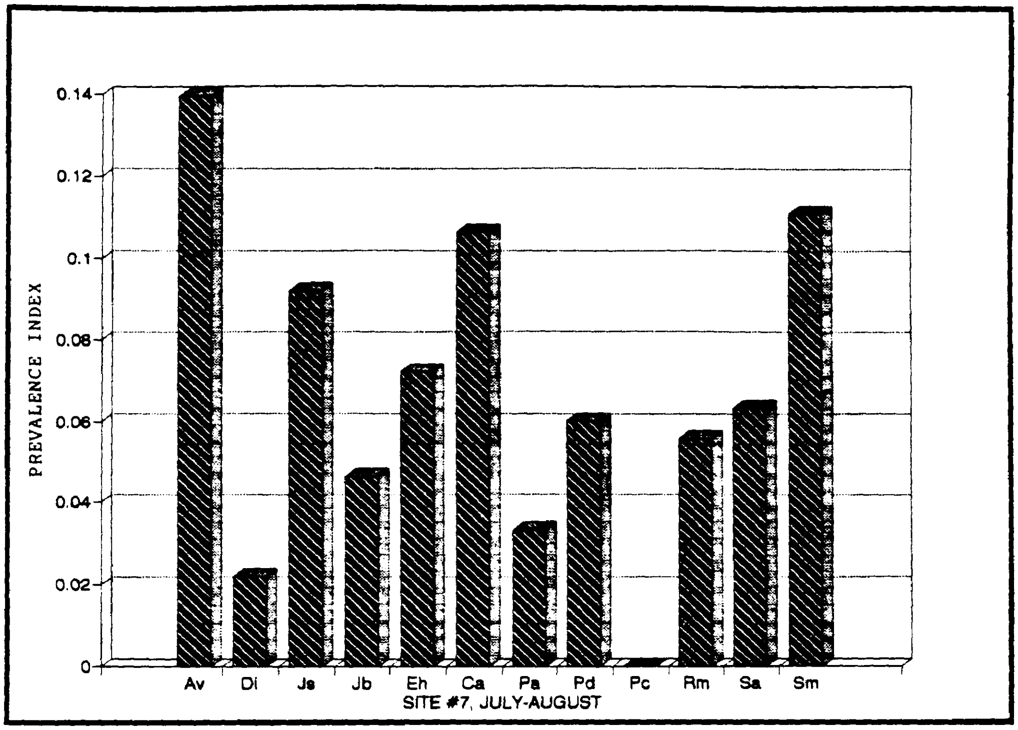
SITE #7, JUNE-JULY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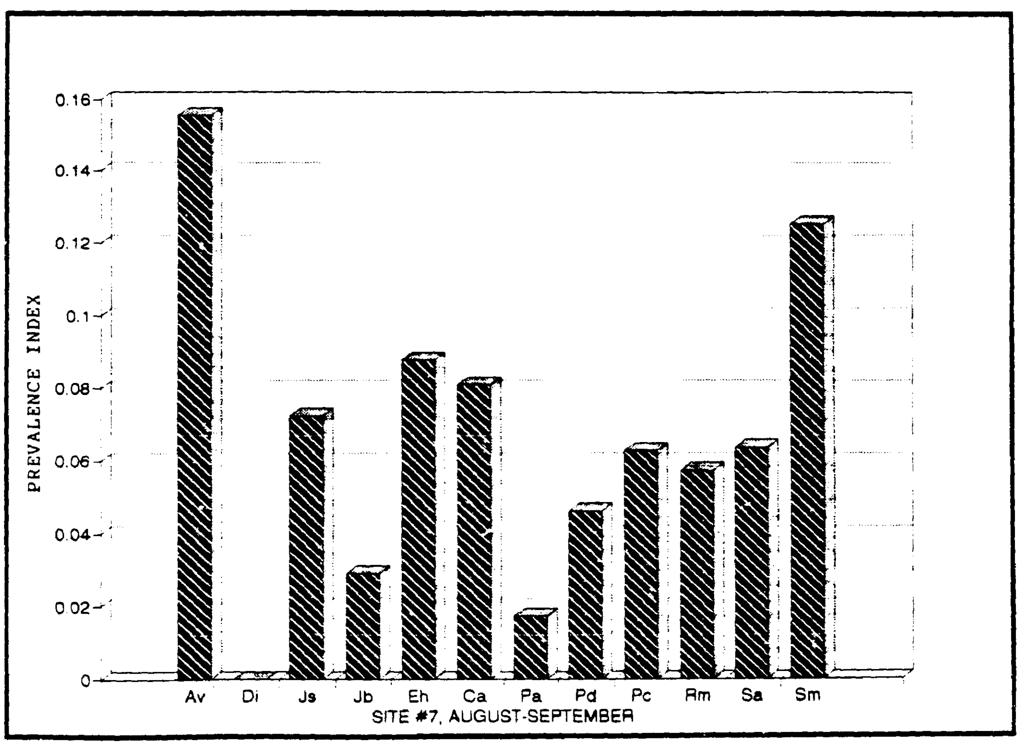
SITE #7, JULY-AUGUST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Di
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Jb
Eh
Ca
Pa
Pd
Pc
Rm
Sa
Sm
SITE #7, AUGUST-SEPTEMBER

site for the given sampling time. The graphs are arranged by site, and the overall appearance of these graphs gives an impression the community structure of each site at each time. In this way, the structure of each site can be compared visually with the structure of the other sites for any given sampling time, and the change in community structure over the course of the summer can be seen for each site. Comparing the figures visually, it is easy to see that *Andropogon virginicus* is by far the dominant species in each of these herb-dominated swales througout the summer. The prevalence index data for the twelve signature species can be seen in tabular form in Tables 1 through 4 as well.

Soils

Analyses of variance were run to compare all sites on the basis of soil pH, phosphorous, potassium, calcium, and magnesium. The means and p-values for each nutrient in these analyses appear in Table 5. The results of the *a priori* contrasts are given in Table 6. As can be clearly seen, there are no significant between site differences in soil quality or pH at the p = .05 level, either overall or when decomposed into specific contrasts between sites.

Analyses of variance were also run on groups of data from collection locations (i.e. dune faces vs. "averages" vs. "lows"). The means and overall p-value for each nutrient in these analyses appear in Table 7. Note that again the pH is not significantly different between groups at the p = .05

Table 1: Comparison of prevalence indices x 100 (P_i x 100) for the twelve signature swale species during the May-June sampling period.

