Fall 1977

Plant Distribution and Succession Within Interdunal Depressions on a Virginia Barrier Dune System

Robert Wayne Tyndall
Old Dominion University

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PLANT DISTRIBUTION AND SUCCESSION WITHIN INTERDUNAL DEPRESSIONS

ON A VIRGINIA BARRIER DUNE SYSTEM

by

Robert Wayne Tyndall

A Thesis Submitted to the Faculty of Old Dominion University
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCES

BIOLOGY

OLD DOMINION UNIVERSITY

December, 1977

Approved by:

Gerald F. Levy (Chairman)

Lytton J. Musselman

Harold G. Marshall
ABSTRACT

PLANT DISTRIBUTION AND SUCCESION WITHIN INTERDUNAL DEPRESSIONS ON A VIRGINIA BARRIER DUNE SYSTEM

Robert Wayne Tyndall
Old Dominion University, 1977
Chairman: Gerald F. Levy

A unique series of interdunal depressions was recognized on the barrier dune system of southeastern Virginia. Plant distribution and succession, and environmental factors controlling them, were studied in the series. Plant community distribution appears to be predominantly controlled by soil moisture, interspecific competition, and feral hog disturbance. Both biotic and physiographic succession are apparent with Quercus virginiana probably climax for both. Salt spray and feral hog and migratory waterfowl activity are important controlling factors of plant succession. Results indicate that the zonal appearance of shrubs and trees on the Virginia and North Carolina coasts is due to the absence of arborescent forms in medium to high salt spray areas because of their intolerance to salt spray. Evidence suggest that soil moisture deficiency is a major factor in determining perennial foredune constituents and that foredune-grass, shrub, and tree zones are not progressive seral stages on stable or degrading sea coasts.
ACKNOWLEDGEMENTS

Appreciation is extended to Dr. Gerald F. Levy for his assistance in the field and in the preparation of this manuscript. Special thanks are extended to Ms. Robin Fields, wildlife biologist for the Back Bay National Wildlife Refuge, who made access to the study areas possible and also to Mr. Warren Beatty, BNWR security officer, for his friendliness and good company after many scorching days of work. Appreciation is also expressed to Dr. Lytton J. Musselman and Dr. Harold G. Marshall for their critical review of this thesis.

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INTRODUCTION

Aerial infrared photographs (1974) revealed a unique series of interdunal depressions on the barrier dune system of southeastern Virginia between the paralleling fore- and reardunes of the Back Bay National Wildlife Refuge and the False Cape State Park (Fig. 1). The uniqueness of the series was attributed to abiotic and vegetative variability not found in any other depression group in this dune system and the contiguous North Carolina Outer Banks.

Depressions are generally bowl-to-saucer shaped with semi-circular-to-irregular perimeters. Depression widths range from ten to 60 m, lengths from ten to 225 m, and depths from 0.5 m below to more than 1 m above maximum water table level. Four of the northernmost depressions in the series are shown in Fig. 2.

This study attempted to determine major plant distribution and succession patterns in the depressions and major ecological forces governing them. Results were also used to help explain plant distribution and succession dynamics on Virginia and North Carolina barrier dune systems.

History

In 1938, the northern study area in Fig. 1 consisted of a barren sand flat westward of a natural foredune (Back Bay Nat. Wild. Ref. Narr. Rept. May-July 1938). Depression formation was apparently initiated by foredune stabilization conducted by the Civilian Conservation Corps. By August 1940, foredune height exceeded 4 m in certain areas.
Fig 1. Location of study areas. The series of interdunal depressions occurring between the fore- and reardunes of the Back Bay National Wildlife Refuge and the False Cape State Park is located in the northern study area. The southern study area represents the location of an interdunal depression, also included in the study, but not part of the series.
Fig. 2. Color infrared photograph showing four of the northernmost depressions in the series.
(Narr. Rept. August 1940). Subsequent establishment of a similar, paralleling dune system west of the foredune (presently not separated by more than 125 m) apparently restricted depression development to the area between these dune systems.

Although wind appears to have been the primary generative force, alluvial sand patterns visible in a 1949 Soil Conservation Service aerial photograph suggest oceanic overwash as a secondary factor. This theory is supported by the presence of isolated stands of *Juncus roemerianus*, a brackish-water marsh dominant, in some depressions. Alluvial patterns are not visible in 1959 and later photographs.

Topographic changes within the series have been substantial, as can be seen from tracings of 1949, 1958, and 1974 Soil Conservation Service photographs (Fig. 3). Depressions have been created, modified, and filled, apparently by the movement of dunes originating in the foredune area. The reardune appears to have remained relatively stable.
Fig. 3. Tracings of 1949, 1958, and 1974 Soil Conservation Service photographs illustrating topographic changes in the depression series. Darkened areas represent depressions. Numbers 1-5 signify intensively studied depressions.
LITERATURE REVIEW

Interdunal depressions are common physiographic features of sea coasts. They have been reported from the Virginia coast (Kearney 1901), the North Carolina Outer Banks (Lewis 1917, Oosting and Billings 1942, Engels 1952, Bordeau and Oosting 1959, and Stalter 1974), the barrier strands of New Jersey (Chrysler 1930 and Martin 1959) and Mississippi (Penfound and O'Neill 1934 and Pessin and Burleigh 1941), as well as the coast of England (Birse 1958 and Willis et al. 1959). A large variety of vegetational associations are reported in the literature.

Martin (1959) described the composition of freshwater marsh communities within depressions on Island Beach, New Jersey as extremely variable. Some of the communities were characterized by a dominance of one or a few species. Others were composed of numerous species none of which were obviously dominant.

Kearney (1901) reported "middle dune" depressions near Ocean View, Virginia as being occupied by xeric species such as Oenothera humifusa, Euphorbia polygonifolia, Triplasis purpurea, Mollugo verticillata, Diodia teres, and Monarda punctata while other depressions were inhabited by marsh species Juncus scirpoïdes, J. dichotomus, Scirpus americanus, and Fimbristylis spadicea. (Original nomenclature has been retained throughout this manuscript to allow independent interpretations.) "Dune marshes" at Cape Henry and at an area
south of Virginia Beach were characterized by *Centella asiatica*, *Hydrocotyle umbellata*, *Drosera intermedia*, *Lycopodium inundatum*, and *Eragrostis infracta*.

On Shackleford Bank of the North Carolina Outer Banks, Lewis (1917) found *Ludwigia palustris*, *Pluchea foetida*, *P. camphorata*, and *Cyperus haspan* dominant in depressions that were characterized by standing water and poor drainage. Similar areas that were subjected to highest winter tides were dominated by *Proserpinaca palustris* and *Aspidium Thelypteris* while *Cladium jamaicense* and *Kosteletskyia virginiana* were dominant in well drained areas.

