AN ECOLOGICAL STUDY OF COASTAL STRAND VEGETATION ON THE WESTERN END OF SANTA ROSA ISLAND NEAR PENSACOLA, FLORIDA

By

James R. Burkhalter

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James Russel Burkhalter

B.S., University of Illinois, 1969

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TABLE OF CONTENTS

ACKNOWLEDGMENTS	iii
LIST OF TABLES	v
LIST OF FIGURES	vii
ABSTRACT	viii
INTRODUCTION	1
LITERATURE REVIEW	4
METHODS	18
RESULTS	34
Description of General Study Area	34
Vegetation	35
The Environment	55
Soil Factors	55
Atmospheric Factors	68
DISCUSSION	91
Vegetation	91
The Environment	109
Soil Factors	109
Atmospheric Factors	135
SUMMARY	169
LITERATURE CITED	173
APPENDIX. ERRONEOUS REPORTS OF PLANT SPECIES IN THE DUNE STRAND OF SANTA ROSA ISLAND	192

LIST OF TABLES

Table		Page
1.	Sea Oats Zone Data	37
2.	Shrub Zone Data	39
3.	Pine Forest Data	42
4.	Bluestem Zone Data	46
5.	Dune Swale Plants	50
6.	Soil Data	57
7.	Temperature Measured at Different Levels in the Soil and 30 cm above the Soil Surface (February 17-18, 1979)	65
8.	Temperature Measured at Different Levels in the Soil and 30 cm above the Soil Surface (April 14, 1979)	65
9.	Temperature Measured at Different Levels in the Soil and 30 cm above the Soil Surface (July 7, 1979)	66
10.	Temperature Measured at Different Levels in the Soil and 30 cm above the Soil Surface (September 16-17,1978)	66
11.	Hourly Air Temperature on Barrier Dune (August 29, 1979)	69
12.	Hourly Air Temperature on Barrier Dune (September 8, 1979)	69
13.	Relative Humidity at Different Seasons	75
14.	Hourly Relative Humidity on Barrier Dune (August 29, 1979)	77
15.	Hourly Relative Humidity on Barrier Dune (September 8, 1979)	77
16.	Amounts of Water Evaporated from Atmometers Exposed for 8 Hours in the Sea Oats Zone	79
17.	Amounts of Water Evaporated from Atmometers Exposed for 8 Hours in the Different Vegetation Zones	79

18. Amounts of Water Evaporated from Atmometers Exposed for 24 Hours in the Different Vegetation Zones 80

19. Amounts of Water Evaporated from Atmometers Exposed for 24 Hours in the Pine Forest and at Adjacent Stations 80

20. Summary of Wind Direction Data Recorded by U. S. Coast Guard Station on Santa Rosa Island 82

21. Summary of Wind Velocity Data Recorded by U. S. Coast Guard Station on Santa Rosa Island 83

22. Results of Salt Spray Study (Sep 19-Nov 18, 1980) 85

23. Results of Salt Spray Study (Apr 2-Jun 1, 1981) 86

24. Results of Salt Spray Study (Nov 28, 1980-Mar 9, 1981) 87

25. Results of Salt Spray Study (Jul 10-Sep 13, 1981) 88

26. Index of Similarity Values for Coastal Strand Vegetation of Santa Rosa Island, Florida, Compared with Coastal Strand Vegetation of Selected Sites along the Atlantic and Gulf Coasts of the United States and Mexico 92

27. Occurrence of Species at Selected Coastal Strand Sites along the Atlantic and Gulf Coasts of the United States and Mexico 97

LIST OF FIGURES

Figure		Page
1.	Study Area on Western End of Santa Rosa Island	19
2.	Diagram of Nested Plot System Used for Quantitative Vegetation Analysis	21
3.	Diagram of Frame Used for Estimating Coverage of Shrubs and Herbaceous Plants	23
4.	Livingston Atmometer	31
5.	Profile across Santa Rosa Island at the Study Site	36

A B S T R A C T

AN ECOLOGICAL STUDY OF COASTAL STRAND VEGETATION ON THE WESTERN END OF SANTA ROSA ISLAND NEAR PENSACOLA, FLORIDA

James Russel Burkhalter

Coastal strand vegetation on the western end of Santa Rosa Island was quantitatively studied to determine coverage, frequency, and constancy for dunal species. A number of environmental factors were examined to determine which ones might be responsible for zonation of the vegetation. The pine forest located at the island's interior was also studied for purposes of comparison.

No soil factor studied (organic content, moisture, pH, chloride, various nutrients, total soluble salts, cation exchange capacity, temperature) was found to correlate with the vegetational zonation. Air temperature and relative humidity patterns also did not coincide with vegetational zonation.

Evaporation was greater where Uniola paniculata was dominant than where Schizachyrium maritimum dominated. The salt spray deposition pattern was observed to correspond with the vegetational zonation. It was concluded that wind-borne salt spray appears to be the primary factor determining and maintaining coastal strand vegetational zonation on Santa Rosa Island.

I N T R O D U C T I O N

> "The best estimate as to the area of the earth covered by sand dunes is 3,200,000,000 acres--nearly twice the total area . . . of the United States."

This quotation (Whitfield and Brown, 1946), which refers primarily to coastal dune systems, provides an indication of the total area of the earth which is occupied by coastal strand habitat--that relatively narrow strip of beaches and dunes with associated vegetation that stretches along many of the coastal areas of the world's continents. On the basis of area alone, the coastal strand must be considered one of the earth's major terrestrial ecosystems. In spite of this, few scientific investigations of this habitat were conducted prior to the 1950s.

In recent years, however, there has been a tremendous increase of interest in the coastal strand habitat and its ecology. To a great extent this has been brought about by the simple realization on the part of many individuals and ecologically-oriented groups that coastal beaches and dunes provide a natural mitigation barrier and protection zone against the ravages of ocean storm surges and hurricanes. It is now common knowledge that disturbance to, or destruction of, coastal strand systems through improper placement of buildings and associated terrain alterations by man leaves the coastline without natural protection and can lead to a catastrophic loss of property and human

lives in the event of a severe storm. The effects of recent hurricanes have provided ample examples of the serious consequences of man's alterations of the coastal zone. As a result of this increased awareness, coastal zone management programs have been developed by many universities, and coastal zone management agencies have been created by the legislatures of most of the coastal states. This resurgence of interest in the preservation of the coastal strand reached a major milestone with the affirmation by President Carter of 1980 as the Year of the Coast.

The coastal strand habitat is characterized by bare beaches and associated dune systems in which the vegetation occurs in distinct zones, and this ecosystem is often referred to as the dune strand. It may be situated along the mainland coast or on offshore barrier islands. In the United States it is found along the Atlantic coast from Maine south to the Florida keys. From Maine to southern Virginia the vegetation of the coastal strand zone just inland from the bare beach is dominated by the grass Ammophila breviligulata, and from that point southward by the grass Uniola paniculata. The west coast of Florida is primarily vegetated by stands (mangals) of mangroves, but Uniola-dominated coastal strand habitat resumes near the mouth of the Ochlockonee River and continues west and south to the southern tip of Texas and into Mexico. Coastal strand is intermittent along the Pacific coast of the United States, being supplanted by coastal marsh in numerous places. The coastal strand species and physiognomy of that area are fundamentally different from those of the coastal strand of the southeastern United States, but similar environmental factors seem to be of importance in both areas.

The purpose of this study was to add to the existing scientific knowledge of the coastal strand of the southeastern United States by studying the ecology of the coastal strand vegetation on the western end of Santa Rosa Island. This was accomplished by the following undertakings:

(1) The vegetation of the dune strand zones was quantitatively analyzed to determine coverage, frequency, and constancy for all species encountered. The vegetation of the pine forest in the interior of the island was also quantitatively studied.

(2) A number of edaphic and atmospheric factors were measured to determine if correlations with vegetational zonation existed.

(3) The findings generated by the field work in this study were compared with results of other investigations to determine if the environmental factors which are important in other coastal locations are also operative in the coastal strand of Santa Rosa Island.

LITERATURE REVIEW

VEGETATION

FLORISTIC COMPOSITION

In the United States Atlantic coastal vegetation has been particularly well-investigated. The pertinent studies may be grouped into two broad categories based on the range of Uniola paniculata, which is the dominant dune grass from southeastern Virginia (Cape Henry) south to Florida and west to Mexico. From Virginia northward Uniola paniculata is replaced by its ecological equivalent Ammophila breviligulata, which is the dominant dune grass where it occurs.

Papers and books describing Ammophila-dominated systems include the following for Atlantic-coast states: Maine--Kuchler (1956); Massachusetts--Jordan (1874), Chrysler (1905), Lewis (1924), Fogg (1930), Moul (1948, 1961, 1969), Boyce (1954), White (1960), Sterling (1967), Hay (1968), MacKeever (1968), Wetherbee et al. (1972), Carlozzi et al. (1975); New York--Taylor (1923), Conard (1935), Art (1971), Stalter (1979); New Jersey--Harshberger (1900, 1902), Stone (1911), Chrysler (1930), Small and Martin (1958), Martin (1959); Delaware--Snow (1902, 1913), Tatnall (1946); Maryland--Chrysler (1910), Shreve (1910), Higgins, Rappleye, and Brown (1971); Virginia--Egler (1942), Harvill (1965, 1967), Clovis (1968), Marsh (1969), Willis and Zaneveld (1971). Additionally, Moul (1973) considered coastal vegetation from

Newfoundland and southern Labrador to the southernmost extent of Ammophila breviligulata, and Godfrey (1977) briefly described Ammophila-dominated coastal strand vegetation on nine barrier islands from Massachusetts to Virginia.

Several authors have described the Uniola-dominated coastal systems of North Carolina. These include the following: Johnson (1900), Kearney (1900), Lewis (1917), Coker (1918), Wells (1928), Oosting and Billings (1942), Rondthaler (1952), Oosting (1956), Stick (1958), Bourdeau and Oosting (1959), Brown (1959), Burk (1961a, 1961b, 1962), Wagner (1964), Au (1969, 1974), Godfrey and Godfrey (1976). The coastal vegetation of South Carolina has been described by Coker (1905), Barry (1968), Stalter (1971, 1972, 1973, 1974, 1975, 1978), Pinson (1973), and Hosier (1975). Descriptions for coastal strand vegetation of Georgia were provided by Johnson et al. (1974) and Hillestad et al. (1975).

The vegetation of Florida's east coast south to Key Biscayne has a Uniola-dominated aspect similar to that found as far north as North Carolina. It has been described by Leeds (1892), Webber (1898), Kurz (1942), Bennett (1961), Mathews (1975), Carlton (1977), Richardson (1977), Austin et al. (1977), and Poppleton et al. (1977). The coastal areas of south Florida and the Keys exhibit a decidedly tropical vegetation, which has been described and/or listed by Millspaugh (1907), Small (1913), Harshberger (1914), Harper (1927), Davis (1942, 1943), and Dickinson et al. (1953). Bowman (1918) and Teas and Schroeder (1971) considered the vegetation of the Tortugas.

The Gulf coastal mainland of Florida's peninsula is devoid of sand strand vegetation. Here the coastal areas are primarily vegetated by mangrove communities, which have been described by Davis (1940), Fuller

(1941), and Carlton (1977). A number of offshore islands along the west coast of Florida's peninsula do, however, exhibit dune strand vegetation to a limited extent, and this vegetation has been briefly considered by Cooley (1955) (Sanibel Island), Fowler (1974) (Caladesi Island), Hilsenbeck and Hilsenbeck (1974) (Mullet Key), and Laessle and Wharton (1959) (Seahorse Key).

Uniola-dominated coastal vegetation resumes in northwest Florida in the vicinity of the Ochlockonee River and is continuous in the panhandle from Franklin County westward. It has been described briefly by Harper (1914). Kurz (1942) reported on the coastal vegetation at Cochran's Beach (St. James Island, Franklin County) and Beacon Hill (near Port St. Joe, Bay County). Livingston et al. (1974) and Carlton (1977) described the strand vegetation of St. George Island (Franklin County). Carlton (1977) also described the coastal vegetation at Cape San Blas (W. T. Stone State Park, Gulf County).

The coastal strand vegetation of Santa Rosa Island has been studied in some detail by McFarlin (1941) (central and eastern portions), Long (1974) (Navarre Beach area), and Carlton (1977) (western end near Ft. Pickens). Blair (1951), in his study of the white-headed beach mouse (Peromyscus polionotus leucocephalus) on Santa Rosa Island, included a brief description of the dune vegetation. A recent series of reports prepared by the National Park Service (1976a, 1976b, 1978a, 1978b) included maps, profile drawings, and verbal descriptions of the vegetation of most of Santa Rosa Island, the eastern end of Perdido Key, and the portion of the Gulf Breeze peninsula coast occupied by the Naval Live Oaks Unit of Gulf Islands National Seashore.

A report from the Escambia County Department of Community Development (1975) included a brief treatment of dune vegetation of Santa Rosa Island with a profile drawing and line drawings of five common coastal strand plants. The Environmental Inventory section of the 201 Facilities Plan for South Escambia and Santa Rosa Counties (Theta Analysis, Inc., 1978) included a description of dune vegetation for the study area and a list of typical northwest Florida coastal strand species.

The vegetation of the dunes and dry sands of the Alabama coast was briefly discussed by Mohr (1901), who referred to the coastal plants as "xerophile psammophytes." Stallard (1950) investigated the coastal vegetation of the Fort Morgan Peninsula, Baldwin County, Alabama. Deramus (1970) studied the dune and strand vegetation of Dauphin Island, Mobile County, Alabama.

Maritime vegetation of Mississippi has been described by Lloyd and Tracy (1901), Lowe (1921), Penfound and O'Neill (1934), Pessin and Burleigh (1941), Richmond (1962, 1968), Miller and Jones (1967), Miller (1975), Eleuterius (1975, 1979), Robinson (1975), Huguley and Eleuterius (1976), and Baron (1979). Recent publications of the National Park Service (1976a, 1976b, 1978a, 1978b) included discussions of strand vegetation for some of Mississippi's islands and maps of the same.

Lloyd and Tracy (1901) also considered coastal strand vegetation of Louisiana, as did Brown (1930), Lemaire (1961), and Gould and Ewan (1975).

Bray (1906), Johnson (1955), Rabalais (1975), Gillespie (1976), Jones (1977), Judd et al. (1977), and Lonard et al. (1978) considered

vegetation of coastal strands and dunes of Texas and its barrier islands.

Oosting (1954) discussed sand strand vegetation occurring in the southeastern United States from southeastern Virginia all the way around Florida and the Gulf coast to Texas. Gulf coast vegetation was also considered by Thorne (1954). Ferguson (1952) considered coastal strand species which have horticultural potential for south Florida and included native as well as cultivated plants in his study.

Strand vegetation of the Gulf coast of Mexico is similar to that of southern Florida. It has been studied by Bequaert (1933), Lundell (1934), Edwards (1954), Bonet and Rzedowski (1962), Poggie (1962), West (1966), Sauer (1967), and Gonzalez-Medrano (1972).

MONOGRAPHS

Several monographers have studied the taxonomy of plants which occur in the coastal strand of the southeastern United States.

Important monographs include those on the genera Atriplex (Hall and Clements, 1923), Balduina (Parker and Jones, 1975), Cakile (Rodman, 1974), Cenchrus (de Lisle, 1963), Iva (Jackson, 1960), Melanthera (Parks, 1973), Uniola (Yates, 1966), the Ipomoea pes-caprae group (St. John, 1970), and the Panicum amarum-P. amarulum complex (Palmer, 1975). The work of Semple (1977, 1978) and Semple et al. (1980) in elucidating the taxonomy of the genera Chrysopsis, Heterotheca, and Pityopsis should be noted here. Thomson (1967) monographed the lichen genus Cladonia in North America.