Site	2	3	4	5	6	7
Species						
Av	17.521	13.989	16.185	18.406	17.162	14.721
Di	16.905	0.236	1.403	4.549	1.846	2.326
Js	4.091	7.416	6.840	8.682	11.864	9.914
Jb	9.092	11.954	5.637	4.258	4.830	4.007
Eh	4.929	6.913	7.817	5.030	11.242	3.822
Ca	0.696	0.666	7.165	2.728	2.069	9.289
Pa	3.774	6.241	6.238	3.260	3.925	1.976
Pd	8.964	12.101	4.685	11.350	10.770	0
Pc	6.554	1.496	0.636	1.670	1.557	6.403
Rm	3.618	0.824	2.956	7.573	3.303	5.002
Sa	3.793	3.627	7.566	2.889	2.587	3.872
Sm	8.524	8.902	12.778	9.273	9.800	9.804

Table 2: Comparison of prevalence indices x 100 (P_i x 100) for the twelve signature swale species during the June-July sampling period.

Site	2	3	4	5	6	7
Species						
Av	18.843	11.651	15.425	17.958	20.486	14.494
Di	1.447	0	0.829	4.277	0.864	2.089
Js	8.323	11.304	10.833	11.205	13.411	7.397
Jb	5.096	6.133	3.724	2.926	3.063	2.149
Eh	4.897	7.248	8.486	4.952	10.842	6.048
Ca	0.593	0.670	5.836	3.802	1.974	12.795
Pa	4.266	7.700	4.458	3.166	2.873	2.999
Pd	10.018	11.200	6.440	10.143	10.523	5.948
Pc	2.033	0.957	1.073	0.368	1.059	8.047
Rm	3.833	0.690	4.288	6.288	3.302	5.348
Sa	2.665	3.247	7.468	2.339	1.774	4.798
Sm	7.980	10.164	12.330	10.031	11.692	10.496

Table 3: Comparison of prevalence indices x 100 (P_i x 100) for the twelve signature swale species during the July-August sampling period.

Site	2	3	4	5	6	7
Species						
Av	20.342	13.064	15.821	17.220	19.664	13.940
Di	0.668	0	0	0.841	0.167	2.191
Js	8.007	9.940	8.699	8.189	11.058	9.210
Jb	4.906	5.428	1.430	1.982	3.518	4.630
Eh	5.749	7.712	9.452	8.475	11.158	7.219
Ca	0.681	0.690	6.061	2.768	1.771	10.654
Pa	3.455	5.813	5.181	4.610	2.827	3.336
Pd	9.328	10.740	4.226	6.988	7.195	6.024
Pc	0.326	3.094	2.507	4.285	6.700	0
Rm	3.874	0.690	4.140	7.479	3.437	5.576
Sa	2.907	1.555	6.793	1.997	1.846	6.323
Sm	8.207	11.140	14.406	10.762	11.608	11.102

Table 4: Comparison of prevalence indices x 100 (P_i x 100) for the twelve signature swale species during the August-September sampling period.

Site	2	3	4	5	6	7
Species						
Av	18.476	14.723	17.551	20.743	22.070	15.540
Di	0.304	0.282	0	1.040	0.313	0
Js	7.989	8.634	7.060	8.805	7.816	7.219
Jb	3.514	4.043	2.565	1.567	1.739	2.908
Eh	7.501	8.579	8.965	7.084	12.281	8.773
Ca	0.417	0.514	4.800	3.955	1.425	8.071
Pa	2.442	6.109	4.765	2.925	2.874	1.704
Pd	6.816	8.195	2.755	7.511	6.592	4.612
Pc	5.588	4.038	4.555	2.731	7.167	6.266
Rm	4.350	0.611	4.365	6.531	3.360	5.715
Sa	2.366	1.607	4.905	1.477	0.463	6.367
Sm	10.169	11.229	14.401	11.093	11.004	12.533

Table 5: Soil nutrient analysis means by study site. The overall p-values represent the probability that samples from each site are from the same statistical population. Numbers in parentheses indicate standard deviation.

GROUP	N	pH	Ca	P	K	Mg
site 2	7	4.557 (.3259)	56.57 (11.41)	2.143 (1.069)	16.29 (9.03)	14.57 (7.25)
site 3	7	4.957 (.3910)	51.43 (11.41)	2.429 (0.535)	19.43 (9.48)	15.43 (4.86)
site 4	7	4.857 (.3867)	63.43 (17.95)	2.571 (0.787)	25.14 (20.62)	20.86 (11.10)
site 5	7	4.871 (.4716)	53.14 (9.44)	2.429 (0.535)	17.57 (10.08)	15.57 (7.55)
site 6	7	4.814 (.3891)	53.14 (11.71)	2.000 (1.000)	17.86 (7.82)	15.43 (6.55)
site 7	7	4.843 (.3207)	58.29 (12.82)	2.000 (0.577)	15.29 (11.08)	14.57 (8.87)
total	42	4.817 (.3841)	56.00 (12.61)	2.262 (0.767)	18.60 (11.82)	16.07 (7.76)

pH: Overall p = .5063
Calcium: Overall p = .5270
Phosphorous: Overall p = .6317
Potassium: Overall p = .7113
Magnesium: Overall p = .6758

Table 6: Soil contrast probabilities - *A priori* tests. The values given are p-values, the probability that the samples being compared are from the same statistical population. No *a priori* test is significant at p = .05 level.

CONTRAST	pH	Ca	P	K	Mg
4 vs. 7	0.941	0.550	0.150	0.294	0.265
2 vs. 3	0.060	0.416	0.543	0.537	0.800
2 vs. 5	0.176	0.552	0.543	0.806	0.805
6 vs. 7	0.883	0.449	1.000	0.626	0.841
5 vs. 6	0.809	1.000	0.343	0.954	0.970

Table 7: Soil analysis means by sample location. Overall p-values indicate the probability that all samples are from the same statistical population. A *** designation indicates a highly significant p-value (.001<p<.01). Numbers in parentheses indicate standard deviations.

GROUP	N	pH	Ca	P	K	Mg
dune face	6	4.850 (0.207)	42.00 (6.57)	3.167 (0.753)	4.17 (0.983)	7.00 (0.000)
average	18	4.911 (0.423)	58.00 (11.82)	2.222 (0.647)	18.11 (8.771)	17.22 (8.121)
low	18	4.711 (0.371)	58.67 (12.27)	2.000 (0.686)	23.83 (12.590)	17.94 (6.708)
total	42	4.817 (0.381)	56.00 (12.62)	2.262 (0.678)	18.57 (11.847)	16.07 (7.757)

pH: Overall p = .2887
Calcium: Overall p = .0099***
Phosphorous: Overall p = .0031***
Potassium: Overall p = .0009***
Magnesium: Overall p = .0053***

Table 8: Soil contrast probabilities - average vs. low. Tukey's Honestly Significant Difference Test was used to create these p-values. Dune face samples were found to be significantly different from the average and low samples at the p = .05 level. Phosphorous is higher on the dune faces than in the swales, and all other nutrients are higher within the swale.