On Bogue Bank, North Carolina, *Fimbristylis castanea* and low clumps of *Myrica cerifera* predominated in depressions that approached the water table (Oosting and Billings 1942). Those that were periodically inundated with seawater were dominated by *Spartina patens*.

Moist to partially submerged depressions alternating with dune ridges on Cat Island, Mississippi possessed either fresh or salt grass-sedge-rush marshes depending upon their distance from the sea (Penfound and O'Neill 1934). Other depressions were dominated by *Andropogon maritimus* and *Centella repanda* while still others were characterized by *Cyperus lecontei* and *Hydrocotyle bonariensis*. On Horn Island, Mississippi, Pessin and Burleigh (1941) reported grass-sedge-rush communities in moist and poorly drained depressions while xeric ones were characterized by dune plants. Grass-sedge-rush-willow communities were found in low-lying slacks and hollows between the coastal dunes at Braunton Burrows, England by Willis et al. (1959).

Theories explaining intra-depressional plant distribution and inter-depressional composition variability are few. Martin (1959),
after a study on Cat Island, Mississippi, stated that "measurements of water table, groundwater pH, groundwater salinity, and substratum composition failed to reveal any obvious environmental gradient along which these variations in composition might be arranged". Costing and Billings (1942) stated that those blowouts on Bogue Bank dominated by Spartina patens were "... unquestionably related to periodic inundation by salt water during storms and high tides" while those moistened with seepage water were dominated by Fimbristylis spadicea. Stalter (1975) suggested that water table depth influenced species distribution in freshwater depressions on the Isle of Palms, South Carolina.
METHODS

Studies began in November 1974 and ended in December 1976. Throughout this period, a floristics list was compiled for the entire depression series. Voucher specimens were deposited in the Old Dominion University Herbarium (ODU). Nomenclature follows Radford et al. (1968) and Breil (1973).

Vegetational Data Collection

Depressions 1-3 (Fig. 3) and six (the southern study area in Fig. 3) were selected to study objectively the distribution, sizes, and ages of shrubs and trees. Selection of depressions 1-3 was based upon their collective possession of all major differences of each of these categories in the entire series. Depression six, although not a member of the series, was studied similarly because of significant shrub and tree compositional differences and its greater distance from the ocean (400 m) as compared to depressions 1-3 (between 160-220 m).

Average diameter of frutescent and arborescent stems was measured at ground level (dgl), by species, in 0.5 x 1.0 m quadrats located contiguously along transects established in the following manner. The lowest point near the middle of depressions one and three was located by measuring winter standing water. A randomly selected compass degree was used to orient a transect extending from this point to about 1 m beyond the depression perimeter. The perimeter was defined subjectively as the area which increased significantly in slope from
the inner region of a depression and was bounded at a higher elevation by plants belonging to the adjacent dune community. Five transects were established at 60° angles in depression one while three transects, 120° apart, were established in depression three. A bisecting transect was established in depression two with largest Prunus serotina individuals on the east and west sides serving as reference points. In depression six, a bisecting transect was randomly positioned using a compass and random numbers table. All transects were marked at 2 m intervals. The varying number of transects per depression was due to differing size, shape, and apparent vegetational homogeneity of each.

Increment borings were taken from shrubs and trees of different sizes and at different locations along depression two and six transects to allow age comparisons of these forms among different sections of the depressions. Age differences of shrubs and trees among different areas of depressions one and three could be sufficiently determined subjectively.

Depression four (Fig. 3) was included in the study because of a significant difference in shrub distribution and its closer proximity to the ocean (100 m). The distribution of shrubs was determined subjectively.

To determine relative ages of dominant perimeter shrubs and trees of the series, increment borings were taken from seven *P. serotina*-*M. pensylvanica* and eight *Baccharis halimifolia*-*M. pensylvanica* "pairs". A "pair" was defined as individuals occurring within 0.5 m of each other. Utilization of several depressions was necessary to satisfy this criterion.

Depressions one and three were utilized for the synthesis of
artificial herbaceous communities. These depressions were utilized because of their collective possession of all major, visibly recognizable, vegetation patterns in the series.

Stem counts were made, by species, for presence and density data in each of two, 4 x 20 cm quadrats randomly located in each meter interval of each transect previously laid for shrub measurements. The long axis of the quadrat was laid parallel to the transect (Bormann 1953). Due to uncertainties associated with subjectively determining non-perimeter community boundaries in the field, a complete accounting of all species belonging to each non-perimeter community was not attempted. However, almost all components of each non-perimeter community were believed to have been sampled.

Characteristic herbaceous species of depressions two, four, six, and mid-region of depression five (Fig. 3) were determined subjectively. The mid-region of depression five was observed periodically because of signs of feral hog and migratory waterfowl activity.

Vegetational Data Analyses

It was impossible to plot graphically individual shrubs in perimeters of depressions 1-3 because of high stem densities and sand burial. Therefore, presence and size data were used to calculate frequency and sum basal area of each perimeter species sampled.

Synthetic herbaceous communities were delimited from Bray-Curtis (1957) multidimensional ordinations constructed using modifications of Beals (1960), Swan and Dix (1966), and Newsome and Dix (1968) with the exception that plots with similarity values equal to 50% were included. Sample plots on each transect were compared with each other on the basis of species presence. Only species with depression frequencies 5% or
greater were included.

Delimitation of artificial communities was based upon comparison of adjacent plots on ordination graphs. All compositionally unique groups of plots were separated. Groups of adjacent plots whose compositions were intermediate between unique groups were delimited with the exception of groups composed of only one or two plots. The latter were combined with the unique group to which they were most similar.

Environmental Data Collection and Analyses

Total soil moisture (expressed as percent of soil oven dry weight) in the upper 10 cm (predominant root zone) of depressions one and three was determined from samples collected monthly, April-August 1975, with a soil auger at 4 m intervals along each transect. Three surface-to-10 cm soil samples were collected from the perimeters of depressions four and six in November 1976. Soil was transported to the laboratory in sealed plastic bags, weighed within 36 hours, and oven dried at 105 °C for at least 48 hours. Hygroscopic water content was determined from randomly selected subsamples. Identical samples were used for soil texture measurements by the hydrometer method (Buoy-oucocos 1936). Inundated sampling points in depressions one and three were noted in November 1974 through November 1975.

After the delimitation of plant communities in depression one, ten surface-to-10 cm soil samples were collected for chemical analyses during November 1976 at randomly selected locations within each of the most unique plant communities. Five soil samples were also collected from the inner region of depression five and two samples each from the perimeters of depressions four and six. After air drying, soil samples were analyzed by the Virginia Truck and Ornamentals Research Station.
(Virginia Beach) for NO$_3$, total salts, and available K, Ca, P, and Mg and pH. Available Ca, P, and Mg were determined colorimetrically, K with a flame photometer, and pH with a glass electrode pH meter.