ECOLOGICAL STUDIES

GENERAL STUDIES

Near the end of the last century, H. C. Cowles (1899) conducted a detailed ecological study of the vegetation of the sand dunes of Lake Michigan southeast of Chicago, Illinois, in northwestern Indiana. His investigations concerned the following factors: light, heat, wind, soil, and water. Although salt spray--the primary ecological factor of the coastal strand--was not considered by Cowles, the other factors he studied are equally operative in both freshwater and coastal marine dune systems. Cowles' study, which is now considered a classic in ecology, influenced other investigators, and a series of similar studies were conducted in the early part of the 1900s, such as those by Harshberger (1900), Snow (1902), Olson-Seffer (1909a), and Martin and Clements (1939).

Later Oosting and Billings (1942) conducted a detailed ecological study of coastal strand vegetation near old Fort Macon at the entrance to Beaufort Harbor on Bogue Bank, North Carolina. Vegetation of two 1-meter-wide transects was mapped by square meters, and density and coverage values for each species were determined. This study included the first quantitative measurements of wind-borne salt spray performed in the United States. The following soil factors were considered: moisture, temperature, and salt content. Air temperature, relative evaporation, and relative humidity were also studied. Phytometric studies were performed in which plants were watered and sprayed with sea water to determine the degree of tolerance to salt spray exhibited by various dune species.

In the same year Wells (1942) discussed the ecological factors which are operative in the coastal areas of the southeastern United States coastal plain. He stressed the role of wind-borne salt spray as being "of major importance in modifying the form of woody plants and in developing a zonation of vegetation related to salt resistance" in coastal areas.

Boyce (1954) conducted a detailed ecological study of coastal strand vegetation in the Cape Fear area of North Carolina and near Cape Cod, Massachusetts. He investigated the following factors: wind, sand-blasting of vegetation, salinity of the substratum, salt spray (including the source, deposition, and intensity of salt spray), plant responses to salt spray (including toxicity of oceanic salts to dune plants, entrance of salt into leaves and stems, patterns of salt spray injury, and chloride-induced hypertrophy), salt spray-selected growth forms, and the effect of nitrogen and phosphorus on the salt spray tolerance of coastal plants. This study included an extensive literature review and is the most detailed study of its type ever undertaken in the United States.

In the same year Oosting (1954) published a review article concerning the ecological processes and vegetation of the coastal strand of the southeastern United States. He cited 62 references and discussed in detail several topics of ecological concern, including topography, soil moisture and soluble salts, temperature, light, precipitation, evaporation, transpiration, wind, salt spray, human and animal influences, and adaptation and xeromorphism of coastal strand plants. The ideas of succession and climax as they relate to coastal strand vegetation were also given special consideration.

Other major ecological studies have been performed in the coastal strand of North Carolina. These include van der Valk (1973, 1974a) and Au (1969, 1974). Similar studies in South Carolina have been conducted by Hosier (1975) on Kiawah Island and by Stalter (1976) at Huntington Beach.

Farther north Higgins et al. (1971) performed an ecological study of the coastal strand of Assateague Island, which is located off the coasts of Maryland and Virginia. Salinity and pH of water samples from the water table were measured and the following edaphic factors were determined at three soil depths (surface, 20 cm, and water table): salinity, pH, magnesium, phosphorus (as P_2O_5), and potassium (as K_2O).

Martin (1959) studied a number of ecological factors during his extensive investigation of the maritime vegetation of Island Beach State Park, which is located on a barrier island off the New Jersey coast. The following were considered: depth of the water table; salinity of the groundwater, bay water, and ocean water; salt spray distribution; and tolerance of plants to salt spray.

SPECIAL STUDIES

In addition to the ecological studies already cited, in which several environmental factors of the coastal strand were considered, a number of investigators have concentrated on a single environmental factor, or a few closely-related factors, operating in coastal strand habitats. Among the factors considered on an individual basis, salt spray has been studied most extensively.

Even before any quantitative studies of salt spray were done, several investigators were aware of the importance of salt spray in coastal areas and reported their observations concerning salt spray damage to coastal vegetation. Salisbury (1805) was the first to report such damage in England. A few years later Beck (1819) made a similar report of salt storms on the northeast coast of the United States. Other authors of the last century also attributed injury of coastal vegetation in Europe to salt particles transported by sea breezes (Focke, 1871; Anderlind, 1897).

Shreve (1910) was the first investigator in the United States to suggest that salt-laden wind, and not salt in the soil, was the factor most injurious to coastal vegetation. This idea was in keeping with the previous findings of Olsson-Seffer (1909b). About the same time in Europe Frodin (1912) and Hayren (1914) attributed the asymmetric growth forms and zonation of various coastal species to the action of salt spray; and Boodle (1920) credited the drying effects of the wind, and perhaps also salt spray, for the production of injury to coastal vegetation.

In the United States, however, it was not until the late 1930s that salt spray carried over the foredunes was recognized as the most important factor influencing zonation, growth-form, and succession of coastal strand vegetation (Wells and Shunk, 1937, 1938a, 1938b). At the same time Bayer (1938) attributed the asymmetrical and stunted growth of coastal plants in South Africa to the effects of wind-borne salt spray.

Somewhat later Wells (1939) studied the flora of Smith island, North Carolina, and interpreted the dominance of live oak (Quercus

virginiana) there as being primarily due to its tolerance to salt spray of moderate intensity. He recognized the apparently stable plant community on Smith Island as a new type of climax, and designated it as the "salt spray climax."

Wallace and Moss (1939) and Moss (1940) gave a remarkable report of salt spray damage to trees that extended as far as 45 miles inland due to the hurricane of September 21, 1938. The area of Connecticut and Rhode Island affected was the same as that examined by Beck (1819) after the hurricane of September 23, 1815.

Doutt (1941) made field observations of the effects of salt spray on the coastal vegetation of the Belcher Islands near Hudson Bay, Canada, the coast of California near San Mateo, and the island of Trinidad, British West Indies. He concluded that wind and salt spray interact as pruning agents in the coastal areas examined and that in certain inland sites far removed from the ocean (e.g. near Mirror Lake, Uinta Mountains, Utah) the action of wind alone results in severe pruning of woody plants. Shortly thereafter a number of authors in many parts of the world published their observations of salt spray as a damaging and zonation-causing factor in regards to coastal vegetation. These papers included Hepburn (1943) for England; Edlin (1943) for the south coast of Africa; Egler (1947) for Hawaii; Gooding (1947) for Barbados; and Numata et al. (1948) and Sekiya (1950) for Japan.

Boyce (1951a, b) studied the sources of atmospheric salt, using a number of different collection methods over the sea and on land, and investigated the relationship of salt spray to succulence of dune plants. In a subsequent study Boyce (1954) investigated the source of

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salt spray, the transportation and deposition of salt particles, the relation of salt spray to the zonation and growth forms of coastal plants, the variation in tolerance of species to salt spray, and the responses of different species to high concentrations of oceanic salts.

Observations of salt storms in various countries and damage to maritime vegetation produced by wind-borne salt spray continued to appear in the literature. Recent reports included Edlin (1957) for England; Nobuhara et al. (1962) and Nobuhara and Toyohara (1964) for Japan; and Zuloaga (1966) for Venezuela.

In recent years quantitative studies of salt spray intensity and distribution have been undertaken in a number of countries. Reports have been published by the following authors for investigations in the countries listed: Japan--Fujiwara and Umejima (1962); Wales--Edwards and Claxton (1964), Rutter and Edwards (1968), Edwards and Holmes (1968); Barbados--Randall (1970); Fiji--Cassidy (1971); England--Malloch (1972); United States (California)--Clayton (1972), Barbour (1978).

Several investigators have studied the tolerance to wind-borne salt spray of coastal strand plants at various sites along the eastern United States seaboard. Some of these studies were included within more extensive ecological studies that have already been cited and are mentioned again here to call attention to them. They include Martin (1959), Boerner and Forman (1975), and Cartica and Quinn (1980) for plants along the New Jersey coast; Wells and Shunk (1938a), Oosting and Billings (1942), Oosting (1945), Boyce (1954), and Au (1969, 1974) for plants along the North Carolina coast; and Stalter (1976) for plants along the South Carolina coast.

Two authors have addressed themselves to the question of whether or not coastal strand plants are truly halophytes.

Kearney (1904) measured the soluble salt contents of dune and beach soils on the coasts of Massachusetts (near Woods Hole), Virginia (near Norfolk), and California (near Long Beach). The sites he studied supported Uniola paniculata and Ammophila breviligulata among other species. He stated that "So far as the data yet available may warrant a generalization, we must therefore conclude that plants of sandy sea beaches and dunes are not generally halophytic, although, as in the case at Long Beach, species that are elsewhere characteristic of strongly saline soils and belong to truly halophytic associations may enter into the vegetation of the sand strand."

More recently Barbour (1970) considered the matter in some detail. Referring to earlier works of Kearney (1904), Davis (1942), Oosting and Billings (1942), and Seneca (1969), and to his own observations concerning Cakile maritima and Lupinus arboreus, he stated that "one may conclude that strand species appear to be intolerant halophytes and cannot be described as either facultative or obligate halophytes."

A number of other investigators have conducted specialized studies into limited aspects of coastal strand ecology. Most of these studies have considered various edaphic factors, but factors such as mineral cycling, effects of wind-borne sand, and the chemical composition of water in dune areas have also been considered.

Kearney (1904) and Olson-Seffer (1909a) studied the relation of soluble salts in soil to vegetation in coastal areas. Gooding (1947) studied soil water content, soil salt content, and soil pH of sand dunes

on Barbados. Wright (1956) measured the levels of total phosphate, potassium, magnesium, sodium, and calcium in dune soils of Morayshire, Scotland. Gillham (1957) measured organic matter, water content, pH, and salinity of dune soils on the islands of Mull and Iona, which are located off the northwest coast of Scotland. Gorham (1958) measured the concentrations of numerous soluble salts in dune soils from Blakeney Point, Norfolk, England, and in well water from the same area; later (1961) he also measured the chemical composition of surface waters from dune slacks at Sandscale, North Lancashire, England. Wilson (1960) conducted a detailed study of pH, organic content, and calcium carbonate content of dune soils at South Haven Peninsula, Dorset, England. Willis and Yemm (1961) investigated the mineral nutrient status of dune soils in North Devon, England, using tomato plants as indicators; and Willis (1963) studied the effects on the vegetation of mineral nutrient additions to dune soils of the same area. Berenyi (1966) studied soil productivity factors on the Outer Banks of North Carolina.

Etherington (1967) studied the cycling of soil potassium in a dune grassland at Kenfig Burrows, Glamorganshire, South Wales. Clayton (1972) studied cycling of sodium, calcium, potassium, and magnesium along the coast of California. Van der Valk (1974b) performed a similar study of cycling of potassium, sodium, calcium, and magnesium in coastal foredune communities on Bodie and Ocracoke Islands, North Carolina.

Farrow (1919) studied the general effects of blowing sand upon vegetation at Breckland, England. Similarly, Ranwell (1958) studied the rate of movement of the dune system at Newborough Warren, Anglesey, England, and how the vegetation was affected by moving sand. In the

United States Kurz (1939) investigated the reactions of certain plants (Magnolia grandiflora, Quercus geminata, Serenoa repens, Callicarpa americana, Ilex vomitoria, Muscadinia rotundifolia, Ilex glabra, Cephalanthus occidentalis, Magnolia virginiana, Pinus caribaea) to the movements of coastal dune sands in northwest Florida (Long Beach, 18 km west of Panama City).

AUTECOLOGICAL STUDIES

A number of autecological studies have been conducted in regards to plants that are important in dune strand habitats.

Laing (1958), Jagschitz and Bell (1966), Seneca (1969, 1972b), and Seneca and Cooper (1971) studied various aspects of the ecology of Ammophila breviligulata. The ecology of Uniola paniculata has been studied in detail by Wagner (1964), Westra and Loomis (1966), Seneca (1969, 1972a, 1972b), and Harper and Seneca (1973). Colosi and McCormick (1978) conducted an autecological study of Iva imbricata. Burk (1961c) studied environmental variation of Heterotheca subaxillaris. The ecology of Quercus virginiana in the coastal strand has been elucidated by Wells (1939), Bourdeau and Oosting (1959), and Laessle and Monk (1961). Cartica and Quinn (1980) investigated various aspects of the ecology of Solidago sempervirens.

METHODS

LOCATION OF STUDY SITE AND FIELD DATA STATIONS

The present study was conducted within the boundaries of the Ft. Pickens Unit of Gulf Islands National Seashore on the western end of Santa Rosa Island, Escambia County, Florida. Ten stations were established for the collection of field data at the widest part of the island, where dune systems and a well-developed pine forest occur (Figure 1). Stations 1 through 7 were located south of Ft. Pickens Road on an imaginary north-south line approximately 1.0 km west of Battery Langdon, and stations 8 through 10 were located north of Ft. Pickens Road on an imaginary north-south line approximately 0.8 km west of Battery Langdon. This offset arrangement in the placement of the stations was necessary to avoid a greatly disturbed area associated with Blackbird Marsh and nearby camping sites.

Stations were chosen so that they constituted representative sites within the different vegetation zones which were studied. Stations 1, 2, 3, 4, and 5 were in the sea oats zone; station 6 in the shrub zone; stations 7 and 8 in the pine forest; and stations 9 and 10 in the bluestem zone. Since stations 1, 2, 3, 4, 5, 6, 9, and 10 were located at sites in exposed dunal areas they were designated as dune stations, in contrast to the two remaining stations (7 and 8) which were not located in open dunal sites and were designated as pine forest stations.

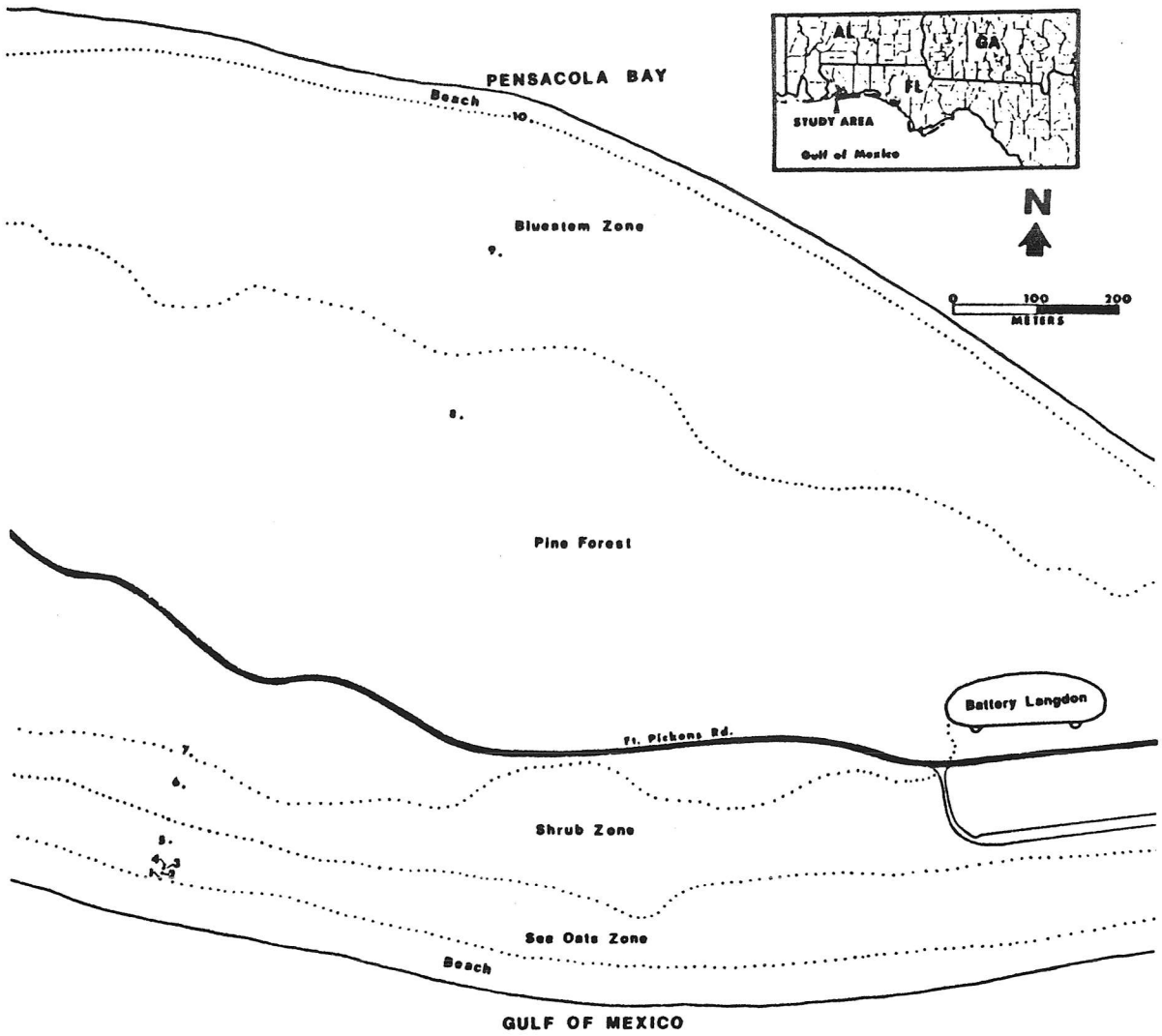


Figure 1. Study area on western end of Santa Rosa Island showing locations of field data stations and approximate boundaries of vegetation zones. Inset shows general location of study area.