CONTRAST	pH	Ca	P	K	Mg
AVG vs. LOW	0.141	0.869	0.324	0.124	0.773

level. The quantity of any given nutrient is also not significantly different between the "average" and "low" samples, as can be seen by the contrast between these groups for each nutrient. However, in doing subsequent *a posteriori* testing using Tukey's Honestly Significant Difference Test, it was found that the levels of phosphorous are higher, and levels of each other nutrient are significantly lower in the dune face samples than in the "average" or "low" samples. These results can be seen in Table 8.

DISCUSSION

The swale is unique among habitat types in Virginia. As such, swales have been the subject of much floristic interest (Fernald 1935, 1936, 1940, 1947; Ludwig, 1990; Tyndall and Levy, 1978). The swale is a habitat of seeming contradictions. Salt-tolerant species such as *Myrica cerifera* are found at most sites, but so are salt-intolerant species. Species range in their water regime requirements from low moisture to semi-aquatic. Rootings by feral hogs create large areas of established swale vegetation disturbance (Ludwig, 1990), but these same areas provide microhabitat islands for the establishment of some rare plant species.

It is necessary to probe into the processes of a swale habitat in order to make sense of these contradictions. As with any ecological area, one must consider the physical stresses of the habitat, including hydrology, soil factors, and geographic location in order to assess the habitat in general.

Vegetation

The vegetation of the FCSP swales is a function of the hydrology, soils, and geographic location of the area. Swale vegetation is composed mainly of marsh species found outside the dune system, and very few species are endemic to the swale habitat (Ranwell, 1959).

Cowardin's (1979) classification of the interdunal swale areas in this study would be either (a) palustrine emergent, or (b) palustrine shrub/scrub, depending on the dominant vegetation type. The species found in the study sites are a mixture of wetland and more upland plants (Appendix A). This mixing occurs because of the differences in soil moisture between sites and within a given site. Since hydrology is the main factor affecting species distribution in the swale (see **Hydrology**) , then the presence of moisture microhabitats in a swale site will allow the establishment of wetland and/or dune species in that site. As previously mentioned, secondary ridges support more xeric species, while hog rooting support more wetland-type species. Tyndall and Levy (1978) found that hog rooting areas were recolonized by hydrophilic *Spartina patens*, while the mounds of sand deposited by the hogs were recolonized almost exclusively by *Andropogon virginicus*. *Andropogon virginicus* is more tolerant to xeric conditions, and is thus found in drier parts of the swale (Oosting and Billings, 1942). Zoladeski (1991) found the vegetation of the Leba Bar slacks to form two distinct series: one in the moist low areas of the slacks, and one on the drier ridges.

The relatively high prevalence of the *Juncus* species is evidence to the wet nature of swales, as rushes tend to thrive in wetland habitats almost exclusively. These wetlands can be freshwater to more brackish in nature, and the species present in the swales may get the needed water from maritime overwash, rainwater, or a high water table.

More interesting even than the rushes is the abundance of

Centella asiatica, *Scirpus americana,* and *Drosera intermedia* in some sites. These species are prevalent enough overall to have been included in the twelve signature species, but their abundance varies considerably from site to site. Site 7 has the largest collection of these predominantly freshwater wetland species, and site 6 has the fewest. Using these species as a guide, one could state with some certainty that site 7 has a fairly constant or regular source of fresh water, whereas other sites, especially site 6, may not have such a reliable source. The source of this freshwater may be a lens of groundwater which is particularly close to the surface (Willis, et al., 1959), or a location which facilitates the use of stochastic events to drive hydrology in that site (Perry, pers. comm.).

The physical form of the swale species is also affected by the harsh variability of the swale's hydrology. Species collected as voucher specimens for this thesis were identified by Dr. Donna M.E. Ware and myself. Many were so depauperate in their form compared to their more robust inland conspecifics as to be very difficult to recognize. Almost every species, it seems, is dwarfed by the swale conditions. There is some evidence that this effect is due, in some species at least, to the effects of waterlogging (Jones and Etherington, 1971; Seliskar, 1990; Ranwell, 1959), instead of stress induced by the lack of water. Waterlogging also stunts root growth and reduces tiller formation in grasses (Jones and Etherington, 1971). Considering the winter flooding as well as the high chance for stochastic flooding in the FCSP sites, the waterlogging theory bears weight in this study as well. Willis and Yemm (1961) found that nutrient deficiency will also stunt the growth of swale plants, and further investigation of plants at the FCSP sites may find this factor to be synergistic.

In general, however, soils play a somewhat less important role in the makeup of the herbaceous community of the swale. Obviously, the low nutrient levels present currently at the FCSP sites will eliminate some less tolerant species from establishing there. However, as the organic content of the soil increases through leaf fall and root decomposition and dune nutrients continue to be leached into the swale, this effect will become negligible (see **Soil Nutrients**).

The geographic location of FCSP also plays a role in the composition of the swale vegetation. There is some argument about the location of the boundary between the northern and southern floras (Hosier, 1991). It seems that, on average at least, FCSP falls somewhere in the ecotone between the two floras. One can find *Hudsonia tomentosa* on the lower dune faces, and *Tillandsia usneoides* in the maritime forest of Wash Woods. FCSP is north of the so-called "Intracapes Zone" (Lazell and Musick, 1973), a floristically depauperate zone between Cape Lookout and Cape Hatteras in North Carolina. This fact may indicate a more northern association of the flora, but both northern and southern species are found in the Park.

In any case, the swale areas of the Park provide a habitat suitable for the geographically wide-ranging species of the Atlantic coast (Moreno-Casasola, 1988) which are generally adapted to rapid dispersal and colonization (Hosier, 1991). The establishment of a species in a swale site is dependent on a seed source which can disperse via wind or birds to the isolated swale areas (Ranwell, 1959), and the randomness of dispersal events accounts somewhat for the vegetational differences between swale sites (Ranwell, 1972). Species come, biogeographically, from surrounding coastal plain and dune areas, as well as other swales along the coast (Lubke and Avis, 1982). Poaceae, Cyperaceae, and Asteraceae are the best represented families for any east coast dune system, and this is certainly true for the FCSP swales, but no one family is characteristic of swale areas (Hosier, 1991). Although plant families from inland are found in dune and slack areas, some families, such as the Fabaceae and Rosaceae are poorly represented (Hosier, 1991). Ranwell (1959) found that a large percentage of plants in dunes and slacks are hemicryptophytes. These plants overwinter as buds near the soil surface (Hosier, 1991). Dunes also have a large percentage of therophytes, which are much less common in swale areas (Ranwell, 1959).

The fact that the herbaceous sites are dominated by *Andropogon virginicus* is not particularly surprising. *Andropogon virginicus* is a wide-spread species (Appendix B) which thrives in a wide range of habitat types (Appendix A).