Mean and extreme values were calculated for total salts, NO$_3$, pH, and available Ca and Mg for the soils of the most unique communities of depression one, for the mid-region of depression five, and for the perimeter soils of depressions four and six. Difference between the means of each possible pair of mean values was statistically determined by use of Student's t-test. Variances for each set of values were compared by means of a variance ratio table to legitimize use of the t-test (Kershaw 1973).

Salt spray was measured on two occasions at 4 m intervals along each transect in depression one by means of salt spray traps made from 15 cm square pieces of cheesecloth stretched across wooden frames. Traps were positioned horizontally about 10 cm above herbaceous vegetation. In shrub dominated areas, one trap was positioned horizontally about 10 cm above the shrub canopy and one directly beneath it about 30 cm above the ground. For comparison, a salt spray trap was also established on the foredune and on the reardune opposite depression one.

Traps were exposed during two severe "northeaster" storms immediately after rain cessation. Traps set during the first storm were exposed for 105 hours during which the National Weather Service at the Norfolk International Airport reported N to S-SE winds of 1.3-5.8 m/sec (3-13 mph) for 93 hours and SW winds of 2.7 m/sec (6-12 mph) for the remaining 12 hours. Traps set during the second storm were exposed for 26 hours. Winds during the initial eight hours were reported from the N-NE decreasing steadily from 6.2-2.7 m/sec (14-6 mph) followed
by calm winds for the remaining 18 hours. A calibrated hand held
anemometer was used to compare Norfolk International Airport with
False Cape beach berm wind velocities and to compare foredune and
reardune wind speeds with those in the middle of depression one.

After exposure, the innermost 10 cm square sections were re­
moved with scissors, stored in sealed, sterilized bottles, and ti­
trated for total salts following the method described by Martin
(1959). Two unexposed cheesecloth squares were processed as con­
trols.

The t-test and the variance ratio table were used similarly
with the salt spray data of depression one to statistically determine
the difference between the means of each community.

Salinity of standing water in depressions one and five was
determined hydrometrically in February 1976.

Soil temperature was recorded at 4 m intervals along each
transect in depression three on a clear summer day (3 August 1975).
Temperatures were recorded at the surface and at depths of ten and
20 cm. Air temperatures were recorded concurrently.

Field Observations

Effects of storms upon vegetation was studied by examining plants
before and after storm occurrence. Offshore and onshore wind producing
storms were utilized.

Several depressions in the series were observed periodically
to study effects of migratory waterfowl and feral hog activity upon
vegetation. Deer occurrence in the entire series was noted during
every field trip.
RESULTS

The bryophytic and vascular flora of the entire depression series is listed in the appendix. The flora consists of at least 129 species representing 88 genera and 48 families.

Perimeter Woody Vegetation

Nearly every depression perimeter in the series was characterized by an almost uninterrupted thicket community dominated by *M. pensylvanica* and *Rhus radicans* as exemplified by depressions 1-3 (Figs. 2, 4-6 and Table 1).

*Myrica pensylvanica* averaged 1.2 years older than *B. halimifolia* and 3.3 years older than *P. serotina*. Age extremes of *M. pensylvanica*, *B. halimifolia*, and *P. serotina* were 7-11, 5-8, and 3-7 years, respectively. Canopy heights of the first two species were similar while *P. serotina* sometimes exceeded the others by 0.5 m. Although very few saplings of *M. pensylvanica* and *B. halimifolia* occurred beneath their canopies, both saplings and trees of *P. serotina* were almost always rooted under shrubs of either species. Shrub branches beneath *P. serotina* canopies possessed noticeably fewer leaves than those not associated with this species.

Depression six differed from all depressions in the series in that *P. taeda* grew abundantly in the perimeter (Fig. 7). Only several individuals were found in the entire series. Note in Fig. 7 that the age differential between *P. taeda* and *M. pensylvanica* was inconsistent.
Fig. 4. Winter photograph of depression one.
Fig. 5. Winter photograph of most of depression two.
Fig. 6. Summer photograph of depression three.
Table 1. Frequencies (F-%) and sum basal areas (B.A.-cm²/m²) of woody species sampled in 0.5 x 1.0 m contiguous plots located on the perimeters of depressions 1-3. Total number of plots sampled in depressions 1-3 were 67, 31, and 43, respectively.

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<td>Rhus radicans B.A.</td>
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<td>11.5</td>
<td>14.3</td>
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<tr>
<td>Baccharis halimifolia F</td>
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<td>77.4</td>
<td>-</td>
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<td>Prunus serotina B.A.</td>
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<td>Rubus sp. F</td>
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<td>Myrica cerifera B.A.</td>
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Fig. 7. Distribution and average dgl of shrubs and trees along the depression six bisect. Thicket boundaries are indicated by vertical slashes. Adjoining bars indicate presence in the same plot. Ages of selected individuals are shown above the appropriate bars.
Non-perimeter Woody Vegetation

Presence of *M. pensylvanica* and *M. cerifera* in non-perimeter areas was highly variable as exemplified by depressions 1-3 (Figs. 8-10) and four. *Myrica pensylvanica* occurred throughout the latter and no other shrubs or trees were present. Both species were always located within *S. patens* dominated areas with *M. pensylvanica* always occurring in lower density regions adjacent to thicket communities than *M. cerifera*. Neither species was found in portions of a depression possessing extremely dense stands of *S. patens*. Only a few *B. halimifolia* were found in non-perimeter regions of the series.

Largest shrubs in non-perimeter areas of depression two were *M. cerifera* with age ranges of 4-6 years (Fig. 9). The largest shrub in adjacent perimeter regions was an eleven year *M. pensylvanica*. Since differences between perimeter and non-perimeter dgl's were much larger in almost every other depression in the series, no other increment borings were made.

Trees were lacking in all non-perimeter areas of all depressions in the series with the exception of a few *Salix nigra* and *Populus heterophylla* individuals. Seedlings and saplings (dgl ≤ 2 cm) of *A. rubrum* and *Liquidambar styraciflua* were not infrequent and occurred in greatest numbers in *S. patens* dominated areas.

Depression six differed from all other depressions in that *P. taeda* and *Vaccinium corymbosum* grew in non-perimeter areas (Fig. 7). Note in Fig. 7 that the former was consistently older and larger than the latter.