Descriptions of the ten station locations are as follows: station 1--the leading edge of vegetation on the gulfward side of the island, or the inland edge of the beach strand; station 2--the south slope, or gulfward slope, of the barrier dune; station 3--the crest of the barrier dune; station 4--the north (or back) slope of the barrier dune; station 5--north of the barrier dune ridge (approximately 25 m north of station 4); station 6--within the shrub zone (approximately 67 m north of station 5); station 7--near the south edge of the pine forest (approximately 39 m north of station 6); station 8--deep within the pine forest (approximately 366 m north of Ft. Pickens Road near the Vitis rotundifolia marker of Blackbird Marsh Nature Trail); station 9--in the bluestem zone approximately halfway between the north edge of the pine forest and Santa Rosa Sound (approximately 195 m north of station 8); and station 10--near the top of the scarp which drops to the bare beach strand along the north side of the island (approximately 161 m north of station 9).

VEGETATION SAMPLING

The vegetation of the four plant communities (sea oats community, shrub community, pine forest community, and bluestem community) in the study area was sampled quantitatively using the nested plot technique described by Daubenmire (1968). Figure 2 shows a diagram of the plot system, which consists of three contiguous rectangular macroplots each measuring 25 x 5 m. All tree species taller than 1 m were counted and catalogued by the following trunk diameter classes in all three of the macroplots of a given set: 0.0-0.5 dm, 0.5-1.0 dm, 1.0-2.0 dm, 2.0-3.0

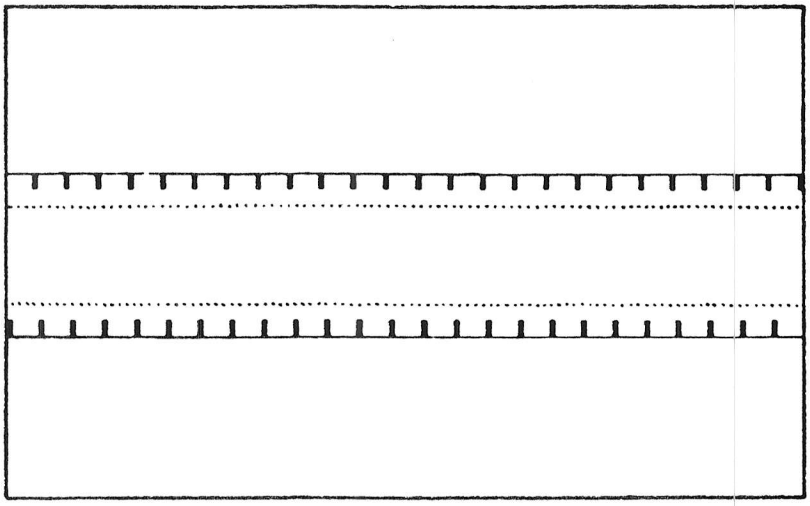


Figure 2. Diagram of nested plot system used for quantitative vegetation analysis in the present study. The three contiguous macroplots each measure 25 m by 5 m. Dotted lines delimit two strips which are each 1 m wide along the sides of the central macroplot. The black rectangles represent coverage microplots measuring 20 cm by 50 cm. (From Daubenmire, 1968.)

dm, 3.0-4.0 dm, 4.0-5.0 dm. Trunk diameters were measured with a pair of calipers. Trees less than 1 m tall (seedlings) were counted in two strips 1 m wide along the side of the central macroplot. Coverage of shrubs and herbaceous species was tallied in the 50 microplots (which measured 20 x 50 cm) at 1-m intervals along the side of the central macroplot.

In the treeless dune zones (sea oats zone, shrub zone, and bluestem zone) only the central macroplot, and its included microplots, was needed to analyze the vegetation. Fourteen such macroplots, with the long axis of each oriented parallel to the long axis of Santa Rosa Island, were examined in the three dune zones. In the sea oats zone one macroplot was examined near each of stations 1, 2, and 5, and two near

each of stations 3 and 4, with one located to the east and the other to the west of each station. However, due to the limited widths of the areas near stations 1, 2, 3, and 4, microplots for determination of vegetation coverage were spaced along both sides of an imaginary line, rather than being placed along the sides of the macroplot. Two macroplots were examined in the shrub zone, with one located to the east and one to the west of station 6. In the bluestem zone one macroplot was examined just north (approximately 5 m) of the pine forest and two macroplots were examined near each of stations 9 and 10, with one to the east and one to the west of each station.

In the pine forest one set of macroplots was examined at each of the following locations: (1) near station 7 at the south edge of the pine forest; (2) approximately 44 m north of Ft. Pickens Road and approximately 1.0 km west of Battery Langdon; (3) approximately 136 m north of Ft. Pickens Road and approximately 1.0 km west of Battery Langdon; (4) near station 8; and (5) near Blackbird Marsh Nature Trail approximately 18 m southwest of "The Marsh Nature Trail" information plaque.

The frame used to estimate coverage of shrubs and herbaceous species (according to the method of Daubenmire (1968)) at the 50 microplots associated with the central macroplot of each macroplot set is shown in Figure 3. The painted pattern on the 20 x 50 cm frame provides areas for visual comparison equal to 5, 25, 50, 75, and 95 percent of the total area enclosed by the frame. Each herbaceous or shrub species enclosed by the frame, or extending over or into the framed area, was scored and its areal coverage estimated, using the markings on the frame

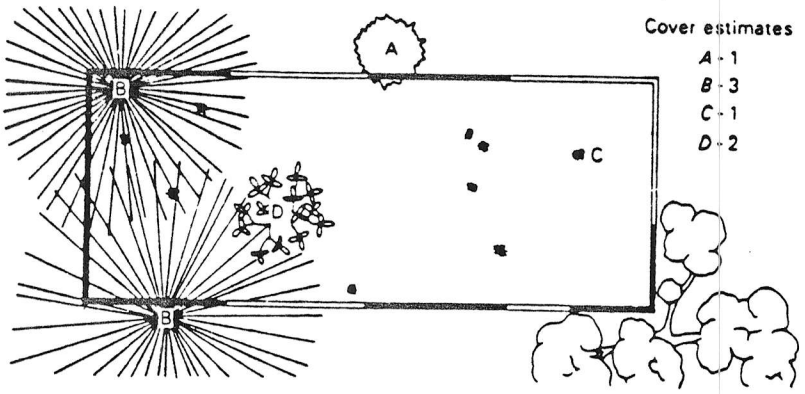


Figure 3. Diagram of frame used for estimating coverage of shrubs and herbaceous plants in the present study. Coverage estimates according to the classes described in the text are shown for hypothetical species A through D. (From Daubenmire, 1968.)

to assign each species to one of the six following coverage classes: (1) 0-5 %, (2) 5-25 %, (3) 25-50 %, (4) 50-75 %, (5) 75-95 %, and (6) 95-100 %. To calculate the coverage of a species in a series of microplots, the midpoint of each coverage class to which it was assigned during the field examination was tallied for each microplot in which the species was encountered, and the sum was averaged by dividing by the total number of plots examined.

Frequency (the percentage of microplots in which a species occurred) and constancy (the percentage of macroplot sets in which a species occurred) were calculated according to Phillips (1959) for each herbaceous and shrub species encountered.

NOMENCLATURE AND IDENTIFICATION OF PLANTS

The vascular plants observed during this study were identified using standard taxonomic techniques (Porter, 1967) and the following

general taxonomic reference works: Small (1933), Kurz and Godfrey (1962), and Radford et al. (1968). Certain genera presented special taxonomic difficulties. For these, monographs or special treatments were consulted to determine identity and proper nomenclature. For the genus Chrysopsis the present study followed the treatment of Semple (1977, 1978); for the genus Cakile, that of Rodman (1974); for the genus Schizachyrium, that of Godfrey and Wooten (1979); and for the genus Quercus, that of Coker and Totten (1945).

Voucher specimens of the vascular plants were collected and deposited at the herbarium of the University of West Florida, Pensacola (UWFP). Voucher specimens of some species were also deposited into the herbarium of the University of Florida, Gainesville (FLAS), whose staff provided assistance in identification of certain species.

The few lichens which were encountered during the present study were identified using primarily Kurz (1942), which included a section on lichens of the coastal dunes and scrub of northwest Florida. Fink (1935), Hale (1961, 1969), Thomson (1967), and Moore (1968) were also consulted for additional lichen identification information.

SORENSEN'S INDEX OF SIMILARITY

Sorensen's index of similarity (Carlton, 1977) was used to numerically compare the vegetation at the present study site with vegetation at other coastal sites along the northern Gulf of Mexico, the eastern seaboard of the United States, and northern Mexico. This index expresses similarity as the percentage of species shared by two sites and is calculated by the following formula: $IS = [2C/(A + B)] \times 100$,

where A = total number of species present at site A, B = total number of species present at site B, and C = number of species shared by both sites. A high index of similarity value indicates great similarity between two communities; conversely, a low index value indicates little similarity between communities.

ENVIRONMENTAL FACTORS

SOIL FACTORS

Organic Matter, Moisture, Nutrients, and Other Chemical Factors

Soil samples for the analysis of organic matter, moisture content, and water-soluble chloride content were collected at depths of 10 cm and 20 cm at stations 1 through 10 on May 12, 1979.

Soil moisture was determined using the method described by Au (1974). In the laboratory soil samples weighing approximately 50 g were oven-dried at 110 ^{o}C for 24 hours and then reweighed. The soil moisture lost was expressed as percentage of oven-dry weight of the soil.

Organic matter was determined by the loss-on-ignition method used by Au (1974). In the laboratory 20 g of soil, oven-dried at 110 ^{o}C for 24 hours, was placed into a porcelain crucible and ignited in a muffle furnace at 650 ^{o}C for one hour, and then reweighed after cooling to room temperature in a desiccator. The organic matter content, i.e. the weight lost during ignition, was expressed as the percentage of soil oven-dry weight.

Water-soluble soil chloride content was determined on an aqueous extract using an Orion Model 407A Ionalyzer with a chloride ion electrode. After being oven-dried at 110 ^{o}C for 24 hours, soil samples of

approximately 20 g were added to 100 ml of deionized water. To prevent sulfide interference 2 ml of a 2 M $Ni(NO_3)_2$ solution was added to each sample. After 30 minutes, during which time the sample was stirred frequently, chloride concentration of the supernatant was read and recorded in parts per million (ppm). The amount of chloride in the soil was calculated from the supernatant chloride concentration.

Soil samples for chemical analyses were collected at depths of 5 cm and 10 cm at stations 1 through 10 on July 12, 1979. These samples were analyzed by the soils laboratory of the Department of Agriculture and Consumer Services of the University of Florida, Gainesville, for the following parameters: pH, calcium, magnesium, potassium, sodium, phosphorus, nitrate, and soluble salts. Analyses for calcium, magnesium, potassium, sodium, phosphorus, and nitrate were performed on an acid extract of the soil; pH and soluble salts analyses employed a simple aqueous extract. Cation exchange capacity was calculated by the sum-of-cations technique (U.S. Soil Conservation Service, 1972).

Temperature

Soil temperature was measured at stations 1 through 10 at the soil surface, 10 cm below the surface, and 25 cm below the surface. Ordinary mercury-bulb thermometers (from Fisher Scientific Company) were used. These were checked against an ice-water solution and boiling water to insure accuracy, and thermometers which varied by no more than 0.5 ^{o}C from expected values were selected for field use. At each station, one thermometer was placed with its bulb at the soil surface and two thermometers were carefully inserted into the soil to the respective depths

of 10 cm and 25 cm. After 90 seconds of exposure to allow stabilization, the temperature at each depth was recorded.

Soil temperatures were read at three times during a single 24-hour study period (6 AM, noon, and 6 PM) during different seasons of the year. The four soil temperature study periods were February 17-18, 1979, April 14, 1979, July 7, 1979, and September 16-17, 1978. Noon and 6 PM soil temperature readings were taken on September 16, 1978, and February 17, 1979, and the 6 AM readings for those two 24-hour periods were taken the following mornings on September 17, 1978, and February 18, 1979, respectively. The reason for reading soil temperatures at midday and evening of one date and then taking readings early in the morning of the following day was to demonstrate the predicted cooling-off effect of the night-time hours in the strand.

It was not possible to read soil temperatures simultaneously at all stations and depths (due to limitations of equipment and personnel). Thus, for a given study date and time, soil temperatures were read in sequence from station to station, starting with station 1 and proceeding as quickly as possible to each successive station until soil temperatures at all ten stations were recorded. A complete run took 45 to 55 minutes to finish, so that, for example, for the 6 AM temperature run on a given study date, soil temperatures at station 1 were recorded at approximately 6 AM and temperatures at station 10 at approximately 6:45-6:55 AM. In the tables of results, temperatures were listed under the time that the particular sampling run was begun.

ATMOSPHERIC FACTORS

Air Temperature

Air Temperature 30 cm above the soil surface was measured concurrently with soil temperatures at all ten stations. The same type of thermometer used to measure soil temperature was also used to measure air temperature. To achieve the proper height above the soil surface, a wooden stake with a small shelf projecting from its side was driven into the ground so that the shelf was 30 cm above the soil surface, and the thermometer, with it bulb resting on the shelf, was held against the stake in an upright position with a rubber band. The thermometer was allowed to stabilize for 90 seconds before the air temperature was recorded. In the tables of results, air temperatures were listed under the time that a particular run was begun.

Two special series of hourly air temperature measurements were made in association with the atmometer studies (q.v.) at stations 1 through 4 from 10 AM to 6 PM on August 29 and September 8, 1979. The same equipment described above was used; however, four stakes and four thermometers were set out and exposed for the eight-hour duration of each run. At the start of each hour the thermometer at station 1 was examined and the air temperature recorded. Subsequently, the other thermometers were similarly examined in sequence as quickly as possible until all four stations had been visited. This process took less than ten minutes to accomplish in each case. Results were tabulated under the hour in which a particular run was started.