It is also quite tall, and therefore able to shade out genetically smaller competitors. *Solidago microcephala* and *Eupatorium hyssopifolium* also do well in each of the sites. These are large, widespread composites, and perhaps compete well for the same reasons listed for *A. virginicus*.

Crawford and Wishart (1966) described three distinct swale vegetation types based on salt tolerance and soil moisture. These types were: young swales with salt tolerant species, older wet swales, and older dry swales. The first type are often close to the sea and presumably get overwashed occasionally, while the older freshwater swales are further inland. As mentioned previously, none of the swales at FCSP, with the possible exception of site #4, were close enough to the ocean for overwash to influence the vegetation therein.

The vegetation recorded in study sites at FCSP, then, represents species which are wide-ranging coastal species and locally abundant inland Virginia-North Carolina species, often in a stunted form, brought in as seeds by wind or birds. These species are subsequently selected by their tolerance to the stringent water regime and soil nutrients of swale sites. They may represent a zonal climax, as suggested by British authors, or they may eventually be overshadowed by trees or washed away by a heavy storm. The most this paper can achieve is a documentation of the current vegetation, and an observation of the conditions under which it grows. Time will change this system, and only the future will show what changes will come.

Hydrology

In any assessment of a wetland habitat, it is necessary to describe the hydrology, soil, and vegetation present at the site (Mitsch and Gosselink, 1986). These factors may be interwoven. For example, larger plants in swale areas may decrease water evaporation, and the higher soil moisture in these areas may decrease temperature fluctuations, thus decreasing water demand (Lubke and Avis, 1982). Of course larger plants may also increase the rate of evapotranspiration, so their effect on hydrology could be negligible. While all three parameters are closely interconnected, an arbitrary separation of the three is useful, and may allow a better view of the links between them.

Of the three wetland parameters, hydrology is certainly the most important (Mitsch and Gosselink, 1986). The hydrology of the swales affects many factors which limit plant growth. The waterlogged soil above the water table causes reduced aeration, lowered pH, lower decomposition rate, and an increase in the carbon:nitrogen ratio (Ranwell, 1959). Van der Laan (1979) found plant community makeup of swales correlated most highly with watertable depth. The other factors highly correlated with vegetation were, in order: % $CaCO_3$, % total organic material, and thickness of the soil A horizon. These other factors, however, were shown to be inseparable from water table effects. An understanding of swale hydrology, then, will prepare the way to understanding the vegetation, and to a lesser extent the soils, of the study site.

The water table forms a dome-shaped lens of water under each swale, being highest (i.e. closest to the soil surface) at the middle of the area, and lowest at the periphery (Willis, et al., 1959). Differences in the rate of subsurface water flow are responsible for this shape (Hosier, 1991). Swale bottoms are often sealed off, wholly or partially, by a layer of sand, silt, and organic material. This layer has a low hydraulic conductivity, and water exchange is therefore more important at the edge of a swale and slower through the bottom (Odum and Harvey, 1988).

Water table fluctuation is the basis of swale hydrology. The water table may change in height over the course of the year, due mostly to the amount of rainfall (Odum and Harvey, 1988; Ranwell, 1959; Van der Laan, 1979; Willis, et al., 1959). At some points during the year, especially the rainy late fall and early spring months, the swales may be partially or entirely flooded (Hosier, 1991). Flooding may also occur after a heavy rainstorm, as evidenced by the effects of hurricane Bob during the study period. Flooding after Bob varied from a few centimeters to knee-deep, depending on the site (pers. obs.). Long -term water table level changes also reflect a 20-year drought cycle in the southeastern U.S., which may completely dry up some swale wetlands during drought years (Odum and Harvey, 1988).

Soil moisture data from most visits, not complete enough to print here, indicate that the soil moisture ranged from

2.5%, the average in all sites, to 10%, which was only rarely found in the wettest parts of the sites (pers. obs.). Tyndall and Levy (1978) found the soil moisture in their sites at Back Bay Refuge and northern FCSP to fall roughly around 3.0% for wet sites and 1.0% for dry sites. The normal pattern, then, would be a high water table with some flooding in the winter, and very dry conditions throughout most of the swale during the summer, with occasional stochastic flooding. This is congruous with findings at other swale sites (Jones and Etherington, 1971; Ranwell, 1959; Seliskar, 1990; Van der Laan, 1979; Willis, 1959). Climate plays a large role in hydrology (see **Climate** section), and its influence cannot be overlooked.

Water table fluctuations may also take place on a daily basis (Ranwell, 1959; Willis, 1959). The high rate of evapotranspiration during the day during the growing season causes a drop in the water table. At night, when water demand is lower, the water table may rise again. In a swale, the water table, even at its lowest, is rarely inaccessible to plants with sufficiently large roots systems. Therefore, the water table has a more direct influence on the types of plants living within a swale than on the dune species which are isolated from it (Ranwell, 1959).

The concept of depth to the water table is also important when assessing microhabitats of the swale. Secondary ridges, formed during the dune-building process, are raised sandy bars in the swale. The soil of these bars is typically drier than that of the lower surrounding swale area (pers. obs.). Areas of feral hog rooting are often deeper into the soil, and therefore closer to the water table than the surrounding area, making the soil within them moister. This effect has been noted by a number of individuals (Ludwig, 1990; Tyndall and Levy, 1978; Rawinski, unpub. data).

The amount of flooding and the soil moisture of a site depends on the specific topography and location of that site (Willis, et al.,1959), creating a wide range of possible water regimes within the same dune system. Ranwell (1959) separated his Newborough Warren sites by depth to the water table after noticing distinct changes in the vegetational associes which accompanied these changes in water table depth. Wet swale associes are found in areas where the water table is always less than one meter from the soil surface. Dry swale associes are found when the summer water table lies between one and two meters from the soil surface. Dune associes occur where the summer water table is more than two meters from the soil surface. Shallow-rooted species are eliminated from dry swales, and even deep-rooted species are independent from the water-table on dunes (Ranwell, 1959). Transition areas have a mixture of xeric and more mesic species, not a completely different flora. Several types of community present at the same flooding index at Braunton Burrows, however, suggests that other factors besides water table level affect the vegetation of any given site. Such factors may include exposure, proximity to seed source, and climatic conditions

(Willis, et al., 1959).

The variable hydrology of the swale, then, exerts strong selective pressure on plant species, on both a holistic and microhabitat level. It is believed by many that water availability is the strongest selection factor in the swale environment (Crawford and Wishart, 1966; Jones and Etherington, 1971; Seliskar, 1990). Swale species are generally adapted to either an excess or deficiency of water. The fluctuation of the water table may well limit germination, growth, and establishment of nonadapted species in the swales (Lubke and Avis, 1982). The vegetation of the FCSP study sites reflects this pressure, as can be seen in the **Vegetation** section.