Herbaceous Communities

Six herbaceous communities in depressions one and three were
Fig. 8. Distribution and average dgl of non-perimeter shrubs (i.e. *M. pensylvanica*) along two transects in depression one. No shrubs occurred along the other transects. Each transect originated in the lowest portion closest to the depression center. The edge of the thicket community is indicated by vertical dashes. Adjoining bars indicate presence in the same plot.
Fig. 9. Distribution and average dgl of non-perimeter shrubs along the depression two bisect. Thicket community boundaries are indicated by vertical dashes. Adjoining bars indicate presence in the same plot. Ages of selected individuals are shown above the appropriate bars.
Fig. 10. Distribution and average dgl of non-perimeter shrubs (i.e. M. cerifera) along depression three transects. Each transect originated in the lowest portion closest to the depression center. The edge of the thicket community is indicated by vertical dashes. Adjoining bars indicate presence in the same plot.
The image contains three graphs, labeled Transect A, Transect B, and Transect C. Each graph plots distance (m) on the x-axis and dry gill (cm) on the y-axis. Transect A shows a peak at around 16 m with a dry gill measurement of 6.0 cm. Transect B has multiple peaks at 16, 20, and 24 m, with dry gill measurements ranging from 2.0 to 4.0 cm. Transect C shows a peak at 24 m with a dry gill measurement of 5.0 cm.
delimited. Ordinations are presented in Figs. 11 and 12 and frequency and density calculations of component species in Tables 2 and 3. Distribution of each community is shown in Figs. 13 and 14. Utilization of the Z axis was helpful in only one case (Fig. 11, transect E). The Spartina dominated community was the only herbaceous community to occur in both depressions.

Spartina patens was at least the second most frequent herb in every perimeter sampled (Table 4) as well as almost every other depression perimeter. Other species sampled in depression 1-3 perimeters are listed in Table 4. Almost every species had very low frequencies.

Non-perimeter areas of depressions 4 and 6 were herbaceously characterized by S. patens, Andropogon virginicus, Lycopodium appressum, Juncus megacephalus, and Solidago tenuifolia. Perimeters of both possessed a few S. patens and Panicum amarulum individuals.

Environmental Parameters

Soil Moisture. Total soil moisture values (capillary plus hygroscopic), expressed as percents of soil oven dry weight, and standing water observations made in depressions one and three are plotted for each transect in Figs. 13 and 14 as are plant community distributions. Hygroscopic water averaged less than 1.0% of soil oven dry weight in both depressions.

In depression one (Fig. 13), the Scirpus-Hydrocotyle dominated community generally occurred in areas of highest soil moisture and longest flood duration. Following in order of decreasing moisture and flood length were the Spartina-Scirpus, Spartina, Andropogon, and thicket communities with the last never experiencing standing
Fig. 11. Ordination of depression one plant communities by transect. Each geometric symbol represents a compositionally unique plot, or plots with similar compositions, and the artificial community in which it occurred. Dominants of each community are:

- Scirpus americanus, Hydrocotyle umbellata
- Spartina patens, Scirpus americanus, H. umbellata
- Spartina patens
- Andropogon virginicus
Table 2. Frequencies (F-%) and densities (D-culms/m²) of species comprising the ordination derived communities of depression one. Total number of plots sampled in the Scirpus-Hydrocotyle, Spartina-Scirpus, Spartina, and Andropogon dominated communities are 71, 29, 39, and 13, respectively.

<table>
<thead>
<tr>
<th>Community</th>
<th>Scirpus-Hydrocotyle</th>
<th>Spartina-Scirpus</th>
<th>Spartina</th>
<th>Andropogon</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>D</td>
<td>F</td>
<td>D</td>
</tr>
<tr>
<td>Scirpus americanus</td>
<td>93.0</td>
<td>415.5</td>
<td>82.8</td>
<td>296.7</td>
</tr>
<tr>
<td>Hydrocotyle umbellata</td>
<td>71.8</td>
<td>431.3</td>
<td>75.9</td>
<td>313.9</td>
</tr>
<tr>
<td>Proserpinaca palustris</td>
<td>49.3</td>
<td>153.1</td>
<td>37.9</td>
<td>107.5</td>
</tr>
<tr>
<td>Eleocharis quadrangulata</td>
<td>42.2</td>
<td>484.2</td>
<td>10.3</td>
<td>90.3</td>
</tr>
<tr>
<td>Ludwigia palustris</td>
<td>22.5</td>
<td>44.0</td>
<td>20.7</td>
<td>30.1</td>
</tr>
<tr>
<td>Eleocharis parvula</td>
<td>21.1</td>
<td>-</td>
<td>6.9</td>
<td>-</td>
</tr>
<tr>
<td>Xyris jupicai</td>
<td>15.5</td>
<td>21.1</td>
<td>6.9</td>
<td>25.8</td>
</tr>
<tr>
<td>Andropogon virginicus</td>
<td>1.4</td>
<td>1.8</td>
<td>3.4</td>
<td>4.3</td>
</tr>
<tr>
<td>Juncus elliottii</td>
<td>7.0</td>
<td>15.8</td>
<td>20.7</td>
<td>55.9</td>
</tr>
<tr>
<td>Spartina patens</td>
<td>0</td>
<td>0</td>
<td>100.0</td>
<td>752.5</td>
</tr>
</tbody>
</table>
Fig. 12. Ordination of depression three plant communities by transect. Each geometric symbol represents a compositionally unique plot, or plots with similar compositions, and the artificial community in which it occurred. Dominants of each community are:

- **Centella asiatica, Juncus elliottii**

- **Spartina patens, C. asiatica, Scirpus americanus**

- **Spartina patens**
Table 3. Frequencies (F-%) and densities (D-culms/m²) of species comprising the ordination derived groups of depression three. Total number of plots sampled in the Centella-Juncus, Spartina-Centella, and Spartina dominated communities are 103, 54, and 38, respectively.

<table>
<thead>
<tr>
<th>Community</th>
<th>Centella-Juncus</th>
<th>Spartina-Centella</th>
<th>Spartina</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>D</td>
<td>F</td>
</tr>
<tr>
<td>Centella asiatica</td>
<td>81.6</td>
<td>1400.3</td>
<td>77.8</td>
</tr>
<tr>
<td>Juncus elliotii</td>
<td>54.4</td>
<td>257.3</td>
<td>24.1</td>
</tr>
<tr>
<td>Scirpus americanus</td>
<td>48.5</td>
<td>118.9</td>
<td>64.8</td>
</tr>
<tr>
<td>Diodia virginiana</td>
<td>41.8</td>
<td>155.3</td>
<td>44.4</td>
</tr>
<tr>
<td>Andropogon virginicus</td>
<td>30.1</td>
<td>149.3</td>
<td>11.1</td>
</tr>
<tr>
<td>Aster tenuifolius</td>
<td>19.4</td>
<td>35.2</td>
<td>14.8</td>
</tr>
<tr>
<td>Juncus marginatus</td>
<td>14.6</td>
<td>38.8</td>
<td>1.8</td>
</tr>
<tr>
<td>Hydrocotyle umbellata</td>
<td>7.8</td>
<td>19.4</td>
<td>7.4</td>
</tr>
<tr>
<td>Panicum dichotomiflorum</td>
<td>6.8</td>
<td>34.0</td>
<td>9.2</td>
</tr>
<tr>
<td>Spartina Patens</td>
<td>0</td>
<td>0</td>
<td>100.0</td>
</tr>
</tbody>
</table>
Fig. 13. Total soil moisture (capillary plus hygroscopic) values, expressed as percents of soil oven dry weight, standing water (cm) (November 1974-March 1975 and September-November 1975), and artificial plant community distributions by transect in depression one. Each geometric symbol indicates the artificial community in which each plot, or pair of plots, occurred per meter sampling interval. Vertical dashes indicate thicket edges. Dominants of each community are:

- **Scirpus americanus, Hydrocotyle umbellata**
- **Spartina patens, Scirpus americanus, H. umbellata**
- **Spartina patens**
- **Andropogon virginicus**
Fig. 14. Total soil moisture (capillary plus hygroscopic) values, expressed as percents of soil oven dry weight, standing water (cm) (November 1974-March 1975 and September-November 1975), and artificial plant community distributions by transect in depression three. Each geometric symbol indicates the artificial community in which each plot, or pair of plots, occurred per meter interval. Vertical dashes indicate thicket edges. Dominants of each community are:

- Centella asiatica, Juncus elliottii

- Spartina patens, C. asiatica, Scirpus americanus

- Spartina patens
Table 4. Frequencies (F-%) and densities (D-culms/m²) of herbs sampled along the perimeter of depressions 1-3. Total number of plots sampled in depression 1-3 were 41, 28, and 44 respectively.

<table>
<thead>
<tr>
<th></th>
<th>Depression 1</th>
<th>Depression 2</th>
<th>Depression 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>D</td>
<td>F</td>
</tr>
<tr>
<td>Spartina</td>
<td>17.1</td>
<td>112.8</td>
<td>3.6</td>
</tr>
<tr>
<td>patens</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juncus</td>
<td>9.8</td>
<td>18.3</td>
<td>10.8</td>
</tr>
<tr>
<td>biflorus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Andropogon</td>
<td>19.5</td>
<td>85.4</td>
<td>0</td>
</tr>
<tr>
<td>virginicus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ammophila</td>
<td>7.3</td>
<td>21.3</td>
<td>0</td>
</tr>
<tr>
<td>brevigulata</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eupatorium</td>
<td>7.3</td>
<td>9.1</td>
<td>0</td>
</tr>
<tr>
<td>capillifolium</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panicum</td>
<td>4.9</td>
<td>6.1</td>
<td>0</td>
</tr>
<tr>
<td>amarulum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Solidago</td>
<td>2.4</td>
<td>3.0</td>
<td>0</td>
</tr>
<tr>
<td>sempervirens</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parthenocissus</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>quinquefolia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aster</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>tenuifolius</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centella</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>asiatica</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eupatorium</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>rotundifolium</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
water (Fig. 13). Scirpus-Hydrocotyle and Spartina-Scirpus dominated communities occur only in areas which were flooded while Spartina and Andropogon dominated communities occurred in both flooded and non-flooded portions of depression one (Fig. 13).

In depression three (Fig. 14), the Centella-Juncus dominated community inhabited areas of highest moisture and longest flood duration and was followed in order of decreasing moisture and flood length by the Spartina-Centella, Spartina, and thicket communities. Like depression one, the thicket community of depression three was never flooded.

Although depression one communities were easily recognizable in the field, Centella-Juncus and Spartina-Centella dominated communities of depression three were not, due to their being interspersed with one another (Fig. 14). Each herbaceous community in both depressions overlapped adjacent communities (Figs. 13 and 14).

Mean and extreme soil moisture values collected in November 1976 in the perimeters of depressions four and six were 3.0%, 2.4-3.4% and 2.8%, 2.6-3.1%, respectively.

Soil Texture. Soil texture was at least 98% sand (0.05-2.0 mm) in all samples tested.

Soil Nutrients and pH. Table 5 lists the means and extremes of available Mg, Ca, NO₃, and total salts concentrations and pH for the three most unique communities in depression one, the middle of depression five, and the perimeters of depressions four and six. Available P and K were undetected. All mean Mg, Ca, and total salts values for each community in depression one were significantly different at the p = 0.05 level with the exception of the mean Ca value of the
thicket community versus the *Scirpus-Hydrocotyle* community. The latter value was not significantly different from the thickets of depressions four and five while the latter two thickets were not significantly different from each other. Depression one NO₃ values and all pH values were not significantly different at the p = 0.05 level.

Soils of the *Spartina* dominated community of depression one possessed the highest levels of available Mg, Ca, and NO₃ while soils of the *Scirpus-Hydrocotyle* dominated community were more than twice as salty as soils of the *Spartina* dominated community with the latter almost twice as salty as soils of the thicket community (Table 5). Soils of the depression four perimeter had higher values in every category, except nitrates, than soils of the perimeter of depression six (Table 5).

**Salt Spray and Standing Water Salinity.** Every comparison of depression one community mean salt spray data, with the exception of the comparison of the *Scirpus-Hydrocotyle* dominated community to the *Spartina-Scirpus* dominated community, was significantly different at the p = 0.05 level. No significant variance differences were detected by the variance ratio method. Total salts means for each community are presented in Table 6 for both salt spray studies. Salt spray deposition was lowest in those areas closest to the thicket and increased towards the depression center but was greatest above the thicket. Salt deposition on the thicket was at least twice as much as on any other community and approached that deposited on the reardune. Deposition on the foredune was about twice as much as on the reardune.

A north wind of 6.2 m/sec (14 mph) reported at the Norfolk International Airport was found to be approximately 8.0 m/sec (18 mph)
Table 5. Mean (X) and extreme (E) values for soil total salts, nitrates, and available calcium and magnesium (in parts per million), and pH in soils of three of the most unique communities of depression one, mid-region of depression five, and perimeter soils of depressions four and six. Communities are arranged in order of increasing distance from depression center.

<table>
<thead>
<tr>
<th>Community</th>
<th>Total Salts</th>
<th>NO₃</th>
<th>CaO</th>
<th>MgO</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>X</td>
<td>E</td>
<td>X</td>
<td>E</td>
<td>X</td>
</tr>
<tr>
<td>Depression one</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scirpus-Hydrocotyle</td>
<td>230.1</td>
<td>116-380</td>
<td>68.2</td>
<td>62-125</td>
<td>127.2</td>
</tr>
<tr>
<td>Spartina</td>
<td>104.2</td>
<td>85-139</td>
<td>80.9</td>
<td>62-125</td>
<td>232.3</td>
</tr>
<tr>
<td>Thicket</td>
<td>57.1</td>
<td>22-133</td>
<td>64.7</td>
<td>50-125</td>
<td>131.6</td>
</tr>
<tr>
<td>Depression four</td>
<td>41.5</td>
<td>32-51</td>
<td>56.0</td>
<td>50-62</td>
<td>162.5</td>
</tr>
<tr>
<td>Depression five</td>
<td>91.2</td>
<td>64-139</td>
<td>57.2</td>
<td>50-62</td>
<td>154.0</td>
</tr>
<tr>
<td>Depression six</td>
<td>26.0</td>
<td>22-30</td>
<td>62.0</td>
<td>62-62</td>
<td>92.5</td>
</tr>
</tbody>
</table>
Table 6. Mean salt spray deposition (total salts) for both salt spray studies in depression one and on the fore- and reardunes. Communities are arranged in order of increasing distance from depression center.