Relative Humidity

A sling psychrometer (Bacharach Instrument Company, Catalog No. 12-7011) was used to determine relative humidity of the air at the ten data stations. The psychrometer was held approximately 0.9 m above the soil surface, with the operator in a kneeling position, and was whirled at approximately two to three revolutions per second for approximately 90 seconds to stabilize the thermometer readings. Then the wet-bulb thermometer temperature was immediately noted and recorded, and afterward the dry-bulb thermometer temperature was read. Later, a psychrometric chart (published by the U.S. National Weather Service) was used to obtain the relative humidity values.

As with soil temperatures, psychrometer readings were taken at 6 AM, noon, and 6 PM during four 24-hour study periods at different seasons. The study dates were October 7-8, 1978, March 11, 1979, April 21, 1979, and August 4, 1979. On October 7, 1978, readings were taken at noon and 6 PM, and the 6 AM readings for that 24-hour period were taken the next morning.

As with soil temperatures, psychrometer readings for a given time and study date were taken in sequence from station to station, starting with station 1 and proceeding as quickly as possible in numerical order to each succesive station until readings had been recorded at all ten stations. In the table of results, relative humidity values were listed under the time that the particular psychrometric run was begun.

Two series of hourly psychrometric readings were taken in association with the atmometer studies at stations 1 through 4 from 10 AM to 6 PM on August 29 and September 8, 1979. At the start of each hour,

psychrometric readings were taken as described above at station 1, and then at the other three stations, as quickly as possible in numerical sequence until all four stations had been visited. Results were tabulated under the hour in which each run was begun.

Evaporation

The evaporative power of the air was measured using Livingston white-bulb atmometers (cf. Livingston, 1935) obtained from Kahl Scientific Instrument Corporation. The Livingston atmometer consists of a thin-walled hollow sphere (5 cm in diameter) of unglazed white porcelain and a cylindrical neck (2.5 cm in diameter) of glazed impermeable porcelain. Water soaks through the wall of the sphere and readily evaporates into the surrounding air. The sphere, with its neck uppermost, was filled with distilled water, and a brass tube which passed through a rubber stopper was inserted into the base of the neck with the stopper forming a leakproof seal against the inside of the neck. The tube was filled with distilled water and the assembly was then inverted with the base of the tube passing through another rubber stopper and into a reservoir bottle containing more distilled water. Thus assembled, the apparatus consisted of a water-filled sphere connected via a water-filled tube to a water-containing reservoir (Figure 4).

The assembled water-filled atmometer, with a plastic bag placed over the porcelain bulb (and held with a rubber band) to prevent premature evaporation, was weighed to the nearest 0.1 g before being taken into the field. In the field the plastic bag was removed and the bulb exposed for a given time period. The assembled atmometer apparatus was placed with the atmometer bulb situated 30 cm above the soil surface and

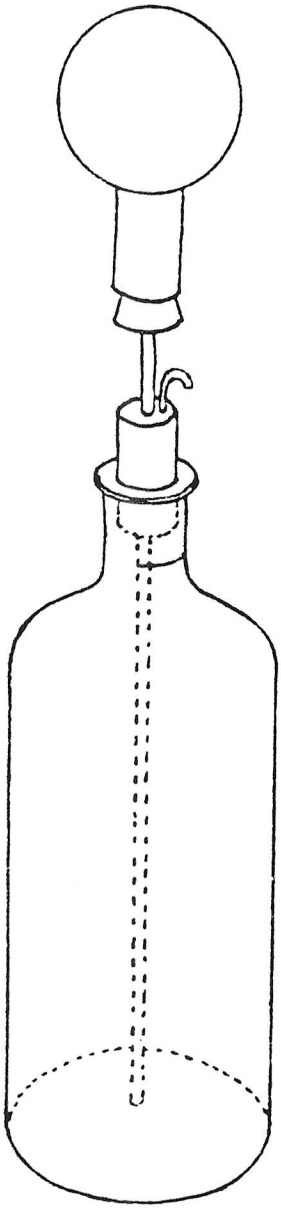


Figure 4. Livingston atmometer consisting of a white porous porcelain sphere mounted atop a glass bottle reservoir via an assembly of rubber stoppers and a brass tube. (From Livingston, 1935.)

the reservoir bottle inside a metal can attached to a wooden stake driven into the ground to prevent it from being overturned. At the end of the exposure time, the plastic bag was replaced and the apparatus was taken back to the laboratory and weighed to determine the weight of water evaporated during field exposure. This loss was expressed as ml/hr of water evaporated.

Two runs, with atmometers exposed at stations 1 through 4 for eight hours, were made on August 29 and September 8, 1979. One run, with one atmometer exposed for eight hours in each of the three dune vegetation zones and one atmometer in the pine forest, was made on October 13, 1979. During this run one atmometer was exposed at each of stations 6, 8, and 9. However, since Hurricane Frederic (September 12-13, 1979) had destroyed the barrier dune at the study site, the sea oats zone atmometer was exposed on a dune remnant somewhat to the northwest of the original location of station 3. A similar run was made on March 14-15, 1980, in which atmometers were exposed for 24 hours at the same locations as on October 13, 1979. On June 19-20, 1982, an additional 24-hour run was made with atmometers exposed at stations 6, 7, 8, and 9.

Wind-borne Salt Spray

Long-term salt spray collectors similar to those described by Malloch (1972) were used. This apparatus consisted of a 40-cm length of cylindrical polyethylene tubing with an inside diameter of 5 cm, sealed at one end and open at the other (illustrated in Chapman, 1976). The tubes were filled to within 5 cm of the top with clean acid-washed fine quartz gravel and were then buried vertically in the ground with the open end upward and projecting 1 cm above the surface. After being

exposed for a given amount of time, the collectors were retrieved, and in the laboratory the gravel from each collector was elutriated with distilled water and the inside of the collector was rinsed with distilled water until a total volume of 500 ml of elutriate was obtained for each collector. Subsamples (100 ml in volume) of the elutriates were measured with an Orion Model 407A Ionalyzer with a chloride ion electrode to determine the amount of chloride collected by each unit. From these results the amount of salt spray received by each collector was calculated using the following formula from Ingmanson and Wallace (1973): Salinity = 1.80655 Chlorinity.

Two long-term salt spray runs of 60 days each, one of 65 days, and a fourth run of 100 days were conducted, with one collector exposed at each of the ten data stations. However, since Hurricane Frederic had destroyed the barrier dune at the original study site, collectors for stations 1 through 5 were placed, instead, on a comparable undamaged barrier dune (and north of it) further east on Santa Rosa Island (approximately 1.4 km east of the intersection of Via DeLuna and Calle Juella); collectors were placed at the original stations 6 through 10. A blank collector in which the gravel was saturated with distilled water and the top sealed with a plastic bag was retained in the laboratory as a control for each field run.

RESULTS

DESCRIPTION OF GENERAL STUDY AREA

Santa Rosa Island is a barrier island located in the Gulf of Mexico approximately 2.5 km south of the extreme northwestern coast of Florida and separated from the mainland by Santa Rosa Sound and the south end of Pensacola Bay. The island's shape is elongate in a basically east-west direction with the long axis extending for 82 km parallel to the mainland's coastline. Most of the island is less than 0.8 km wide, but for its westernmost 5 km it is considerably broader, with the maximum width being approximately 1.25 km.

The most outstanding feature of Santa Rosa Island is the gleaming-white incoherent sand which constitutes the main component of the island's soils and forms a line of low barrier dunes (also termed foredunes or primary dunes) near the south side of the island inland from a bare beach strand. Scattered secondary sand dunes are located inland from the barrier dune line in some places. Low areas, known as swales, with a water table that is close to the surface and shallow standing water at certain times of the year, occur in the dune system.

On the narrow parts of Santa Rosa Island the bare beach strand and the dune-and-swale system occupy the entire width of the island and there is an absence of trees, the vegetation being dominated by herbs and low shrubs. On wider portions of the island a forest occurs inland

from the treeless dune-and-swale zone and a salt marsh community may be found on the soundward side. At other points a narrow bare beach strand is situated on the north side of the island along Santa Rosa Sound and Pensacola Bay.

The wide western end of Santa Rosa Island within the boundaries of Gulf Islands National Seashore, where this study was conducted, supports a well-developed pine forest, in addition to a treeless dune-and-swale system, and has bare beaches along its north and south shores.

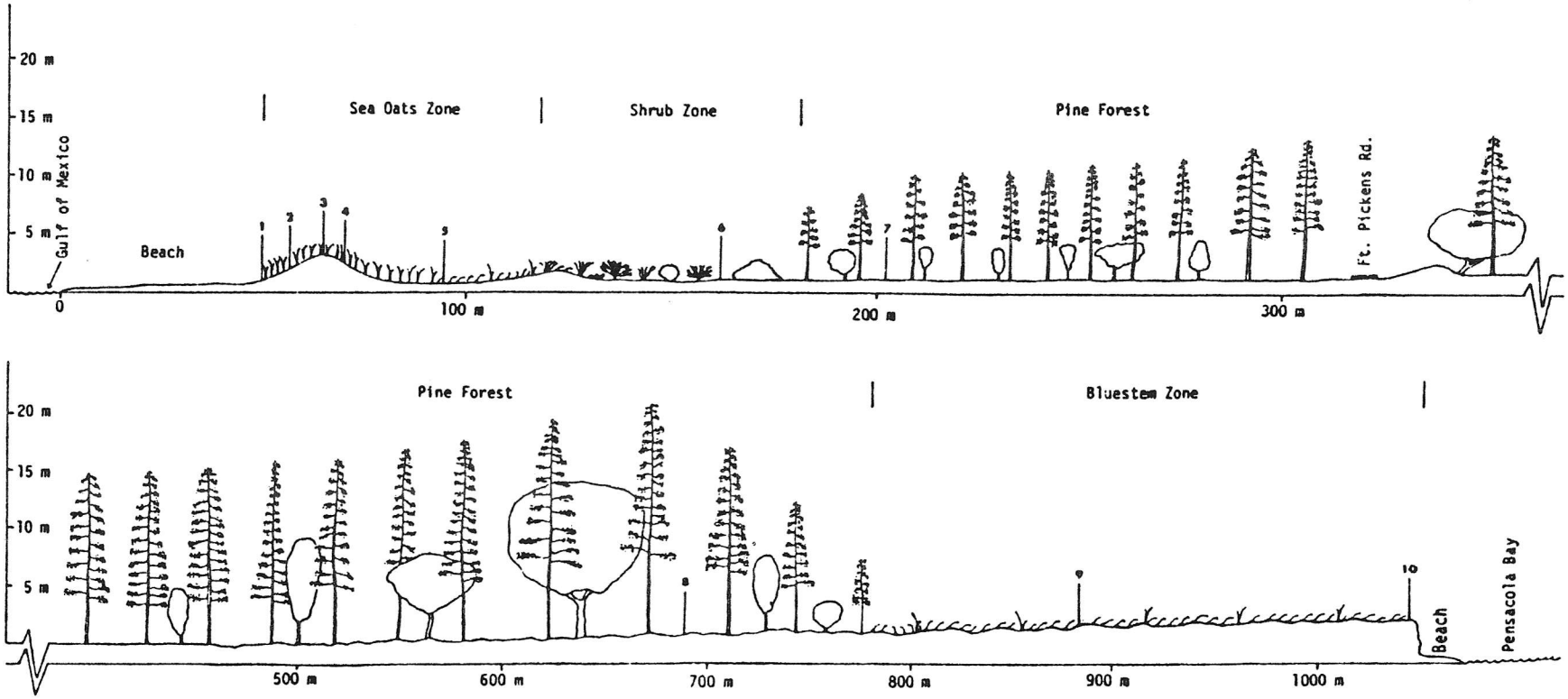
VEGETATION

Four distinct vegetation communities, or zones, were observed at the study site: (1) sea oats zone, (2) shrub zone, (3) pine forest, and (4) bluestem zone. Figure 5 is a profile across Santa Rosa Island at the study site, showing the location and approximate width of these zones. Each zone is considered separately below.

SEA OATS ZONE

The sea oats zone of this study is equivalent to the pioneer zone described by Davis (1975). Quantitative data for this community is presented in Table 1. This zone extended from the inland edge of the bare beach strand on the Gulf side of Santa Rosa Island across the primary dune ridge (approximately 2.1 m high) and secondary dunes and measured approximately 73 m in width.

As the name of this zone indicates, Uniola paniculata was the dominant species. The coverage of U. paniculata, however, varied across the zone. At the southernmost edge adjacent to the bare beach it was only 4.8 percent. This increased somewhat on the front (south) slope of the



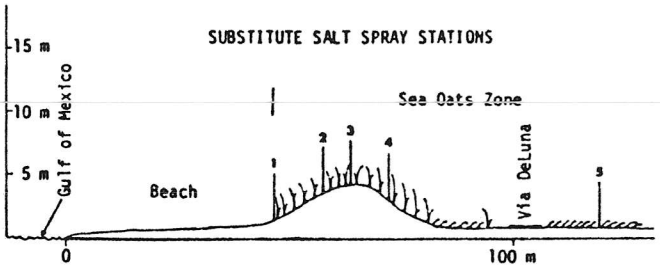


Figure 5. Profile across Santa Rosa Island at the study site showing the width and stylized physiognomy of the vegetation zones and the locations of the field data stations. Profile showing locations of substitute salt spray Stations 1 through 5 is at the bottom left.

Table 1

Sea Oats Zone Data

Coastal Strand Vegetation

Santa Rosa Island, Florida

	Initial Edge		Front Slope of Dune		Crest of Dune		Rear Slope of Dune		North of Dune		Combined		
	Cov.(%)	Freq.(%)	Cov.(%)	Freq.(%)	Cov.(%)	Freq.(%)	Cov.(%)	Freq.(%)	Cov.(%)	Freq.(%)	Cov.(%)	Freq.(%)	Const.(%)
Herbaceous Angiosperms:													
Uniola paniculata	4.8	56.0	5.7	82.0	41.5	99.0	17.8	92.0	3.3	64.0	18.9	83.4	100.0
Galactia microphylla					3.9	32.0	2.5	36.0	0.4	14.0	1.9	21.4	71.4
Schizachyrium maritimum					2.1	16.0	<0.1	3.0	4.0	78.0	1.2	16.0	57.1
Conyza canadensis var. pusillus			0.2	6.0	1.5	51.0	1.4	50.0	<0.1	2.0	0.9	30.3	85.7
Chrysopsis godfreyi					0.6	17.0	0.9	19.0	1.5	38.0	0.7	15.7	71.4
Polygonella gracilis					0.4	15.0	0.8	32.0	0.5	18.0	0.4	16.0	71.4
Hydrocotyle bonariensis	<0.1	2.0	0.2	6.0	0.7	23.0	0.7	18.0			0.4	12.9	85.7
Oenothera humifusa	0.4	6.0	1.3	24.0	0.5	9.0	0.2	6.0			0.4	8.6	85.7
Chamaesyce ammannioides			<0.1	2.0	0.3	11.0	0.3	12.0	0.2	8.0	0.2	8.0	71.4
Balduina angustifolia					0.2	4.0	0.1	5.0	0.6	24.0	0.2	6.0	42.9
Paronychia erecta					<0.1	2.0	0.1	5.0	0.9	26.0	0.2	5.7	42.9
Panicum portoricense									1.7	28.0	0.2	4.0	14.3
Polypremum procumbens									0.6	22.0	0.1	3.1	14.3
Heterotheca subaxillaris									0.5	10.0	0.1	1.4	14.3
Ipomoea stolonifera	0.1	4.0	*		0.2	2.0			<0.1	2.0	0.1	1.4	42.9
Panicum amarum	*		*						0.3	10.0	<0.1	1.4	14.3
Helianthemum corymbosum									0.4	6.0	<0.1	0.9	14.3
Asclepias humistrata									<0.1	2.0	<0.1	0.3	14.3
Cakile constricta	<0.1	2.0	*								<0.1	0.3	14.3
Sesuvium portulacastrum	*												
Linaria floridana							*						
Shrubs and Woody Vines:													
Chrysoma pauciflosculosa									1.8	6.0	0.3	0.9	14.3
Smilax auriculata									0.4	8.0	<0.1	1.1	14.3
Iva imbricata	0.3	2.0	*								<0.1	0.3	14.3
Opuntia humifusa									*				
Cryptogams:													
Usnea strigosa									<0.1	2.0	<0.1	0.3	14.3
	5.6		7.4		51.9		25.0		17.0		26.3		

* Present, but not encountered in coverage plots.

barrier dune, reached a maximum of 41.5 percent on the crest of the dune, then decreased on the rear slope to 17.8 percent, and finally reached a minimum of 3.3 percent north of the dune ridge, where Schizachyrium maritimum actually had slightly greater coverage (4.0 percent).