Climate

An important key to hydrology and plant distribution, as well as to the dune-building process itself, is the prevailing climatic conditions of the area. Factors involved in this are listed below.

Wind

Wind affects dune swales mostly as a vector for sand, which will eventually cover or expose swale habitat in a dune area. Godfrey (1977) reports prevailing winds in the FCSP area for 5 months of the year as north-northeast at approximately 5.5 m/s. During 5 spring and summer months, the winds are southwest at 5.1 m/s. During 2 months of the fall, the winds are northeast and south-southwest at 5.0 m/s (Godfrey, 1977).

Temperature

FCSP lies north of Cape Hatteras, which is a natural ecological break. This break is due to the warm oceanic winds, which keep the winter minimum temperature above 4 degrees F all season for Cape Hatteras and southward. FCSP, on the other hand, experiences 2-3 months, on average, during which temperatures can fall below 0 degrees F (Godfrey, 1977). Mean winter temperature at Cape Henry is around 45 degrees F (Oosting, 1954), and mean annual temperature is 60 degrees F (Wright, et al., 1990). Winter highs are around 50 degrees F, lows are around 30 degrees F, and the temperature range is from 5 degrees to 100 degrees F (Wright, et al. 1990). Relative humidity in the summer is around 90% (Wright, et al. 1990).

Precipitation

Precipitation at Cape Hatteras averages 1.3 m/yr., evenly spaced throughout the year (Godfrey, 1977). Wright, et al. (1990) reports 44.22 inches of annual rainfall, with slightly higher precipitation in August and somewhat lower precipitation in November and April, at Cape Henry. Significant rainfall occurs on 120 days per year at Cape Henry. FCSP, being not so far from the Cape, would have similar rainfall. Total yearly rainfall patterns, however, do not take into account that water table levels are likely to increase in winter, due to lower evapotranspiration rates. Godfrey (1977) states that the even distribution of precipitation throughout the year should rule out water stress as a plant distribution factor. However, higher evapotranspiration rates in the summer, due to increased bioactivity and temperature, will lead to water stress under low precipitation conditions due to a depletion of the water table (pers. obs.).

Storms

Storm frequency determines the frequency of overwash and dune erosion. Godfrey (1977) reports that the coastal area from southeastern North Carolina to New England is highly susceptible to storms, including cyclones which create heavy surf, storm surges, and high winds. Cyclones of the late summer and fall follow the Atlantic coast northward from the Caribbean. Winter and early spring storms come from the southeastern coast and move northward (Godfrey, 1977). The effects of the storms on swale habitats may include flooding due to high precipitation, oceanic overwash of swales near the primary dune, or salt spray carried far inland by high winds (Hosier, 1991).

Tide range

The tidal stage and tidal range at the time of a storm affect the overwash and erosion potential of that storm. The tidal range in Virginia is rarely more than one meter (Godfrey, 1977). This indicates that there is no oceanic overwash into swales and no saltwater contamination of groundwater during normal tidal activity.

Soil

Soils in FCSP swale areas are, with the exception of higher nutrient values (see **Soil Nutrients**), much like the soils of the dunes. They consist of fairly coarse yellow sand, moistened by the water table and occasionally crusted with a very thin layer (1-2 mm) of organic material (pers. obs.)

Older swale areas in other areas typically have a high humus content due to the slow decomposition of plant material in the reducing conditions of the moist swale soil. An increase in vegetation leads to an increase in organic debris. The slow buildup of organic matter in a swale lowers the pH of the moist swale soil steadily (Lubke and Avis, 1982). This reducing chemistry leads to a gleying of the B horizon of the soil over the course of hundreds of years (Hosier, 1991; Ranwell, 1959; Willis, 1959). The study sites at FCSP, however, have not had enough time to develop these types of hydric soils. The dune system has been active since the 1930's, and all of the present topography has developed since that time (Hennigar, 1977). The soils of FCSP swales, therefore, are very young, undeveloped soils. There is no organic muck, as is found in slacks of Great Britain (Crawford and Wishart, 1966; Jones and Etherington, 1971; Willis, et al., 1959) or in the swales studied at the Park by Ludwig in 1990, the pH values are high for a wetland ecosystem (Perry, pers. comm.), and there is no distinct gleying of the B horizon (pers. obs.). As time progresses, the soils will become more organic (Ranwell, 1959), and the reducing conditions in the soil will lower the pH and cause the gleying of the soil so indicative of a wetland. Of course, this scenario only holds true if the present conditions remain in place. Zoladeski (1991) described the major factor limiting vegetation in the slacks of Leba Bar to be the instability and infertility of the sand, with moisture being a secondary factor. Should dune destabilization occur at FCSP due to human activity, overgrazing by wild horses and pigs, or natural disaster, the sands will be free to build a new dune and swale system with new soils and altered hydrology.

Soil Nutrients

The primary sources of nutrients in the swale soil are rainfall and salt aerosols (Hosier, 1991). Salt spray, however, may not be an important factor to soil nutrients or plant salt tolerance. Most salt spray is dropped on the foredune, and most of the remaining airborne salt is carried to the face of the reardune, with little salt dropped in the intervening swale areas (Oosting and Billings, 1942). Salt content of soil measured by Oosting and Billings (1942) was less than 1.81 mg salt per 100 g of soil, not enough to affect the plants chemically or osmotically. With the exception of calcium, which may be released due to weathering of shell material, no nutrients are contributed by the sandy parent material of the soil. The soils of these study sites are characteristically poor in nutrients, but with a significant increase in soil nutrients (except phosphorous) from dune to swale (see **Results**). This is in keeping with results from other swale soil studies (Crawford and Wishart, 1966; Ranwell, 1959; Salisbury, 1952; Willis, et al., 1959). However, in contrast to these findings, the soils of the FCSP sites are not gleyed (see **Soils**), nor are the nutrient values as high. The reason for this is simply that nutrients found in the swales have been leached into them from dune soils by rainwater (Hosier, 1991; Ranwell, 1959; Willis, et al., 1959). The dune system at FCSP has only been active since the 1930's (Hennigar, 1977), so the "new" dune soil has not yet been so highly leached, and these leachates have not had the chance to build up in the swales.

Another reason for higher nutrients in swale soils of former studies is the buildup of organic matter. Waterlogged conditions of the soil allow for the slow decomposition of plant material, including dead leaves and roots of annuals (Ranwell, 1959), thereby enriching the soil. The earlier developmental stage of the dunes and swales of FCSP, then, accounts for the lower nutrient levels found there.