<table>
<thead>
<tr>
<th>Community</th>
<th>Study One</th>
<th>Study Two</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean$_2$ (mg/dm$^2$)</td>
<td>Mean$_2$ (mg/dm$^2$)</td>
</tr>
<tr>
<td><strong>Depression one</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Community:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scirpus-Hydrocotyle (6)</td>
<td>1.60</td>
<td>0.76</td>
</tr>
<tr>
<td>Scirpus (3)</td>
<td>1.48</td>
<td>0.80</td>
</tr>
<tr>
<td>Spartina (5)</td>
<td>0.66</td>
<td>0.48</td>
</tr>
<tr>
<td>Inside Thicket (4)</td>
<td>0.74</td>
<td>0.60</td>
</tr>
<tr>
<td>Above Thicket (2)</td>
<td>3.32</td>
<td>1.70</td>
</tr>
<tr>
<td>Foredune (1)</td>
<td>7.40</td>
<td>2.17</td>
</tr>
<tr>
<td>Reardune (1)</td>
<td>3.57</td>
<td>1.15</td>
</tr>
<tr>
<td>Controls (2)</td>
<td>0.38</td>
<td>0.38</td>
</tr>
</tbody>
</table>
at the False Cape beach berm. Concurrent foredune, depression one-middle, and reardune wind speeds were measured at 7.6 m/sec (17 mph), 1.8 m/sec (4 mph), and 6.7 m/sec (15 mph), respectively.

Salinity of late winter standing water in depressions one and five was less than 0.5 parts per thousand.

Soil Temperature. Surface, ten, and 20 cm soil temperatures and air temperatures measured in depression three are plotted, by transect, in Fig. 15. Highest values at each soil level were always recorded at the periphery of each transect.

Field Observations

Following a severe "northeaster" storm (westward winds) on 15 April 1975, virtually all *P. serotina* leaves projecting above shrub canopies in the depression series were observed to be necrotic while leaves in shrub interiors were visibly unharmed. Within several weeks, however, most leaves on the original stems were replaced. *Prunus serotina* trees which were not surrounded by shrubs possessed espalier shapes, exhibited necrosis on almost every leaf following the storm, and regained leaves almost solely on the western half. Effects of the storm upon *L. styraciflua*, *R. radicans*, *Populus heterophylla*, *Salix nigra*, *A. rubrum*, and *Pinus taeda* appeared to be relatively similar to *Prunus serotina*. *Myrica pensylvanica*, *M. cerifera*, *B. halimifolia*, and *Q. virginiana* exhibited necrosis almost solely on canopy leaf tips. No shrubs or trees were noticeably affected in depression six. A storm with high velocity westward winds in the winter of 1976 was observed to produce the same effects. No shrub or tree leaves appeared to be visibly harmed following high velocity eastward winds.

Following the 15 April storm, a 1-3 mm layer of sand was de-
Fig. 15. Surface, ten, and 20 cm soil temperatures (°C) and air temperatures (°C) measured in depression three. Vertical dashes represent thicket boundaries.
posited in the eastern half of depression one and lesser amounts in the western half. Similar accumulations were also found in depressions two and three.

Hogs are usually released in False Cape in the fall for grazing and not usually collected until spring. Collection, however, is seldom complete and a population is usually present year-round. Uprooting in the depression series occurred almost exclusively in rhizome-rich *Spartina patens* dominated areas, oftentimes of such great intensity that an uninterrupted increase in depression depth up to 0.6 m resulted. Such disturbance noticeably increased summer soil moisture and usually caused a September-May flood stage. Following uprooting in depression five during winter 1974, *Spartina patens* was replaced the following spring by *Scirpus americanus*, *Eleocharis parvula*, *E. quadrangulata*, and other species common to the *Scirpus-Hydrocotyle* dominated community of depression one. Maximum density of these species occurred in late summer and was followed by autumn flooding and subsequent arrival of Canada geese, snow geese, and other migratory waterfowl. Complete removal of *Scirpus americanus*, *E. parvula*, *E. quadrangulata*, and associated species ensued. Similar species reinvaded the next growing season and were subsequently removed by migrating waterfowl during winter 1975. *Panicum dichotomiflorum*, however, became dominant during the 1976 growing season with *Scirpus americanus* and *Eleocharis* spp. much less abundant.

Low hog uprooting intensity (winter 1975) resulted in mounds of sand deposited beside excavated potholes. The latter were either re-invaded by *Spartina patens* or invaded predominantly by *Scirpus americanus* and *Eleocharis* spp. Sand mounds were almost always invaded.
by Andropogon virginicus.

An almost uninterrupted, diurnal migration of deer into the depression series was either directly or indirectly observed on almost every field trip. Bedding signs were common. Other effects upon vegetation were not obvious.
DISCUSSION

Plant Establishment and Succession

Although *B. halimifolia* averaged 1.2 years younger than *M. pensylvanica*, dependence of the former upon the latter for establishment is improbable since both had similar canopy heights and both were shade intolerant. Since *P. serotina* was virtually always associated with *M. pensylvanica* in the depressions, averaged 3.3 years younger than the latter, and was tolerant of the shade produced by it, *P. serotina* establishment is probably dependent upon *M. pensylvanica* presence. Reduction in shrub vigor beneath the taller growing *P. serotina* indicates this species represents a succeeding seral stage. Since *P. serotina* trees not surrounded by mature shrubs appeared to be near death as a result of salt spray and possessed seedlings of *M. pensylvanica* beneath them, linear succession appears to be diverted to a *M. pensylvanica*-*P. serotina* cycle. Presence of *Q. virginiana* seedlings and seedlings beneath *M. pensylvanica* shrubs and the relative salt spray tolerance of mature *Q. virginiana* forms on adjacent dunes suggests this species may break the cycle and become climax.

Hog uprooting caused a regressive successional effect by significantly increasing and decreasing soil moisture in *S. patens* dominated areas. Succession in the more xeric habitat, after *A. virginicus* invasion, could not be projected. After species such as *Scirpus americanus* invaded the more hydric habitat, succession appeared to be inhibited by migrating waterfowl. *Panicum dichotomiflorum* invasion in
depression five indicates that succession does occur, however. Succession is probably inhibited in Spartina patens dominated areas where hog uprooting results in the removal of vegetation but no significant change in soil moisture.