At the initial edge of this zone, adjacent to the bare beach, the total vegetation coverage was quite sparse (5.6 percent). Here occurred a number of plants which grow primarily (but not exclusively) at this point in the coastal strand: Hydrocotyle bonariensis, Sesuvium portulacastrum, Cakile constricta, and Iva imbricata.

The general aspect of this zone was that of a moderately-vegetated (26.3 percent overall coverage) landscape punctuated with dunes and swales and dominated by herbaceous plants. Three herbaceous plants (Uniola paniculata, Galactia microphylla, and Schizachyrium maritimum) covered most of the vegetated area. A few woody species (Chrysoma pauciflosculosa, Smilax auriculata, and Opuntia humifusa) were found in the rear of this zone behind the barrier dune ridge. One low shrub (Iva imbricata) occurred in front of the barrier dune line.

SHRUB ZONE

Table 2 presents quantitative data for this zone, which is equivalent to the scrub zone described by Davis (1975). It was situated inland from, and adjacent to, the sea oats zone, and was approximately 73 m wide.

This zone was dominated by shrubs, which had a combined coverage of 21.2 percent. Chrysoma pauciflosculosa and Ceratiola ericoides, with coverages of 7.4 and 7.0 percent, respectively, were co-dominants. The

Table 2

Shrub Zone Data
Coastal Strand Vegetation
Santa Rosa Island, Florida

	Coverage (%)	Frequency (%)	Constancy (%)
Shrubs and Woody Vines:			
Chrysoma pauciflosculosa	7.4	64.0	100.0
Ceratiola ericoides	7.0	23.0	100.0
Smilax auriculata	3.9	39.0	100.0
Ilex vomitoria	2.0	6.0	50.0
Quercus virginiana var. *geminata*	0.9	5.0	100.0
Herbaceous Angiosperms:			
Polygonella polygama	3.4	37.0	100.0
Polygonella gracilis	0.6	23.0	100.0
Balduina angustifolia	0.4	16.0	100.0
Helianthemum corymbosum	0.4	14.0	100.0
Panicum portoricense	0.3	5.0	100.0
Schizachyrium maritimum	0.3	10.0	100.0
Agalinis filifolia	<0.1	1.0	50.0
Galium hispidulum	<0.1	1.0	50.0
Chrysopsis godfreyi	*		
Cuscuta pentagona	*		
Paronychia erecta	*		
Cryptogams:			
Cladonia spp.**	17.4	85.0	100.0
Usnea strigosa	1.0	41.0	100.0
	45.4		

* Present, but not encountered in coverage plots.
** Two species were observed: *C. evansii* and *C. leporina*.

general aspect of this zone was similar to that of a desert landscape: scattered shrubs were interspersed with sparse herbaceous plants and bare expanses of white sand.

Three other woody plants (Ilex vomitoria, Quercus virginiana var. geminata, and Smilax auriculata) were less prominent in this zone. Although I. vomitoria and Q. virginiana var. geminata may achieve arborescent proportions elsewhere, here they occurred only as shrubs having the low, lopsided habit produced by salt spray pruning and sculpturing (cf. Boyce, 1954). The vine Smilax auriculata was the only woody vine observed in this zone, and, with a coverage of 3.9 percent, ranked third in dominance among woody plants here.

Coverage of herbaceous angiosperms was sparse in this zone. Of the ten species common here, only one, Polygonella polygama (which is actually somewhat suffrutescent), had a coverage of greater than 1.0 percent. This species, with a coverage of 3.4 percent, was the dominant herbaceous angiosperm of the zone. Another species of the same genus, P. gracilis, was the second-ranked dominant herbaceous angiosperm, with a coverage of 0.6 percent. Together these two species had a greater coverage than the combined coverages of all other herbaceous angiosperms in this zone.

Interestingly, in this zone the greatest area was occupied by lichens of the genus Cladonia, which covered 17.4 percent of the sand's surface. The two species of Cladonia also had the greatest frequency (85.0 percent) of the plants in this zone.

PINE FOREST

Table 3 presents the quanitative data for the well-developed slash pine forest located at the study site. This forest, which was approximately 561 m in width, was situated in an area of old stabilized low dune ridges and swales with an irregularly-shaped, well-developed freshwater marsh (Blackbird Marsh) in its center.

The dominant tree of this zone was Pinus elliottii, as demonstrated by the large number of this species scored in the study plots and by the fact that it had the greatest total basal area. Most individuals of P. elliottii were less than 0.5 dm in diameter, and the numbers of individuals decreased progressively for each larger diameter class, with no individuals encountered exceeding 5 dm in diameter. A few specimens of P. elliottii with trunk diameters greater than 5 dm were observed outside the study plots.

Quercus virginiana var. geminata and Persea palustris ranked second and third, respectively, in number of individuals in the forest canopy. As with P. elliottii, the majority of these two trees were less than 0.5 dm in trunk diameter. Other than P. elliottii, they were the only trees of considerable importance in this forest. The remaining four tree species were each scored only once, indicating their minimal importance. A single specimen of Pinus clausa was seen near, but not within, a study plot.

In the higher, drier areas (e.g. atop the old dune ridges) of the forest Quercus virginiana var. geminata was abundant and achieved massive size, but none of these old trees was encountered in the study plots. In the lower areas Persea palustris, a hydrophylic tree, was

Table 3

Pine Forest Data

Coastal Strand Vegetation

Santa Rosa Island, Florida

	Diameter Classes (dm)								
	0-0.5	0.5-1	1-2	2-3	3-4	4-5	Totals	Density (trees/ha)	Basal Area (m^2/ha)
Trees:									
Pinus elliottii	139	50	35	38	16	3	281	1499	25.01
Quercus virginiana var. *geminata*	30	11	14				55	293	1.65
Persea palustris	13	1					14	75	0.04
Quercus myrtifolia	1						1	5	<0.01
Nyssa biflora		1					1	5	0.08
Diospyros virginiana	1						1	5	<0.01
*Pinus clausa**									
							353		
Seedlings:									
Quercus virginiana var. *geminata*	69								
Persea palustris	16								
Pinus elliottii	10								
	95								

	Coverage (%)	Frequency (%)	Constancy (%)
Shrubs and Woody Vines:			
Ilex glabra	14.5	44.0	80.0
Smilax auriculata	7.3	30.0	100.0
Vitis rotundifolia	4.1	21.0	80.0
Myrica cerifera	3.0	9.0	60.0
Hypericum reductum	2.7	8.0	40.0
Ilex vomitoria	1.5	4.0	60.0
Ceratiola ericoides	1.5	5.0	20.0
Gaylussacia mosieri	1.3	4.0	20.0
Conradina canescens	0.9	2.0	20.0
Vaccinium darrowi	0.8	4.0	40.0
Smilax bona-nox	0.8	9.0	20.0
Rubus trivialis	<0.1	1.0	20.0
Toxicodendron radicans	<0.1	1.6	60.0
Ampelopsis arborea	<0.1	0.8	20.0
Kalmia hirsuta	<0.1	0.8	20.0
	38.4		

Table 3
(Continued)

	Coverage (%)	Frequency (%)	Constancy (%)
Herbaceous Angiosperms:			
Monocots			
Andropogon capillipes	0.7	4.8	60.0
Panicum portoricense	0.2	6.0	60.0
Schizachyrium maritimum	<0.1	0.4	20.0
Fuirena scirpoidea	<0.1	1.6	20.0
Juncus scirpoides	<0.1	0.8	20.0
Lachnanthes caroliniana	<0.1	0.8	20.0
Xyris caroliniana	<0.1	0.8	20.0
Dicots			
Polygonella polygama	0.3	6.4	60.0
Centella asiatica	<0.1	3.2	20.0
Polygonella gracilis	<0.1	2.0	20.0
Balduina angustifolia	<0.1	1.6	20.0
Euthamia minor	<0.1	1.6	20.0
Mikania scandens	<0.1	0.8	20.0
Drosera capillaris	<0.1	0.8	20.0
Helianthemum corymbosum	<0.1	0.4	20.0
Ipomoea sagittata	<0.1	0.4	20.0
Lippia nodiflora	<0.1	0.4	20.0
	1.2		
Cryptogams:			
Osmunda regalis	0.9	3.2	20.0
Cladonia spp.**	0.9	16.8	60.0
Usnea strigosa	0.1	3.6	40.0
Mosses	0.1	2.4	60.0
	2.0		

* Present, but not encountered in study plots.
** Two species were observed: *C. evansii* and *C. leporina*.

common, but none of the individuals observed were very large, with only one specimen having a trunk diameter greater than 0.5 dm.

In the seedling plots, specimens of only the three major tree species were encountered. Seedlings of Q. virginiana var. geminata were most abundant, being almost four times as abundant as those of Persea palustris and almost seven times as numerous as those of Pinus elliottii.

The understory of the pine forest was dominated by shrubs and woody vines. Ilex glabra was the dominant understory species, with a coverage of 14.5 percent--nearly twice that of Smilax auriculata, the next most abundant understory plant.

The general aspect of this forest, then, was that of a stand of Pinus elliottii (1499 trees/hectare) with a few other arborescent species intermixed and a moderately-dense (approximately 38.4 percent total coverage) understory of Ilex glabra and other shrubs. However, in some low areas with shallow standing water throughout the year, the shrub cover was absent and freshwater marsh existed, with species such as Typha domingensis, Cladium jamaicense, and Sagittaria lancifolia common there.

The heterogeneity of this forest, as shown by the mixture of the hydric and xeric species in the tree canopy influenced by topographic variation, was also seen in the shrub layer. Species such as Ilex glabra, Hypericum reductum, and Myrica cerifera occurred in low moist sites, whereas Ceratiola ericoides and Conradina canescens were found in relatively dry areas. These xeric species were common in the southern part of the pine forest, where it met the shrub zone, and on the higher old dune ridges within the forest. In the center of the forest near

Blackbird Marsh and in scattered swale areas, hydric shrubs dominated the understory stratum.

The herbaceous layer was not well developed in the pine forest, except in the freshwater marsh area and in exposed clearings. In the study plots the total herbaceous coverage was only approximately 3.2 percent. Most of the species encountered had less than 0.1 percent coverage, and all had less than 1.0 percent coverage.

As with the tree and shrub layers, the herb layer showed a heterogeneous mixture of hydric and xeric species correlated with topography. In fact, the highest coverage value (0.9 percent) was reported for the hydric fern species Osmunda regalis, which was found in and near the central freshwater marsh area of the forest, and for the two xeric lichens of the genus Cladonia, which were found in the southern part of the forest and on scattered old dune ridges. The species with the next greatest coverage (0.7 percent) was the hydrophilic grass Andropogon capillipes. This plant and others of hydric affinity (e.g. Fuirena scirpoidea, Juncus scirpoides, Centella asiatica, Drosera capillaris, Lachnanthes caroliniana, and Xyris caroliniana) were found primarily in the old swale areas of the forest. Other hydric species (Ipomoea sagittata, Lippia nodiflora, and Mikania scandens) were found in and near the central freshwater marsh area.

BLUESTEM ZONE

This vegetation zone was approximately 280 m wide and extended from the north edge of the slash pine forest to the bare beach strand paralleling the north side of Santa Rosa Island. Table 4 presents the

Table 4

Bluestem Zone Data
Coastal Strand Vegetation
Santa Rosa Island, Florida

	Coverage (%)	Frequency (%)	Constancy (%)
Shrubs and Woody Vines:			
Opuntia pusilla	*		
Smilax auriculata	*		
Herbaceous Angiosperms:			
Schizachyrium maritimum	23.2	90.8	100.0
Heterotheca subaxillaris	6.6	78.4	100.0
Uniola paniculata	6.2	42.0	100.0
Oenothera humifusa	0.7	14.4	100.0
Chamaesyce ammannioides	<0.1	0.8	20.0
Hydrocotyle bonariensis	<0.1	0.2	20.0
Ipomopsis rubra	*		
Rumex hastatulus	*		
Panicum amarum	*		
Triplasis purpurea	*		
Cryptogams:			
Usnea strigosa	*		
	36.7		

* Present, but not encountered in coverage plots.

quantitative data collected in the bluestem zone, which derives its name from the dominance of coastal bluestem (Schizachyrium maritimum).

Total vegetation coverage in this zone was a moderate 36.7 percent, and Schizachyrium maritimum, with 23.2 percent coverage, was clearly the dominant species. This grass formed a low-growing layer of herbage punctuated by scattered protruding plants of two taller species, Uniola paniculata and Heterotheca subaxillaris. With coverages estimated at 6.6 percent and 6.2 percent, respectively, H. subaxillaris and U. paniculata ranked second and third in dominance after S. maritimum. The other species encountered in this community had low coverage, with values of less than 0.1 percent each.

Almost all of the species scored in this zone were also found in the sea oats zone on the Gulf side of the island, and the two zones were physiognomically similar in that both were dominated by grasses. However, no prominent dune ridge occurred here (only scattered very low elevations), and the general aspect was that of an expanse of irregular, very low rises vegetated primarily by grasses.

In the main study area an abrupt cliff-like scarp, dropping approximately 2.5 m straight down to the beach strand at the northern edge of this zone, was noted. This scarp was actually the northern edge of the sandy spoil deposited here when the turning basin in Pensacola Bay was dredged in 1958-59. It was several hundred meters long, extending to the east approximately 0.5 km west of the site of the former U.S. Coast Guard station. Stapor (1975) presented a diagram that outlined the boundaries of the spoil area underlying the bluestem zone. Aerial photographs on file at the J. C. Pace Library showed that all of the spoil was deposited north of the pine forest, primarily into shallow

waters of Pensacola Bay, thus widening the island approximately 274 m. The north edge of the pine forest at the present study site was observed to be located exactly where it had been prior to spoil placement.

At the base of the scarp a heterogeneous assemblage of plants was found at irregular intervals. In addition to Heterotheca subaxillaris, Schizachyrium maritimum, and Uniola paniculata, which were common on top of the scarp, a number of plants found here were also abundant at the inland edge of the beach strand on the south side of the island: Cakile constricta, Hydrocotyle bonariensis, Ipomoea stolonifera, Iva imbricata, and Sesuvium portulacastrum. Conyza canadensis var. pusillus, which was common in the sea oats zone on the south side of the island, was found here. A number of halophytic species found on the mainland strand to the north were here as well; these included Atriplex arenaria, Spartina patens, Strophostyles helvola, Physalis angustifolia, and Paspalum distichum. Several plants found here were weedy species common to other sandy habitats and existed here as nonpersistent waifs. These were Cenchrus sp., Conyza bonariensis, Erechtites hieracifolia, Lepidium virginicum, Froelichia floridana, Xanthium strumarium, Ambrosia artemisiifolia, Diodia teres, and Actinospermum australe. Seedlings of Carya sp., Quercus hemisphaerica, Taxodium distichum, and Crinum americanum found here were obviously derived from propagules washed ashore in the flotsam from Santa Rosa Sound and did not mature nor persist.