Nevertheless, nutrient levels do differ somewhat between sites at FCSP. There is some evidence (Willis, 1963) that changes in nutrient status of swale soils will change the composition of the vegetation found therein. Crawford and Wishart (1966) described ten distinct swale types at their study site in Scotland. These types were based on soil moisture and salinity (see **Vegetation**), but trends in swale nutrients were noted and graphed. These findings led to the graphing of nutrient data from the FCSP sites. Even though there were no statistically significant differences between sites for any given nutrient, there is a distinct trend in the graphed data. Site #4 is consistently more nutrient-rich than the other sites. This site is low and wet, and is the only site in which *Salix nigra* and *Juncus roemerianus* were noted, although the latter did not fall on a transect.

Soil nutrients in dune systems come occasionally from overwash (Boyce, 1954; Hosier, 1991). It has been suggested (Tyndall and Levy, 1978) that oceanic overwash is responsible for isolated stands of *Juncus roemerianus* behind the foredunes. Since *J. roemerianus* is found in site #4, and *J. roemerianus* is a brackish-water species, it would seem logical that oceanic overwash occurred in the site at some point, allowing the species to establish itself while increasing soil nutrients. Along the same lines, and even more plausible theory is that dune building at FCSP took place after major dune destabilization (Hennigar, 1977), thus allowing sand to build up on previously stabilized areas. In this case, perhaps site #4 was previously a brackish-water marsh, like many along the Virginia coast. The subsequent buildup of sand into dunes and blowout into swales brought the sandy swale soil in contact with the water table. This water table, as it fluctuates throughout the year, brings nutrients up from the rich organic marsh soil into the otherwise poorer swale soil. Recession of the water table then leaves the swale soil enriched (Hosier, 1991; Willis, 1959).

Rare Species

No assessment of interdunal vegetation at FCSP would be complete without mention of the rare and watched plants contained in the swale sites. The unique habitat afforded by the low, wet, sheltered swales plays host to many species which are not found in any abundance elsewhere in the Commonwealth (Ludwig, 1991). In 1990, a team from Virginia Natural Heritage surveyed the Park for rare species and found 30 of note. Of those, 11 were found in swale areas. In the current study, five rare species were identified, including: *Cyperus haspan, Drosera intermedia, Erigeron vernus, Ludwigia brevipes,* and *Rhynchospora fascicularis*. With the exception of *Ludwigia brevipes*, which I was unable to relocate at any site, all of these species have been collected and duly recorded. It should be noted that while these species are rare, all were well represented in the swale flora except *L. brevipes*.

As an index of the current status of these plants, the Commonwealth-published Natural Heritage Resources of Virginia: Rare Vascular Plant Species (Ludwig, 1991) was consulted. Rare plants include *Erigeron vernus, Ludwigia brevipes,* and

Rhynchospora fascicularis. Each of these has a global ranking of G5, meaning that there is no particular threat to these species on a global scale. On the state level, these each rank S2, meaning that they are

> very rare and imperiled with 6 to 20 occurrences or few remaining individuals in Virginia, or because of some factor(s) making it vulnerable to extirpation in Virginia. (Ludwig, 1991)

Each also has an RSC notation for its entry, meaning Recommended Special Concern. Since the swales of False Cape are special habitats, as noted previously, the presence of these species here when they are rare elsewhere in the Commonwealth is not altogether surprising.

Also occurring in the study sites are plants on the Virginia Natural Heritage Watch List (Ludwig, 1991). These species include *Drosera intermedia, Hudsonia tomentosa, Lechea maritima, Oenethera humifusa,* and *Solidago fistulosa*. Each rates a G5 global ranking, per above, and an S3 state ranking. The S3 ranking indicates

> rare to uncommon in Virginia with between 20 and 100 occurrences; may have fewer occurrences if found to be common or abundant at some of these locations; may be somewhat vulnerable to extirpation in Virginia. (Ludwig, 1991)

Again, the location and physical processes of the swale sites make it a suitable habitat for these plants which are unable to occur in abundance in other parts of the Commonwealth.

Succession

Succession in swale areas begins on bare, damp sand and is considered a truncated hydrosere (Ranwell, 1959). As soon as sand is cleared away at the foot of a receding parabolic dune, seeds carried in by wind or birds will colonize the damp exposed soil. Alternatively, swales may begin as blowouts during the dry summer months, leaving bare moist patches of sand. These areas may flood in the fall and winter, allowing algal growth. when the ponds dry, this algae may help bind the soil into a suitable substrate for mosses. After the mosses, rushes, grasses, and sedges may come in. Species needing the shelter of other plants, such as *Hydrocotyle*, will establish themselves after that (Willis, et al., 1959). The grass, rush, and sedge communities, no matter how they begin, may become thick enough to exclude species of trees and bushes, thus becoming an herbaceous climax (Willis, et al., 1959). On the other hand, invasion by trees and shrubs may lead to a maritime forest climax.

With organic material increasing in the swales and hydrology remaining essentially the same, the flora should become more diverse at the FCSP sites. This prediction, however, is based on the assumption that trees will not take over the sites. Ranwell (1959), Willis et al. (1959), and Crawford and Wishart (1966) found that the dune systems of Great Britain were stable, and the particular soils and hydrology of their study sites did not allow the invasion of these sites by native trees. The loblolly pine, *Pinus taeda*, however, is a facultative wetland (FAC) species in Virginia (Perry, pers. comm.). In the sheltered swale areas behind the dunes with minimal salt spray and/or overwash, there is no foreseeable reason why they should not become established. In fact, some pines have already been located at the swale sites. Also noted at the FCSP sites is live oak, *Quercus virginiana*, which in the absence of salt spray can form a climax maritime forest (Oosting, 1954; Tyndall and Levy, 1978; Wright, et al., 1990) with other oak species such as the *Quercus laurifolia* found in the remaining maritime forest of FCSP. *Quercus virginiana* is fairly shade and salt-spray tolerant, and can become quite abundant in xeric dune or swale sites (Tyndall and Levy, 1978). Paucity of trees in swale areas may be due to salt spray effects (Willis, et al., 1959), and or deer browsing (Tyndall and Levy, 1978). The former affects *Q. virginiana* to a lesser degree than it affects *Pinus taeda*. The result is that *P. taeda* may be easily outcompeted by *Q. virginiana* in drier, more exposed sites (Tyndall and Levy, 1978), leading quickly to a maritime forest climax. It may be that the only way to maintain the herbaceous swale habitat at FCSP is through continuous dune-building activity. Only time will tell whether the present swale community is a viable long-term vegetation type in this area.

Ludwig (1991) points to invasion of swale areas by *Phragmites australis*, the common reed, as a possible threat to natural vegetation at the FCSP swale sites. It is this researcher's belief that the hydrology is not suitably wet year-round to support such a genetically large hydrophyte. However, should such invasion take place, the succession to a maritime forest climax could be severely altered.