Inconsistent age differentials between M. pensylvanica and P. taeda in depression six (Fig. 7) suggest that neither species is dependent upon the other for establishment. The taller growing P. taeda, however, will most likely succeed the apparently shade intolerant M. pensylvanica.

Age differences between perimeter and non-perimeter shrubs in almost every depression indicate that shrub establishment occurs first in the perimeter. This is possibly a result of interspecific competition since non-perimeter areas possessed more mesic conditions.

Major topographic changes illustrated in Fig. 3 and sand accumulations observed in depressions 1-3 suggest that an inward progression of species succession may exist as a result of decreasing soil moisture. Because of Q. virginiana's relative tolerance to shade and salt spray and its occurrence on xeric dunes between depressions, this species probably represents the climax of physiographic succession.

Plant Distribution and Environmental Factors

A definite relationship between community distribution and soil moisture is obvious in Figs. 13 and 14. In non-perimeter areas, M. pensylvanica occurred only in the Spartina patens dominated community while M. cerifera occurred in both Spartina patens and Centella-Juncus dominated communities (Figs. 8, 10, 13, and 14). Since the distribution of these communities is controlled, at least partially, by soil moisture, it appears reasonable to assume that distribution of these shrubs
is also controlled, at least in part, by soil moisture with M. cerifera inhabiting areas of higher soil moisture than M. pensylvanica. Soil moisture tolerances of each species, however, cannot be determined from the results because of possible interspecific competition interactions. For example, absence of M. cerifera in the Spartina patens dominated community of depression one (Fig. 8) may be a result of competition since it occurs in noticeably lower density Spartina patens areas of depression two. Lower density of Spartina patens may be due to allelopathy rather than moisture differences. Absence of Scirpus americanus in the Spartina patens dominated community of depressions two and three (Tables 2 and 3) may also be due to competition rather than the former's intolerance to lower moisture. A complete understanding of soil moisture and competition interactions will require extensive experimentation.

Interspersion of Centella-Juncus and Spartina-Centella dominated communities in depression three (Fig. 14) is probably the result of low intensity, feral hog uprooting. Increased soil moisture resulting from increases in soil depth apparently allows establishment of the more hydric species. This suggests the presence of such species in the depression series may be dependent almost completely upon feral hog uprooting. Presence of uprooting signs in virtually every area of the depression series dominated by species belonging to Centella-Juncus and Scirpus-Hydrocotyle dominated communities lend support to this theory. Alluvial currents, however, may have produced similar effects in some depressions.

Relatively lower soil moisture in sand mounds produced by low intensity hog uprooting is apparently responsible for the sparse dist-
ribution of *A. virginicus* throughout the interior of depression three (Fig. 14). Occurrence of this species towards the perimeter of depression one (Fig. 13) is probably related to signs of high uprooting intensity in inner areas.

Seneca (1969, 1972) has shown that *S. patens* seeds and seedlings are capable of tolerating soil salt concentrations of 4.0% yet this species occurred most abundantly in depression one in areas of medium soil salt concentrations which never exceeded 0.014% (Table 5). Based upon these autecological studies, a correlation between total soil salts and plant community distribution does not appear likely even though almost all total salt means were significantly different statistically.

Lack of P and K detection may indicate that these nutrients are primary limiting growth factors in the depression series and probably are not important in controlling plant community distribution. Available Ca is apparently not significant in limiting community distribution since non-adjacent communities had similar means (Table 5). Available Mg is also not apparently important in limiting community distribution since the depression one thicket and depression five non-perimeter communities had similar values (Table 5).

Higher Ca, Mg, and total salts values in depression four than in depression six (Table 5) are probably due to the former's close proximity to the ocean which results in greater nutrient deposition by salt spray (van der Valk 1974).

Although depression one community salt spray means were significantly different statistically (Table 6), laboratory tap water was found to have higher concentrations of total salts (1.5 mg/dm²) than
70% of the titration solutions. Salt spray is therefore eliminated as a community distributional limiting factor. The possibility of salt water influence upon vegetation was discounted by hydrometer results.

Paucity of trees in the depression series is probably attributable, at least partially, to salt spray since severe damage to all tree species was observed after the 15 April storm. Deer browsing may also be a factor (Marquis 1974).

Results of this study (Fig. 15) do not suggest that soil temperature influences the distribution of non-perimeter vegetation. Although relatively higher soil temperatures were recorded from the periphery of depression three, other sampling points in the thicket community had values similar to non-perimeter areas. Therefore, soil temperature is not believed to control the distribution of perimeter vegetation.

Barrier Island Plant Zonation

Abundance of P. taeda and V. corymbosum in depression six (Fig. 7) is attributed to insufficient salt spray deposition since they were visibly harmed in the depression series by the 15 April storm but not in depression six or areas westward. In addition, soil moisture, NO₃, pH, and herbaceous associates were similar in depression four and six perimeters while total salts, CaO, and MgO were more plentiful in depression four (Table 5). These findings support those of Wells (1942) in that the zonal appearance of shrubs and trees, at least on the Virginia and North Carolina barrier dune systems, is due to the absence of arborescent forms in medium to high spray areas because of their intolerance to salt spray. (Quercus virginiana is not regarded as a
tree near the ocean because of its shrubby growth habit.) In areas of low or no spray, usually located farther from the ocean, establishment of an arborescent zone by P. taeda is permitted.

Results of this study are insufficient to allow deductions regarding the salt spray dependence of the foredune-grass zone. However, results of this study, in conjunction with those of Costing (1945), do not support Wells and Shunk's (1938) conclusion that "... the dominants of the ocean front dune are dominant because of their resistance to salt spray." Costing (1945) found Spartina patens, an infrequent member of most foredunes, to be more salt spray tolerant than Uniola paniculata, a foredune dominant on the North Carolina Outer Banks. Distribution and soil moisture correlations in this study suggest that the paucity of S. patens on the foredune is controlled, at least in part, by insufficient soil moisture. Studies by Wagner (1964), Woodhouse and Hanes (1966), and van der Valk (1974) suggest that excessive sand movement may be a major factor, also.

Costing and Billings (1942) stated that "the zonal distribution (on the North Carolina Outer Banks) of the major species is ... explainable on the basis of tolerance to wind born salt." Stalter (1975) concluded that "salt spray is the most important parameter affecting vegetation distribution in the coastal dunes of South Carolina." Results of this study and Costing (1945), however, indicate that distribution of S. patens is independent of salt spray and that, although the occurrence of M. pensylvanica appears to be indirectly related to salt spray, its distribution is independent of it.

Barrier Island Plant Succession

Wells (1939) reported that dune-grass, shrub, and arborescent
zones represented progressive successional stages. He stated that "... the pioneer on the sand flats is, in the Cape Fear region (North Carolina), the sea oats (U. paniculata) ... . On older areas in the medium spray zone, Myrica cerifera, Ilex vomitoria, and often Juniperus virginiana come in as shrub stage. This will be followed by the live oak forest climax." Penfound and O'Neill (1934) similarly recognized vegetational zones as representing stages in succession on Cat Island, Mississippi. Chrysler (1930) believed that the zonation-succession relationship applied to Sandy Hook, New Jersey, also.