All of the species encountered at the base of the scarp had coverages less than 0.1 percent; and, since most of the species were nonpersistent waifs, or were found farther inland on the island, this melange of species was considered to be merely the heterogeneous flotsam-influenced edge of the bluestem zone. This concept was

supported by the fact that the same admixed array of species was also found beyond the eastern limit of the scarp.

Farther to the east on Santa Rosa Island, where it was narrower and devoid of trees, this bluestem zone was found to be contiguous with the sea oats zone (but was still situated on the soundward side of the island), and the two communities, having similar species compositions, intergraded imperceptibly. The feature which distinguished this zone from the sea oats zone, however, was the clear dominance of Schizachyrium maritimum.

DUNE SWALES

Swales are low areas located inland from the primary dune ridge. They were observed to be scattered, without any discernible distributional pattern, primarily in the sea oats and shrub zones and also in certain parts of the pine forest. They were found to be characterized by a very high water table, and usually retained shallow standing fresh water for some time after rainfall. In the swales this condition of shallow inundation persisted for a protracted period of time during the rainier months of the year.

Plants observed in the swales were primarily non-halophytes that also occurred in moist sandy sites at inland areas removed from the coastal strand. The species were predominantly herbaceous, but a few shrubs (e.g. Ilex glabra and Hypericum reductum) were also found in the swales. Table 5 lists the plants which were observed in five dune swales examined within the Fort Pickens Unit of Gulf Islands National Seashore.

Table 5

Dune Swale Plants

Santa Rosa Island, Florida

Calopogon pallidus

Centella asiatica

Cynanchum angustifolium

Cyperus lecontei

Drosera capillaris

Eriocaulon decangulare

Euthamia minor

Fimbristylis caroliniana

Fuirena scirpoidea

Habenaria repens

Hedyotis uniflora

Hypericum cistifolium

Hypericum reductum

Ilex glabra

Juncus abortivus

Juncus marginatus

Juncus scirpoides

Lachnanthes caroliniana

Lachnocaulon engleri

Linum floridanum

Ludwigia alata

Lycopodium appressum

Panicum caerulescens

Panicum chamaelonche

Pogonia ophioglossoides

Polygala balduinii

Polygala balduinii X *P. ramosa*

Polygala lutea

Polygala ramosa

Psilocarya nitens

Rhexia cubensis

Rhynchospora fascicularis

Rhynchospora tracyi

Sabatia stellaris

Scleria reticularis

Scleria verticillata

Spartina patens

Spiranthes praecox

Syngonanthus flavidulus

Utricularia cornuta

Utricularia subulata

Xyris caroliniana

Xyris elliottii

Xyris flabelliformis

RECONNAISSANCE OBSERVATIONS

Reconnaissance observations of Santa Rosa Island to the east of the primary study site, and on Perdido Key to the west, showed that the coastal strand vegetation was similar in all three areas. However, to the east on Santa Rosa Island two outstanding vegetation features, which were not found in the primary study area within Gulf Islands National Seashore, were noted.

First, a number of high sand dunes (to 4.5 m in height), with lee-side communities dominated by stunted and gnarled specimens of Magnolia grandiflora in association with other characteristically mesic inland species, were observed. A good example of this unusual dune community was located to the west of the Dunes Motel along Ft. Pickens Road. Here M. grandiflora was growing with Persea borbonia, Ilex vomitoria, Lonicera sempervirens, Ampelopsis arborea, Toxicodendron radicans, and Erythrina herbacea. Another example was located to the north of Via DeLuna on the Santa Rosa Island property of the University of West Florida. Kurz (1939, 1942) reported similar plant associations in Florida coastal dune systems farther to the east.

Secondly, a number of areas along the north side of the island, adjacent to Santa Rosa Sound, were found supporting well-developed coastal marsh communities. An example of such a site was located on the Santa Rosa Island property of the University of West Florida. The marsh there was dominated by Juncus roemerianus and contained such typical salt marsh species as Spartina alterniflora, S. patens, S. spartinae, Limonium carolinianum, and Baccharis halimifolia.

It should also be noted that four species of plants characteristic of coastal strand habitats in northwest Florida were observed to be

absent from the western end of Santa Rosa Island within the boundaries of Gulf Islands National Seashore, but are documented to occur to the east on the island and/or the coastal mainland of northwest Florida. They were Croton punctatus, Chrysopsis cruiseana, Ipomoea pes-caprae, and Lupinus westianus.

Croton punctatus was found on Santa Rosa Island in the area of Quiet Water Beach and along Via DeLuna in the town of Pensacola Beach. McFarlin (1941) reported it as "frequent along Santa Rosa Sound east of the Pensacola Beach Casino on Santa Rosa Island." I did not find C. punctatus on Perdido Key, but Stallard (1950) reported it from the Ft. Morgan peninsula and Deramus (1970) reported it from Dauphin Island, Alabama. Croton punctatus is generally considered to be common along the Gulf coast of northwest Florida and west to the east coast of Texas. Why this plant was apparently absent from the western end of Santa Rosa Island and Perdido Key is not known.

Chrysopsis cruiseana was observed to be abundant in the white sand dune systems to the east of Pensacola Beach. Ward (1979) stated that C. cruiseana "is found only on Santa Rosa Island, from Escambia County east to Walton County, and to a very limited extent on the adjacent mainland" and that "vacation housing, in the form of condominiums and other buildings placed directly on the dunes, has obliterated the western end of its range on Santa Rosa Island and part of its eastern range near Destin." Thus human activity was at least partially responsible for the absence of this plant from the main study area. This species was first described by Dress (1954), and so was not listed by McFarlin (1941), even though it was obviously present on Santa Rosa Island at the time of his survey.

Ipomoea pes-caprae is considered to be a common plant of seaside dunes from Georgia and Florida to Texas, and is also found on seashores of warmer areas throughout the world. This plant was not recorded for Santa Rosa Island by McFarlin (1941), but Long (1974) later reported it from the Navarre Pass area of the island, and I recently collected it in the area of Pensacola Beach. Carlton (1977) did not observe I. pes-caprae near Fort Pickens, and I did not observe it on Perdido Key during the present study. Deramus (1970) did not report it from Dauphin Island, but Stallard (1950) listed it for the Fort Morgan Peninsula. Apparently I. pes-caprae is rare on Santa Rosa Island and is absent from the far western end of the island within the Ft. Pickens Unit of Gulf Islands National Seashore.

Lupinus westianus is an endemic plant of Gulf Coast dunes and scrub habitats from Florosa, Okaloosa County, eastward to St. Vincent Island. Ward (1979) stated that formerly (1936) it also occurred in coastal areas as far west as the Gulf Breeze Peninsula, Santa Rosa County. This species, which was first described by Small (1926), was not reported on Santa Rosa Island by McFarlin (1941). Apparently L. westianus has not extended as far as the western end of Santa Rosa Island within recent historical times.

Two interesting plants found in dune swales to the east of the main study area are worthy of special attention: Ophioglossum petiolatum and an unnamed hybrid of Polygala balduinii and P. ramosa.

Ophioglossum petiolatum is a small fern that has been observed on Santa Rosa Island in only four dune swales at the following locations: (1) John C. Beasley State Park, Okaloosa County, at the eastern end of the island; (2) south of Florida Highway S399 approximately 0.2 km east

of Navarre Pier Road; (3) near the southwest corner of Via DeLuna and Avenida 18, near Pensacola Beach; and (4) north of Ft. Pickens Road approximately 0.2 km west of the Mai Kai Motel. The inconspicuous size of O. petiolatum, and the fact that it usually grows within dense stands of Fuirena scirpoidea, make it easy to overlook this fern and may explain why McFarlin (1941) did not report it from Santa Rosa Island. It was not observed in any of the swales examined within the Fort Pickens Unit of Gulf Islands National Seashore during the present study. Whether or not it is actually totally absent from the Ft. Pickens Unit will require additonal intensive searching to determine. However, since the plant appears to be infrequent to rare, it is highly possible that it does not occur on the extreme western end of Santa Rosa Island, although suitable habitats for it exist there.

A distinctive member of the genus Polygala, with pale-yellow wings and a lemon-yellow corolla tube, was discovered in the large swale just south of Ft. Pickens Road across from Battery Langdon. This is apparently a hybrid of Polygala balduinii and P. ramosa, both of which occur in the area where the putative hybrid grows. A number of specimens of this hybrid collected in other locations in Florida are in the herbarium of Florida State University, Tallahassee. This putative hybrid Polygala was briefly mentioned by Smith and Ward (1976), who noted that Torrey and Gray (1838) apparently referred to this entity as variety chlorgena of P. balduinii.

THE ENVIRONMENT

SOIL FACTORS

General

Carlisle (1960) designated the soil type of the entire western end of Santa Rosa Island as "Coastal Dune Land and Beach." He further described the soil as being composed of sand deposited by wave action along the coast, and noted that white sand comprised the entire profile in most areas. McFarlin (1941) stated that the beaches and dunes of Santa Rosa Island were composed of Galveston Sand, for which he gave the following grain size composition: coarse sand (1.0-0.5 mm)--15.5 percent; medium sand (0.5-0.25 mm)--56.1 percent; fine sand (0.25-0.1 mm)--28.3 percent; very fine sand (0.1-0.05 mm)--0.1 percent.

Carlisle (1960) noted that in the dune swale depressions a very thin layer of organic matter had developed at the surface. To this should be added the observation that in the slash pine forest considerable organic matter was found to have accumulated in the soil. The organic matter reached its maximum development at lower sites deep inside the forest near the central marsh area (e.g. at station 8), where a 5 to 8 cm layer of pine needles and leaf litter overlay a horizon of peat-like organic matter intermixed with incoherent white sand nearly 20 cm thick.

The soil in the bluestem zone (stations 9 and 10) consisted of sand which was dredged from Pensacola Bay in 1958-59, as noted previously. This dredged material formed a cliff-like scarp dropping approximately 2.5 m straight down to the beach strand just north of station 10.

The results of all soil analyses are presented in Table 6, and all concentrations stated from the present study in the following subsections refer to this table.

Organic Matter, Moisture, Nutrients, and Other Chemical Factors

Organic Matter. Understandably, the soils of the dune stations (1, 2, 3, 4, 5, 6, 9, and 10) were extremely low in organic content, with all samples from both depths having concentrations less than 1.0 percent.

Due to buildup from tree leaves and other plant debris, the soil of the pine forest community tended to have greater organic content than that of the treeless dune communities. The extreme example of this occurred at station 8, deep within the forest, where the peat-like upper soil layer had an organic content of nearly 12.0 percent.

Moisture. Soil samples from the sea oats, shrub, and bluestem communities were generally low in moisture at the two depths sampled, with the soil from a depth of 20 cm having slightly more moisture than soil from 10 cm depth. At station 2, however, both depths had identical moisture content.

Soil samples from the pine forest were noticeably higher in moisture content than were the dune soil samples, particularly so at station 8, where the water table was at a depth of only 26 cm at the time of soil sample collection. The fact that the soil at 10 cm depth at this station had a higher moisture content than did the soil at 20 cm depth is explained by the great water-retention properties of the peat-like soil occurring at the 10 cm depth.

Chloride. Soil chloride measurements in the present study were indicative of the NaCl content of the soil samples. These measurements

Table 6

Soil Data
Coastal Strand Vegetation
Santa Rosa Island, Florida

Parameters	Sea Oats Zone					Shrub Zone	Pine Forest		Bluestem Zone	
	Sta. 1	Sta. 2	Sta. 3	Sta. 4	Sta. 5	Sta. 6	Sta. 7	Sta. 8	Sta. 9	Sta. 10
Organic Matter (%)										
10 cm	0.003	0.055	0.038	0.062	0.174	0.184	0.235	11.616	0.351	0.292
20 cm	0.040	0.055	0.029	0.041	0.107	0.194	0.093	2.496	0.424	0.518
Moisture (%)										
10 cm	3.5	1.1	1.0	1.7	1.9	2.1	7.1	47.8	2.3	1.9
20 cm	3.6	1.1	1.7	2.2	2.7	2.8	17.9	35.6	2.5	2.5
Chloride (ppm)										
10 cm	5.2	4.1	2.4	1.1	2.1	1.6	4.6	27.0	1.8	2.8
20 cm	5.2	2.9	1.8	1.3	1.7	1.4	9.1	10.8	1.9	2.7
pH										
5 cm	6.9	6.7	6.7	6.5	6.2	5.5	5.1	4.7	6.4	6.9
10 cm	6.1	6.0	6.1	6.2	5.9	5.1	5.1	4.9	6.6	7.1
Calcium (ppm)										
5 cm	T	8	T	12	T	32	20	921	1321	1121
10 cm	T	T	T	4	T	12	T	520	1161	1841
Magnesium (ppm)										
5 cm	4	4	4	4	4	8	8	128	12	12
10 cm	4	4	4	4	4	4	4	60	8	12
Potassium (ppm)										
5 cm	T	4	4	4	4	4	4	16	4	4
10 cm	4	T	4	4	4	4	4	8	4	4
Phosphorus (ppm)										
5 cm	1	<1	T	T	<1	<1	T	<1	3	7
10 cm	<1	T	T	<1	T	T	T	<1	8	5
Sodium (ppm)										
5 cm	32	20	20	9	8	20	24	80	28	36
10 cm	20	4	16	8	20	8	12	44	48	36
Nitrate (ppm)										
5 cm	2	10	8	<1	<1	2	<1	3	9	11
10 cm	3	2	3	4	2	2	2	2	9	10
Soluble Salts (ppm)										
5 cm	56	42	1	1	1	1	14	168	84	70
10 cm	14	7	7	7	4	3	4	70	70	70
C.E.C. (meq/100 g)										
5 cm	—	0.12	0.22	0.06	0.06	0.15	0.28	32.70	1.56	0.06
10 cm	0.06	0.03	0.04	0.02	0.03	0.08	0.09	3.81	1.56	1.52
Depth to Water Table (m)	1.07	—	—	—	1.07	1.37	0.39	0.08	>3.0	—

T = trace

showed that salinity of the dune soils on Santa Rosa Island was very low.

Soil chloride concentrations for dune stations ranged from a minuscule 1.1 ppm (station 4, 10 cm depth) to a high value of 5.2 ppm (station 1)--a range of much less than 1 ppt. One of the eight dune stations (station 1) had the same chloride concentration at both soil depths. Five of the dune stations (2, 3, 5, 6, and 10) had a higher soil chloride concentration at 10 cm than at 20 cm depth, and the two remaining dune stations (4 and 9) had a slightly greater chloride concentration at 20 cm than at 10 cm depth.

The pattern of soil chloride content was the same at both depths sampled at the dune stations. Soil chloride concentrations were greatest at the southern edge of the sea oats zone and on the front slope of the barrier dune (stations 1 and 2) (presumably due to greater salt spray inputs than at other stations), with somewhat higher concentrations at station 1 than at station 2. Concentrations dropped off considerably at the crest of the barrier dune, and decreased further on the rear slope of the barrier dune (station 4). Near the northern edge of the sea oats zone (station 5) the soil chloride concentration was somewhat greater than for the rear slope of the barrier dune (station 4) but somewhat less than soil chloride content on the barrier dune crest (station 3). Soil chloride content was somewhat less in the shrub zone (station 6) than at the northern edge of the sea oats zone (station 5), and then showed an increasing trend in the bluestem zone. Soil chloride at station 9 (in the middle of the bluestem zone) was slightly greater than at station 6, and soil chloride at station 10 (the north edge of the bluestem zone) was somewhat greater than at station 9

and about equal (though slightly greater than) the soil chloride content on the barrier dune crest (station 3).