Other Areas

In order to place the composition of the FCSP swale vegetation and flora in context, studies of swale vegetation in the United States and worldwide were examined (Appendix D). Based on the review of the studies summarized in Appendix D, the swales at FCSP seem on inspection to be more closely related floristically to the swales to their immediate north than to the barrier island swales of North Carolina. Additionally, the types of plants found in the FCSP swale sites are found in swales and slacks worldwide, showing the distinctiveness of this community type; dominated by rushes and sedges in the wetter areas, and grasses in the drier areas, with occasional bushes and/or small trees for good measure.

CONCLUSION

Odum and Harvey (1988) point out that freshwater interdunal swales are fragile, unique ecosystems which must be managed wisely to avoid their loss. Withdrawal of water from an aquifer near a swale area can greatly lower that swale's water table (Odum and Harvey, 1988), thus altering, or even destroying that swale area's vegetational community. Swale habitats are rare in Virginia, and activities which seek to bulldoze or dredge dune and swale areas can be devastating to the few remaining swale areas in the state. Development of areas such as Virginia Beach and Chincoteague Island have already caused irreparable damage to these habitats (Odum and Harvey, 1988). The fate of the FCSP swale sites depends largely on wise management of the area.

Appendix A
Regional and National Wetland Indicator Status of FCSP Species

	Regional	National
Acer rubrum L.	FAC	FAC
Andropogon virginicus L.	FACU	FACU,FACW
Bulbostylis capillaris (L.) C.B. Clarke	FACU	FACU,FAC
Centella asiatica (L.) Urban	FACW	FACW
Cyperus haspan L.	OBL	OBL
Dichanthelium scoparium (Lam.) Gould	FACW	FACW,FAC
Diodia teres Walter	NOT LISTED	
Diodia virginiana L.	FACW	FACW,OBL
Diospyros virginiana L.	FAC-	FACU,FAC
Drosera intermedia Hayne	OBL	OBL
Drosera rotundifolia L.	OBL	OBL
Eleocharis quadrangulata (Michx.) Roem.	OBL	OBL
Erianthus giganteas (Walter) F.T. Hubb.	FACW+	FACW,FACW+
Erigeron vernus (L.) Torr. & Gray	OBL	OBL
Eupatorium hyssopifolium L.	NOT LISTED	
Eupatorium rotundifolium L.	FAC-	FAC-,FAC
Hudsonia tomentosa Nutt.	NOT LISTED	
Hydrocotyle umbellata L.	OBL	OBL
Hypericum gentianoides (L.) BSP	NOT LISTED	
Juncus biflorus Elliott	FACW	FACW
Juncus canadensis J. Gay ex LaHarpe	OBL	OBL
Juncus scirpoides Lam.	FACW	FACW,FACW+
Lechea maritima Leggett	NOT LISTED	
Leersia oryzoides (L.) Swartz	OBL	OBL
Linaria canadensis (L.) Dum.-Cours.	NOT LISTED	

Ludwigia brevipes B. Long ex Britton	OBL	OBL
Lycopodium appressum (Chapm.) Lloyd	FACW+	FACW+,OBL
Myrica cerifera L.	FAC	FAC,FAC+
Myrica pennsylvanica Loiseleur	FAC	FAC
Panicum amarum Elliot	FACU-	FACU-,FAC
Panicum dichotomiflorum Michx.	FACW-	FACW-,FAC
Panicum virgatum L.	FAC	FAC,FACW
Pinus taeda L.	FAC-	FAC,UPL
Polysticum commune var. perigonale	NOT LISTED	
Proserpinaca palustris L.	OBL	OBL
Quercus virginiana Mill.	FACU	FACU,FACU+
Rhexia mariana L.	OBL	FACW+,OBL
Rhynchospora fascicularis (Mich.) Vahl	OBL	FACW+,OBL
Salix nigra Marshall	FACW+	UPL,OBL
Scirpus americanus Pers.	OBL	OBL
Solidago fistulosa Mill.	FACW	FAC+,FACW
Solidago microcephala	NOT LISTED	
Sphagnum sp.	NOT LISTED	
Toxicodendron radicans (L.) Kuntze	FAC	FACU,FACW
Vaccinium corymbosum L.	FACW-	FACW-,FACW
Viola lanceolata L.	OBL	OBL
Xyris jupicai L.C. Rich.	OBL	OBL

Appendix B
Distribution of FCSP Species

NOTE: N=northern, S=southern, C=coastal, W=western, *=widespread

	Distribution
Acer rubrum L.	*
Andropogon virginicus L.	*
Bulbostylis capillaris (L.) C.B. Clarke	*
Centella asiatica (L.) Urban	C
Cyperus haspan L.	VA only
Dichanthelium scoparium (Lam.) Gould	C,S
Diodia teres Walter	*
Diodia virginiana L.	*
Diospyros virginiana L.	*
Drosera intermedia Hayne	*
Drosera rotundifolia L.	N
Eleocharis quadrangulata (Michx.) Roem.	S
Erianthus giganteas (Walter) F.T. Hubb.	S
Erigeron vernus (L.) Torr. & Gray	C,S
Eupatorium hyssopifolium L.	C
Eupatorium rotundifolium L.	*
Hudsonia tomentosa Nutt.	N
Hydrocotyle umbellata L.	*
Hypericum gentianoides (L.) BSP	*
Juncus biflorus Elliott	*
Juncus canadensis J. Gay ex LaHarpe	N
Juncus scirpoides Lam.	*
Lechea maritima Leggett	N,C
Leersia oryzoides (L.) Swartz	*

Linaria canadensis (L.) Dum.-Cours.	*
Ludwigia brevipes B. Long ex Britton	C,S
Lycopodium appressum (Chapm.) Lloyd	C
Myrica cerifera L.	C,S
Myrica pennsylvanica Loiseleur	N,C
Panicum amarum Elliot	C
Panicum dichotomiflorum Michx.	*
Panicum virgatum L.	*
Pinus taeda L.	S
Polysticum commune var. perigonale	*
Proserpinaca palustris L.	C
Quercus virginiana Mill.	C,S
Rhexia mariana L.	*
Rhynchospora fascicularis (Mich.) Vahl	C,S
Salix nigra Marshall	*
Scirpus americanus Pers.	*
Solidago fistulosa Mill.	C,S
Solidago microcephala	S
Sphagnum sp.	
Toxicodendron radicans (L.) Kuntze	*
Vaccinium corymbosum L.	*
Viola lanceolata L.	C,S
Xyris jupicai L.C. Rich.	C,S

SOURCE: Gleason, H.A, and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United states and Adjacent Canada, 2nd ed. New York: New York Botanical Garden. 910 pp.

Appendix C
Diversity Indices for Sites Over the Study Time

The table below compares the diversity indices (D.I.'s) for all sites over the course of the summer. Note the lower D.I. values in site 6 at each sampling time. All other sites are in the same statistical population subset, and therefore not significantly different at the 95% confidence level.