However, Martin (1959) found that, at least for Island Beach, New Jersey, each topographic unit had its own plant composition and successional pattern. He suggested that succession is primarily controlled by physiography but that biotic succession also occurs. "... it seems reasonable to conclude that plant succession on Island Beach, and perhaps on barrier beaches in general, is largely an interzonal phenomenon. The herbaceous, shrubby, and arborescent zones do not necessarily represent seral stages in biotic succession."

In 1942, Wells altered his succession and climax theories. He suggested that the dune-grass, shrub, and forest communities persist for centuries and thus represent climates.

Results of this study support those of Wells (1959) and Wells (1942) in that the zones do not represent progressive seral stages on a stable or degrading coast. It appears unlikely that the grasses of the foredune zone and shrubs of the shrub zone will be succeeded by trees, on a stable or degrading coast, due to excessive salt spray.
APPENDIX

Floristics List of the Bryophytic and Vascular Flora of the Entire Depression Series

Bryophyta

Polytrichum sp.  POLYTRICHACEAE

Sphagnum sp.  SPHAGNACEAE

Pteridophyta

Thelypteris palustris Schott  ASPIDIACEAE

Woodwardia areolata (L.) Moore  BLECHNACEAE

Osmunda regalis var. spectabilis (Willd.) Gray  OSMUNDACEAE

Spermatophyta

Acer rubrum L.  ACERACEAE

Sagittaria graminea Michaux  ALISMATACEAE

Rhus copallina L.
   R. radicans L.
   R. vernix L.  ANACARDIACEAE

Centella asiatica (L.) Urban
   Hydrocotyle umbellata L.
   Ptilimnium capillaceum (Michaux) Raf.  APIACEAE
AQUIFOLIACEAE

Ilex glabra (L.) Gray
I. opaca Aiton

ASCLEPIADACEAE

Asclepias incarnata ssp. pulchra (Willd.) Woodson

ASTERACEAE

Aster tenuifolius L.
A. puniceus L.
Baccharis halimifolia L.
Carduus sp.
Coreopsis latifolia Michaux
Erechtites hieracifolia (L.) Raf.
Erigeron canadensis var. pusillus (Nuttall) Ahles
Eupatorium capillifolium var. capillifolium (Lam.) Small
E. rotundifolium L.
E. serotinum Michaux
Gnaphalium obtusifolium L.
Heterotheca nervosa var. nervosa (Willd.) Shinners
Hieracium gronovii L.
Mikania scandens (L.) Willd.
Pluchea festida (L.) DC
P. purpurascens (Swartz) DC
Solidago graminifolia (L.) Salisbury
S. puberula Nuttall
S. sempervirens L.
S. tenuifolia Pursh
Sonchus oleraceus L.
Sonchus sp.

CAPRIFOLIACEAE

Lonicera sempervirens L.

CARVOPHYLLACEAE

Paronychia riparia Chapman

CONVOLVULACEAE

Calystegia sepium (L.) R. Brown

CUPRESSACEAE

Juniperus virginiana L.

CYPERACEAE

Bulbostylis ciliatifolia (Ell.) Fernald
Cyperus erythrorhizos Muhl.
C. haspan L.
C. polystachyos var. texensis (Torrey) Fernald
C. strigosus L.
Eleocharis flavescens (Poiret) Urban
E. parvula (R. & S.) Link
E. quadrangulata (Michaux) R. & S.
Scirpus americanus Persoon
S. cyperinus (L.) Kunth
S. robustus Pursh
S. validus Vahl

Drosera capillaris Poiret

Diospyros virginiana L.

Vaccinium corymbosum L

Euphorbia polygonifolia L.

Cassia fasciculata Michaux
Lespedeza sp.
Strophostyles helvola (L.) Ell.

Quercus virginiana Miller

Sabatia stellaris Pursh

Proserpinaca palustris L.

Liquidambar styraciflua L.

Hypericum gentianoides (L.) BSP
H. muticum L.
H. prolificum L.

Juncus acuminatus Michaux
J. biflorus Ell.
J. dichotomus Ell.
J. elliottii Chapman
J. marginatus Rostk.
J. megacephalus M.A. Curtis
J. roemerianus Scheele
J. scirpoides Lam.

Lycopus rubellus var. angustifolius (Ell.) Ahles
Stachys nuttallii Shuttlew.
LILIACEAE

Smilax bona-nox L.

LINACEAE

Linum virginianum L.

LYCOPODIACEAE

Lycopodium appressum (Chapman) Lloyd and Underwood

MALVACEAE

Hibiscus moscheutos ssp. moscheutos L.

MELASTOMATACEAE

Rhexia mariana L.

MYRICACEAE

Myrica cerifera var. cerifera L.  
M. pensylvanica foisel

ONAGRACEAE

Ludwigia alternifolia L.  
L. brevipes (Long) Eames  
L. linearis Walter  
L. palustris (L.) Ell.  
Genothera humifusa Nuttall

ORTHIDACEAE

Spiranthes cernua (L.) Richard

PHYTOLACCACEAE

Phytolacca americana L.

PINACEAE

Pinus taeda L.

POACEAE

Ammophila breviligulata Fernald  
Andropogon scoparius Michaux  
A. virginicus L.  
Echinochloa walteri (Pursh) Heller  
Eragrostis elliottii Watson  
E. spectabilis (Pursh) Steudel  
Erianthus giganteus (Walter) Muhl.  
Leersiaabyrinthes (L.) Swartz  
Panicum amarum Hitchcock and Chase  
P. amarum Ell.  
P. anceps Michaux  
P. dichotomiflorum Michaux  
P. scoparium Lam.  
Phragmites communis Trinius  
Sacciolepis striata (L.) Nash  
Spartina patens (Aiton) Muhl.  
Triplasis purpurea (Walter) Chapman
POLYGONACEAE
Polygonum hydropiperoides var. opelousanum (Riddell ex Small) Stone
P. punctatum Ell.
Rumex acetosella L.

ROSACEAE
Prunus serotina var. serotina Ehrhart
Rubus sp.

RUBIACEAE
Diodia teres Walter
D. virginiana L.
Galium tinctorium L.

SALICACEAE
Populus heterophylla L.
Salix nigra Marshall

SCROPHULARIACEAE
Agalinis sp.
Linaria canadensis (L.) Dumont
Lindernia anagallidea (Michaux) Pennell

TYPHACEAE
Typha angustifolia L.
T. latifolia L.

VITACEAE
Parthenocissus quinquefolia (L.) Planchon
Vitis rotundifolia Michaux

XYRIDACEAE
Xyris jupicae Richard
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