On September 28, 1981, a set of three soil samples was collected for chloride analysis near substitute salt spray dune station 3 east of Pensacola Beach. One sample was collected at the surface and the other two at depths of 5 cm and 10 cm, respectively. The samples were extracted in the same manner as other soil chloride samples, and the extracts were analyzed with a Dionex IC 10 ion chromatograph. The chloride concentrations for the three samples were as follows: surface--18.0 ppm; 5 cm--1.8 ppm; 10 cm--2.4 ppm. Thus, at the very surface, soil chloride was 10 times as great as at 5 cm depth and 7.5 times as great as at 10 cm depth.

Soil chloride content in the pine forest (stations 7 and 8) was high in comparison with results from most of the dune stations. Soil chloride at 10 cm depth for station 7 was somewhat less than the corresponding soil chloride level at dune station 1, while at station 8 the 10 cm soil chloride reading was nearly six times as great as at station 7 and five times as great as at station 1. For 20 cm depth the soil chloride concentrations at stations 7 and 8 were similar to each other in magnitude and both were approximately twice as great as corresponding soil chloride concentration at station 1. For both depths soil chloride concentration at station 8 exceeded that of all other stations.

pH. Dune soil samples were generally somewhat acidic at both depths, except for station 10 which had slightly basic (pH 7.1) soil at 10 cm depth. With the exception of stations 9 and 10, dune soil samples were slightly more acidic at 10 cm depth than at 5 cm depth.

Generally, the dune soil showed increasing acidity from the foredune to the pine forest, and decreasing acidity north of the forest to the soundward side of the island.

Understandably, the pH values of the pine forest soil samples (which had greater organic content than the dune soil samples) were lower than those of the dune stations, with the lowest readings being reported for station 8.

Calcium. Calcium concentrations of the dune soil samples were low, particularly so in the sea oats zone, where seven of the ten samples had no more than a trace of calcium. The shrub zone soil was somewhat higher in calcium content than the sea oats zone soil. Similarly, the bluestem zone soil had about 100 times as much calcium as the soil of the sea oats zone and over 40 times as much calcium as the shrub zone soil. The high levels of soil calcium in the bluestem zone were most probably due to the presence of abundant seashell fragments observed during field sampling.

Pine forest soil calcium content at station 8 was considerably greater at both depths than was the soil calcium content at all dune stations except stations 9 and 10. At station 7, however, the soil calcium content was less than that of the adjacent shrub zone at both depths and was also less than the average for all sea oats zone samples at 10 cm depth, but was somewhat greater than the average for the sea oats zone stations at 5 cm depth.

Magnesium. Soil samples from the dune stations were all very low in magnesium content, with the range being only 8 ppm between the maximum (12 ppm) and the minimum (4 ppm) values.

All stations in the sea oats zone had the same soil magnesium concentration (4 ppm) at both depths sampled. The shrub zone soil had twice as much magnesium (8 ppm) at the 5 cm depth as did the sea oats zone, but the same concentration (4 ppm) at 10 cm depth. At the 5 cm depth of stations 9 and 10, and the 10 cm depth of station 10, the bluestem zone had three times as much soil magnesium (12 ppm) as did the sea oats zone stations, and at the 10 cm depth of station 9 soil magnesium concentration (8 ppm) was twice as great as at the same depth in the sea oats zone.

At the southern edge of the pine forest, soil magnesium concentrations at station 7 were identical to corresponding soil magnesium concentrations for dune station 6 at both depths sampled. However, the pine forest soil at station 8, which was considerably more organic than the soil of all other stations, had a much greater magnesium content than did the other stations.

Potassium. Soil potassium concentrations at all dune stations were extremely low. Soil samples at both depths measured 4 ppm potassium, except for station 1, which had only a trace of potassium at 5 cm depth, and station 2, which also had only a trace at 10 cm depth.

The southern part of the pine forest (station 7) also had the same low level of soil potassium (4 ppm) as did the dune stations. However, station 8, deep within the pine forest, had somewhat higher soil potassium concentrations (16 ppm at 5 cm and 8 ppm at 10 cm).

Sodium. Soil sodium concentrations for dune stations showed an irregular pattern (which did not correspond with the observed vegetational zonation), with the highest values occurring in the bluestem zone, rather than, as might be expected, in the sea oats zone. And the

dune soil sodium concentrations were not very great, with the range from the highest value (48 ppm) to the lowest (4 ppm) being only 44 ppm.

Soil sodium concentrations in the pine forest were unexpectedly high, with station 7 having concentrations in the same range as those of dune stations to the south, and station 8 having the highest reading (80 ppm) of all samples measured at the 5 cm depth and the second highest concentration (44 ppm) of all samples at 10 cm depth.

Phosphorus. Phosphorus concentrations of the dune soils were extremely low, with a maximum of only 8 ppm measured for station 9 at 10 cm depth. Of the 16 dune soil samples, all samples from stations 1 through 6 had either less than 1 ppm (five samples) or only a trace (eight samples) of phosphorus. Soil phosphorus values for the bluestem zone were only slightly greater, with values ranging from 3 to 8 ppm.

Surprisingly, the pine forest soil, with its apparently greater fertility, was as low in phosphorus content as the dune soils to the south.

Nitrate. Soil nitrate concentrations at the dune stations were also very low, with the highest concentration being only 11 ppm at station 10 (5 cm depth). The pattern of concentrations was irregular and did not show an apparent relationship with the vegetational zonation.

Soil nitrate concentrations of the pine forest stations were in the same range as those observed in the dunes to the south, being lower, in fact, than most of the concentrations reported from the sea oats zone.

Soluble Salts. Whereas the individual soil cations just discussed were analyzed in an acid extraction which removed each cation totally from the soil, the analysis for soluble salts content was performed on a simple aqueous extract and thus measured only water-soluble cations. As

such, the soluble salts concentration of a soil is an indicator of all nutrients readily available to plants and may not equal the sum of the individual total cation concentrations.

Soluble salts content of soil at all dune stations was low. Concentrations were extremely low at stations 3, 4, 5, and 6, with all values at 5 cm depth being 1 ppm and the highest concentration at the four stations being only 7 ppm (10 cm at stations 3 and 4). Concentrations at stations 1 and 2 were somewhat greater than at the other sea oats zone stations, particularly so at 5 cm depth.

Soil data for soluble salts did not show a pattern which suggested a strong relationship with the observed vegetational zonation. Low and high readings were reported for the sea oats zone, those for the shrub zone station (6) were almost identical with those of the adjacent sea oats zone station (5), and those for the bluestem zone were considerably higher than those in the sea oats zone. Soluble salts data indicated, however, that all dune station soils were quite infertile.

Expectedly, soluble salts concentration of soil in the pine forest was considerably higher at 5 cm depth at station 8 (168 ppm) than at the same depth at any dune station. This was attributed to the great organic content of soil at this station. At 10 cm depth at station 8, however, soluble salts concentration (70 ppm) was the same as that reported for 10 cm at dune stations 9 and 10. Soil soluble salts concentration at 10 cm depth at station 7 (4 ppm) was the same as that of dune station 5 at 10 cm. However, the 5 cm reading for station 7 was considerably greater than 5 cm concentrations at dune stations 3, 4, 5, and 6, but was considerably lower than 5 cm soluble salts concentrations at the other dune stations (1, 2, 9, and 10).

Cation Exchange Capacity. Soil cation exchange capacities for the dune stations were very low, indicating that the dune soil was very low in available nutrients (since cation exchange capacity is the maximum amount of exchangeable cations a soil can hold). All results for samples from the sea oats and shrub zones were similar in magnitude, with all values being less than 1.0 meq/100 g and the range being from 0.02 meq/100 g (station 4, 10 cm depth) to 0.22 meq/100 g (station 3, 5 cm depth). One sample from the bluestem zone (0.06 meq/100 g at 5 cm depth, station 10) had the same cation exchange capacity as did a number of samples from the sea oats zone (stations 1, 4, and 5).

Soil cation exchange capacities for the southern part of the pine forest (station 7) were in the same range of magnitude as cation exchange capacity values for samples from the sea oats and shrub zones, despite the fact that the vegetation of the pine forest differed considerably from that of the areas to the south. Soil samples from station 8, deep within the forest, had somewhat higher cation exchange capacities, which were indicative of greater fertility and were probably a result of the higher soil organic content. The cation exchange capacity values from station 8, however, were not considered to be very high.

Temperature

General. Soil temperature readings taken at all ten stations at the soil surface and at depths of 10 cm and 25 cm at different seasons of the year are presented in Tables 7, 8, 9, and 10. Air temperature values measured at 30 cm above the soil surface are also included in these tables. All statements concerning soil temperature and air temperature in the following subsections refer to these tables.

Table 7

Temperature (°C) Measured at Different Levels in the Soil and 30 cm above the Soil Surface

Coastal Strand Vegetation, Santa Rosa Island, Florida

February 17-18, 1979

Station	30 cm above Soil Surface			Soil Surface			10 cm below Soil Surface			25 cm below Soil Surface		
	6 AM	12 N	6 PM	6 AM	12 N	6 PM	6 AM	12 N	6 PM	6 AM	12 N	6 PM
1	11.0	14.0	13.5	11.0	14.0	13.0	12.0	14.0	13.0	12.0	13.0	13.0
2	11.0	14.0	13.0	11.0	13.0	12.0	11.0	13.0	13.0	12.0	12.5	13.0
3	11.0	14.0	13.0	11.0	15.0	13.0	11.0	12.0	14.0	12.0	13.0	13.0
4	11.0	14.0	13.5	11.0	14.0	12.0	11.0	10.0	13.0	11.5	10.5	12.0
5	11.0	13.0	13.5	11.0	14.0	14.0	11.0	12.0	14.0	12.0	12.5	13.0
6	11.0	15.0	13.0	11.0	16.0	13.5	12.0	12.0	14.0	12.0	12.0	13.0
7	11.0	16.0	13.5	11.0	16.0	13.5	12.0	14.0	14.0	13.0	14.0	14.0
8	12.0	14.5	14.5	12.0	14.5	12.0	11.5	12.0	12.0	11.5	12.0	12.0
9	11.0	14.0	14.0	11.0	15.0	12.0	11.0	13.0	13.0	12.0	12.0	12.5
10	11.0	14.5	13.5	11.0	16.0	12.5	11.0	13.0	12.5	11.5	12.0	12.0

Table 8

Temperature (°C) Measured at Different Levels in the Soil and 30 cm above the Soil Surface

Coastal Strand Vegetation, Santa Rosa Island, Florida

April 14, 1979

Station	30 cm above Soil Surface			Soil Surface			10 cm below Soil Surface			25 cm below Soil Surface		
	6 AM	12 N	6 PM	6 AM	12 N	6 PM	6 AM	12 N	6 PM	6 AM	12 N	6 PM
1	19.5	35.0	22.0	17.5	37.0	21.5	20.0	24.0	23.5	20.0	23.0	22.5
2	19.5	32.0	22.0	18.0	34.0	22.0	20.0	24.5	25.0	21.0	22.5	24.0
3	19.5	34.0	22.0	18.0	42.5	22.0	21.0	25.0	26.0	22.0	24.0	24.5
4	19.0	38.0	22.0	18.5	39.0	22.5	21.0	24.0	26.5	22.0	23.0	24.0
5	19.5	34.0	21.5	19.0	39.5	22.0	21.0	24.0	24.0	22.0	24.0	24.0
6	20.0	35.5	21.5	18.0	46.0	22.0	21.0	24.5	26.0	21.5	23.0	25.0
7	19.5	33.0	21.5	19.0	33.0	21.5	21.0	24.0	24.0	21.0	22.0	23.5
8	20.0	29.0	21.5	18.5	26.0	21.0	19.5	20.5	21.0	19.5	20.0	20.0
9	20.5	31.0	21.0	20.0	35.0	22.0	21.0	26.5	26.0	22.0	25.0	25.0
10	21.0	29.0	21.0	21.0	33.0	22.0	21.5	25.0	25.0	22.0	24.0	25.0

Table 9

Temperature (°C) Measured at Different Levels in the Soil and 30 cm above the Soil Surface

Coastal Strand Vegetation, Santa Rosa Island, Florida

July 7, 1979

	30 cm above Soil Surface			Soil Surface			10 cm below Soil Surface			25 cm below Soil Surface		
Station	6 AM	12 N	6 PM	6 AM	12 N	6 PM	6 AM	12 N	6 PM	6 AM	12 N	6 PM
1	27.0	36.0	30.0	25.0	42.0	30.0	27.0	29.0	28.5	27.0	28.5	28.5
2	27.0	34.5	29.5	25.0	42.0	29.5	28.5	30.0	30.0	28.5	29.0	29.5
3	27.0	35.5	29.5	26.0	44.0	31.0	30.0	31.0	31.5	30.0	32.5	31.0
4	27.0	42.0	29.0	26.0	54.0	31.0	30.0	32.0	31.0	30.5	33.5	30.5
5	27.0	38.5	29.0	26.0	49.0	30.0	29.0	33.0	31.0	29.0	33.0	30.0
6	27.0	39.5	29.0	26.0	53.0	30.0	30.0	34.0	33.0	30.0	33.5	30.0
7	27.0	39.0	29.0	26.0	40.5	29.0	28.0	31.0	29.0	28.0	33.0	29.5
8	27.5	35.0	28.5	26.5	34.0	28.5	24.5	25.5	24.5	24.5	27.5	26.5
9	28.0	36.0	30.0	27.5	51.0	30.0	30.0	34.0	31.0	30.5	34.0	31.0
10	28.5	35.0	30.0	27.5	45.5	30.0	30.5	32.0	31.0	31.0	32.5	31.5

Table 10

Temperature (°C) Measured at Different Levels in the Soil and 30 cm above the Soil Surface

Coastal Strand Vegetation, Santa Rosa Island, Florida

September 16-17, 1978

	30 cm above Soil Surface			Soil Surface			10 cm below Soil Surface			25 cm below Soil Surface		
Station	6 AM	12 N	6 PM	6 AM	12 N	6 PM	6 AM	12 N	6 PM	6 AM	12 N	6 PM
1	26.5	34.0	29.0	25.0	38.0	29.0	27.0	32.0	29.0	27.5	29.0	29.0
2	25.5	36.0	29.0	24.5	41.0	30.0	27.0	33.0	32.5	28.5	30.0	30.0
3	26.0	35.5	28.5	25.5	45.0	30.5	28.0	33.5	33.0	29.5	32.0	31.0
4	26.0	43.5	29.0	26.0	45.0	30.5	27.0	34.0	30.5	28.5	32.0	30.0
5	26.0	39.5	29.0	25.5	45.5	30.0	27.0	36.5	32.0	28.5	31.0	30.0
6	26.0	41.5	29.0	25.0	48.0	29.0	27.0	37.0	32.5	28.5	33.5	31.0
7	26.0	39.0	29.0	26.0	46.0	28.5	27.0	33.5	30.0	28.0	30.5	29.5
8	26.0	34.0	28.0	26.0	35.5	27.5	26.0	27.0	27.0	26.0	27.0	26.0
9	26.5	34.0	27.0	26.0	43.0	27.5	28.5	38.0	31.0	29.5	34.0	31.0
10	27.0	36.0	26.5	26.5	42.0	28.5	28.0	34.0	29.0	29.0	33.0	30.0

Dunes. The results for soil temperatures at the dune stations may be summarized as follows: (1) the soil surface on a given date warmed up faster than did the deeper strata and achieved a higher maximum than the other strata, with the surface maximum being greater than the air temperature at the same time; (2) the soil surface had the highest maximum (54.0 ^{o}C) and the lowest minimum (11.0 ^{o}C) temperatures of all dune soil strata measured; (3) soil temperature at 10 cm and 25 cm depths changed more slowly than did surface temperature and generally showed less variation from station to station; and (4) the 10 cm and 25 cm dune soil strata had temperature maxima which were lower, and minima which were higher, than corresponding soil surface maxima and minima on a given day. A few exceptions to these general trends did occur (as examination of Tables 7 through 10 will reveal), but the overall patterns shown by the soil temperature data were as stated.