Site	**2**	**3**	**4**	**5**	**6**	**7**
Sample						
May-June	2.9134	2.8018	2.8830	2.8262	2.7502	2.8659
June-Jul	2.9701	2.8645	2.8675	2.8666	2.6165	2.9005
July-Aug	2.9809	2.9196	2.8907	2.9427	2.7200	2.8741
Aug-Sept	2.9868	2.9775	2.9348	2.8582	2.6776	2.8694

Appendix D
Comparison of FCSP Flora with the Floras of Other Swale Areas

In order to have a floristic background against which to compare the vegetation of FCSP,studies of swale vegetation in the U.S. and elsewhere are reviewed in this Appendix.

United States

North Carolina

The classification of North Carolina wetlands includes a listing for Maritime Wet Grassland, which is roughly similar in parameters to the swale sites at FCSP, although this classification also includes interdunal areas which are subject to overwash. These herbaceous areas are usually dominated by *Spartina patens, Fimbristylis spp.,* or *Muehlenbergia filipes*, showing a more saline association of the flora. Some conspecifics include *Scirpus americanus, Andropogon virginicus, Diodia virginica, Hydrocotyle umbellata, Panicum spp., Xyris jupicai, Centella asiatica,* and *Rhexia mariana* (Schafale and Weakley, 1990). Sixteen other typical species of North Carolina swale areas were not found in the FCSP sites. The findings of Godfrey and Godfrey (1976) at Cape Lookout show those swales to be somewhat similar to FCSP sites, but also with a more saline set of dominants.

Maryland

No information was available on swale areas of Maryland.

Delaware

Swale areas of Delaware occupy a thin strip from Cape Henlopen in the north to Fenwick Island to the south. Many of these areas have been threatened and/or destroyed by beach development (Clancy, pers. comm.). Conspecifics include *Acer rubrum, Andropogon virginicus, Drosera intermedia, Juncus biflorus, Juncus canadensis, Juncus scirpoides, Lycopodium appressum, Ludwigia spp., Myrica cerifera, Panicum virgatum, Pinus taeda, Proserpinaca palustris, Rhus radicans, Solidago fistulosa, Sphagnum spp., Vaccinium corymbosum,* and *Viola lanceolata*. Thirty other listed species were not found at FCSP. Of those thirty, eight are congeneric. the species present in Delaware swale sites are less saline than those of North Carolina, and therefore more closely allied to the FCSP swale communities.

New Jersey

The interdunal communities of New Jersey take the form of Coastal Interdunal Marshes (Breden, 1989). These areas, quite unlike the FCSP sites, are dominated by *Typha latifolia, Phragmites australis, Hibiscus palustris,* or *Thelypteris palustris*, all freshwater marsh dominants. Conspecifics include *Andropogon virginicus, Cyperus filicinus, Scirpus americanus, Toxicodendron (Rhus) radicans, Vaccinium corymbosum, Myrica pennsylvanica,* and *Acer rubrum*. Eleven other typical species are not found at FCSP. Of these eleven, three are congeneric, despite the more marshy association of species.

New York

Ecological Communities of New York State (Reschke, 1990) has a listing for Maritime Interdunal Swales, which are dominated by sedges and herbs with occasional low shrubs. These areas vary in size and species composition. Characteristic species include *Cladium mariscoides, Cyperus spp., Rhynchospora capitellata,* and *Juncus canadensis*. Conspecifics include *Cyperus spp., Juncus canadensis, Drosera rotundifolia, Myrica pennsylvanica,* and *Vaccinium corymbosum*. Five other characteristic species do not occur at the FCSP sites. Of these five, four are congeneric

Connecticut

There is limited dune activity in Connecticut, and no work has been done on these habitats (Kenneth Metzler, pers. comm.).

Rhode Island

Again, there is no swale habitat in Rhode Island (Thomas Rawinski, pers. comm.).

Massachusetts

Interdunal areas of Massachusetts take the form of cranberry meadows (Benedict, 1977; McDonnell, 1979)/ Conspecifics include *Sphagnum spp., Scirpus americana, Juncus spp., Drosera rotundifolia, Acer rubrum,* and *Vaccinium corymbosum*. Twelve other characteristic species do not occur at the FCSP sites. Of these, three are congenerics.

The Cape area of Massachusetts has interdunal thickets of *Myrica cerifera, Rosa rugosa, Prunus maritima,* and *Rhus radicans* (Moul, 1969). The herbaceous wet depressions are dominated by *Festuca rubra* and *Spartina patens*, and share no conspecifics with the FCSP sites. It is likely that these areas are more saline than the FCSP sites.

Maine

Maine has a very rocky coast, and is unsuitable for the type of dune-and-swale topography of much of the rest of the Atlantic coast.

South Carolina, Georgia, Florida

The beach dynamics of these southern states are such as to create long, flat beaches, often with extensive tidal marshes (Silberhorn, pers. comm.). These forces are not proper for creating a dune-and-swale topography.

Other Areas (Worldwide)

Other countries around the world have dunes and swales. The best studied examples are in Great Britain and the Netherlands. Studies have also been done in Poland and South Africa. While it is very unlikely to have conspecifics between these sites and the FCSP sites, it is exciting to note the number of congenerics present, thus showing a distinct similarity between these habitat areas worldwide.

Great Britain

Willis, et al. (1959) found congenerics *Erigeron, Eleocharis, Juncus, Linaria, Linum, Oenothera, Salix, Viola,* and the lichen *Cladonia* in the Braunton Burrows sites. Ranwell (1959) additionally found *Hydrocotyle* at the Newborough Warren sites, although these sites were more floristically depauperate than the Braunton Burrows sites. Crawford and Wishart (1966) found *Salix, Juncus, Hydrocotyle,* and *Cladonia* at their Tentsmuir sites.

Poland

The Polish slacks described by Zoladeski (1991) are particularly interesting to this study because of the two conspecifics, *Polytrichum commune var. perigonale* and *Drosera intermedia*, found there. Other congenerics include *Salix, Linaria, Juncus, Pinus, Vaccinium,* *Lycopodium,* and *Cladonia*.

South Africa

Lubke and Avis (1982) report rather sparsely-vegetated slacks in South Africa. These slacks, however, do have congenerics *Myrica* and *Scirpus*.

In summary, the swales at FCSP seem on inspection to be more closely related floristically to the swales to their immediate north than to the barrier island swales of North Carolina. Additionally, the types of plants found in the FCSP swale sites are found in swales and slacks worldwide, showing the distinctiveness of this community type; dominated by rushes and sedges in the wetter areas, and grasses in the drier areas, with occasional bushes and/or small trees for good measure.

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