Pine Forest. Soil temperature at the two forest stations (7 and 8) showed patterns which were distinctly different from each other.

Soil temperature at station 7 showed a pattern similar to that of soil temperature at dune station 6, with the following exceptions: (1) in spring, summer, and autumn, the maximum temperature achieved on a given date was always somewhat lower at station 7 than at station 6 at all depths; and (2) in winter the maximum temperature achieved at station 7 at all depths was equal to, or slightly greater than, the corresponding maximum reported at station 6.

Soil temperature readings at station 8 (deep inside the pine forest) were conspicuously different from the dune soil temperatures, with all readings at all times at all depths in spring, summer, and autumn being lower than corresponding temperatures at station 9 in the bluestem

zone. With the exception of two occasions (September 17, 1978, 6 AM, soil surface and July 7, 1979, 6 AM, soil surface) all spring, summer, and autumn soil temperature readings at station 8 were also lower than corresponding temperatures measured at station 7, which was at the south edge of the pine forest. Winter soil temperature readings (measured February 17-18, 1979) at station 8 at noon and 6 PM at all depths were equal to, or less than, corresponding temperatures at station 9 and were consistently less than the corresponding temperatures at station 7. The 6 AM winter soil temperature at station 8 was slightly greater at the surface and 10 cm depth than corresponding temperatures at station 9 and was slightly less than the corresponding station 9 temperature at 25 cm depth; but the 6 AM winter soil temperature at station 8 was slightly less than the corresponding temperature at station 7 for 10 and 25 cm depths, and was slightly higher at station 8 than at station 7 for the surface.

ATMOSPHERIC FACTORS

Air Temperature

General. Air temperature 30 cm above the soil surface was measured at the same time as soil temperature (see Tables 7, 8, 9, and 10) and has already been mentioned in connection with it for comparison. Additional air temperature readings 30 cm above the soil surface were made every hour over an eight-hour period at dune stations 1 through 4 in connection with atmometric studies (see Tables 11 and 12).

Dunes. Understandably, the air temperature at 6 AM at all dune stations on all study dates was the lowest air temperature recorded on any given date, with the exceptions of station 10 on April 14, 1979,

Table 11

Hourly Air Temperature (°C) on Barrier Dune
Santa Rosa Island, Florida
August 29, 1979

Station	10 AM	11 AM	12 N	1 PM	2 PM	3 PM	4 PM	5 PM	6 PM
Edge of Beach (1)	33.0	35.0	36.0	36.0	38.0	36.0	35.0	35.0	30.0
Front Slope of Dune (2)	34.0	35.0	35.0	35.0	38.0	37.0	36.0	36.0	30.0
Crest of Dune (3)	36.0	37.0	37.0	37.0	40.0	38.0	36.0	35.5	30.5
Rear Slope of Dune (4)	37.5	39.5	42.0	46.0	46.5	48.5	46.0	39.5	31.5

Table 12

Hourly Air Temperature (°C) on Barrier Dune
Santa Rosa Island, Florida
September 8, 1979

Station	10 AM	11 AM	12 N	1 PM	2 PM	3 PM	4 PM	5 PM	6 PM
Edge of Beach (1)	37.0	40.0	44.0	44.0	43.0	44.0	43.0	40.0	35.0
Front Slope of Dune (2)	36.5	41.0	43.0	44.0	43.5	44.0	43.0	39.0	35.0
Crest of Dune (3)	35.0	39.0	43.5	42.0	41.0	42.0	41.0	36.0	33.0
Rear Slope of Dune (4)	34.5	38.0	42.5	42.5	42.5	42.0	41.5	36.5	34.0

when the 6 AM and 6 PM air temperatures were equal (21.0 ^{o}C) and at station 10 on September 16, 1978, when the 6 PM air temperature (26.5 ^{o}C) was 0.5 ^{o}C lower than the air temperature measured at 6 AM the next morning. Air temperature at 6 AM in the dunes did not vary greatly from station to station, with air temperature at all stations at 6 AM on February 18, 1979, being the same and the greatest station-to-station range for 6 AM air temperatures being only 2.0 ^{o}C (April 14, 1979).

The noon air temperature at a given dune station was always higher than the corresponding 6 AM air temperature at the same station, with the difference between the 6 AM and noon readings often being considerable. For the April, July, and September study dates, the greatest difference between noon and 6 AM air temperatures at a given dune station was 19.0 ^{o}C (station 4, April 14, 1979) and the least such difference was 6.5 ^{o}C (station 10, July 7, 1979). Winter dune air temperatures measured in February showed less of a difference between 6 AM and noon readings within the 24-hour study period at a given station, with the greatest such difference being 4.0 ^{o}C (station 6) and the least such difference being 2.0 ^{o}C (station 5).

The noon air temperature at a given dune station was usually the highest temperature recorded during a given 24-hour study period. This trend was observed for all study dates except February 17, 1979, when the noon air temperature at station 5 (13.0 ^{o}C) was 0.5 ^{o}C less than the corresponding 6 PM air temperature and the noon air temperature at station 9 (14.0 ^{o}C) was the same as the corresponding 6 PM air temperature. Since temperatures were recorded only three times during a given 24-hour period, this data did not necessarily mean that the highest air temperature at a given dune station was achieved at noon on a given date. As

indicated by hourly air temperatures recorded in August and September, 1979, at dune stations 1 through 4 between 10 AM and 6 PM (Tables 11 and 12), it was possible for the maximum air temperature to be reached at noon or in the early afternoon (usually by 2 PM or 3 PM). Thus, the two exceptions just mentioned (in which the 6 PM air temperature was equal to, or greater than, the corresponding noon air temperature) probably indicated that the air temperature at the stations involved had reached its maximum in the afternoon and had not yet cooled down by 6 PM to a temperature below that of the corresponding noon reading.

Noon air temperature at dune stations showed greater variation from station to station than did the corresponding 6 AM air temperature on a particular date. The greatest range for noon air temperature readings on a given date at the dune stations was 11.0 ^{o}C on April 14, 1979 (on which date the range of 6 AM readings was only 2.0 ^{o}C), and the least such range was 1.5 ^{o}C on February 17, 1979 (when the air temperature at 6 AM the next morning was the same at all dune stations).

By 6 PM on a given date the sun had either set (February, 1979) or was approaching its nadir, and consequently air temperature at dune stations had usually dropped below the noon temperature (which may, or may not, have been the maximum for the day) and often showed a considerable decrease from the noon temperature reading. With the exceptions of stations 5 and 9 on February 17, 1979, the 6 PM air temperature measured at all dune stations on all study dates was less than the corresponding noon temperature. In April, July, and September, the 6 PM air temperature at a given dune station was usually several degrees less than the corresponding noon temperature, with the greatest difference between noon and 6 PM readings at a given station being 16.0 ^{o}C (station 4,

April 14, 1979), and the least such difference being 5.0 °C (stations 2 and 10, July 7, 1979). In February, 6 PM air temperature at dune stations was usually only slightly lower than the corresponding noon temperature, differing by a maximum of only 2.0 °C (station 6).

Air temperature at 6 PM at dune stations varied only slightly from station to station, with considerably less variation than was observed for noon temperature readings. In February, April, and July, 1979, the station-to-station range for 6 PM air temperature readings at dune stations was only 1.0 °C; in September, 1978, the range was 2.5 °C.

The range of air temperature readings at a particular dune station during a single 24-hour period varied with the season of the year and varied from station to station within a given season. In winter (February 17-18, 1979) the greatest such range was 4.0 °C (station 6), and the least such range was 2.5 °C (station 5). These are modest ranges in comparison with the results for the 24-hour spring study period (April 14, 1979), which varied as much as 19.0 °C for the air temperature readings at station 4, but only 8.0 °C for the readings at station 10. For dune station air temperature readings in summer (July 7, 1979) the maximum range for a single station during the 24-hour study period was 15.0 °C (station 4) and the minimum such range was 6.5 °C (station 10). During the remaining study period (September 16-17, 1978) the maximum range for dune station air temperature readings at a given station was 17.5 °C (station 4) and the minimum such range was 7.5 °C (stations 1 and 9).

Pine Forest. Air temperature readings in the pine forest (stations 7 and 8) were similar to corresponding readings at the nearest dune stations (6 and 9). The air temperature at station 7 was the same as the

corresponding air temperature at station 6 on six occasions, was slightly higher (maximum difference 1.0 ^{o}C) than the corresponding air temperature at station 6 on two occasions, and was slightly less (maximum difference 2.5 ^{o}C) than the corresponding air temperature at station 6 on four occasions. The air temperature at station 8 was equal to the corresponding air temperature at station 9 on one occasion, was slightly higher (maximum difference 1.0 ^{o}C) than the corresponding air temperature at station 9 on five occasions, and was slightly less (maximum difference 2.0 ^{o}C) on six occasions.

On all study dates the air temperature measured at 6 AM and 6 PM did not differ greatly for stations 7 and 8, with the greatest difference being only 1.0 ^{o}C between corresponding air temperature readings at the two stations. At 6 AM the air temperature at station 8 was usually (three out of four times measured) slightly higher than the corresponding air temperature at station 7; it was equal to the air temperature at station 7 on one occasion.

At noon on all study dates the air temperature at station 8 was less than the corresponding air temperature at station 7. In winter (February 17, 1979) the difference in noon air temperature readings at the two stations was not great, being only 1.5 ^{o}C, but for the other seasons the difference was 4.0 ^{o}C on two dates (April 14 and July 7, 1979) and 5.0 ^{o}C on the remaining date (September 16, 1979).

On all study dates the highest air temperature reading at stations 7 and 8 was recorded at noon, and the lowest reading at 6 AM. The 6 PM air temperature at stations 7 and 8 was intermediate between the 6 AM and noon temperatures, except on one occasion (February 17, 1979) when the noon and 6 PM readings at station 8 were the same (14.5 ^{o}C).

Air temperature readings at station 7 on a given date always had a greater range than did air temperature readings at station 8 on the same date. The greatest range for air temperature readings at station 7 during a 24-hour period was 13.5 ^{o}C (April 14, 1979), and the least such range was 5.0 ^{o}C (February 17-18, 1979). The greatest range for air temperature readings at station 8 during a 24-hour period was 9.0 ^{o}C (April 14, 1979), and the least such range was 2.5 ^{o}C (February 17-18, 1979).

Relative Humidity

Dunes. Relative humidity data for all dune stations at different seasons of the year is presented in Table 13. This table also contains the relative humidity data for the two pine forest stations (7 and 8).

Relative humidity measured at noon at dune stations on all study dates showed greater variation from station to station than did relative humidity values recorded at 6 AM and 6 PM on the same date, with the greatest range for noon relative humidity values in the dunes being 21 percent (March 11, 1979), and the least such range being 13 percent (August 4, 1979). For relative humidity measured at 6 AM at dune stations on a given date, the greatest range of values was 13 percent (April 21, 1979, and October 8, 1978); the least such range was observed on March 11, 1979, when the relative humidity at all dune stations was the same (79 percent) at 6 AM. The greatest range of relative humidity values at 6 PM at dune stations was 9 percent (October 7, 1978, and March 11, 1979), and the least such range was 2 percent (April 21, 1979).

Relative humidity was a very unstable parameter in the dunes, and it fluctuated considerably throughout the day at a given station. The

Table 13

Relative Humidity (%) at Different Seasons

Coastal Strand Vegetation

Santa Rosa Island, Florida

Station	Spring			Summer			Autumn			Winter		
	6 AM	12 N	6 PM	6 AM	12 N	6 PM	6 AM	12 N	6 PM	6 AM	12 N	6 PM
1	83	75	89	93	66	75	73	43	39	79	44	40
2	86	75	89	93	72	75	67	40	39	79	47	40
3	86	75	89	89	72	77	60	49	36	79	56	40
4	86	69	89	89	59	73	60	47	36	79	53	43
5	88	75	89	89	59	74	65	48	37	79	39	43
6	83	65	89	91	68	74	63	52	37	79	35	43
7	83	72	86	91	68	74	65	42	43	79	54	43
8	82	79	91	91	71	77	69	41	41	79	46	45
9	75	75	91	90	71	72	63	43	45	79	37	49
10	82	79	91	88	66	72	69	36	45	79	45	47

Study dates: Spring, April 21, 1979; Summer, August 4, 1979; Autumn, October 7-8, 1978; Winter, March 11, 1979.

greatest difference between high and low relative humidity values recorded at a single dune station within a 24-hour period was 44 percent (station 6, March 11, 1979); the least such difference was 12 percent (station 10, April 21, 1979).

Hourly relative humidity readings at stations 1 through 4 (Tables 14 and 15) also showed considerable variation with time and from station to station. Only six times during all runs was the relative humidity at a given station the same for two consecutive hourly measurements.

Pine Forest. Relative humidity readings at stations 7 and 8 were similar to corresponding readings for dune stations to the north and south of the forest. On seven occasions out of twelve, the relative humidity at station 7 was the same as the corresponding relative humidity for at least one dune station. On eight occasions out of twelve, the relative humidity for station 8 was the same as the corresponding relative humidity for at least one dune station. On the five occasions when the relative humidity at station 7 was not equal to a corresponding relative humidity value for a dune station, the relative humidity for station 7 differed by no more than 3 percent from at least one corresponding dune station's relative humidity value. On the four occasions when the relative humidity at station 8 was not equal to a corresponding relative humidity value for a dune station, the relative humidity at station 8 differed by no more than 2 percent from at least one corresponding dune station's relative humidity value.

Evaporation

Dunes. Average amounts of water evaporated by atmometers exposed at dune stations 1 through 4 (the sea oats zone) for an eight-hour period are shown in Table 16, and data for atmometers exposed in all

Table 14

Hourly Relative Humidity (%) on Barrier Dune
Santa Rosa Island, Florida
August 29, 1979

Station	10 AM	11 AM	12 N	1 PM	2 PM	3 PM	4 PM	5 PM	6 PM
Edge of Beach (1)	77	78	78	83	81	85	83	78	82
Front Slope of Dune (2)	74	78	78	85	78	79	78	78	81
Crest of Dune (3)	76	78	81	81	75	78	81	76	80
Rear Slope of Dune (4)	73	72	69	69	75	70	69	72	79

Table 15

Hourly Relative Humidity (%) on Barrier Dune
Santa Rosa Island, Florida
September 8, 1979

Station	10 AM	11 AM	12 N	1 PM	2 PM	3 PM	4 PM	5 PM	6 PM
Edge of Beach (1)	67	77	63	56	47	45	47	47	46
Front Slope of Dune (2)	65	65	64	56	48	48	45	49	49
Crest of Dune (3)	68	67	68	55	49	47	49	50	49
Rear Slope of Dune (4)	70	67	65	60	48	47	50	49	50

three dune zones and in the pine forest is presented in Tables 17 and 18. The data presented in Table 19 focuses upon the pine forest and was obtained by exposing atmometers for 24 hours at stations 7 and 8 and at adjacent dune stations 6 and 9.

The pattern of evaporation rates for the two dates on which only stations 1 through 4 were studied were slightly different. On August 29, 1979, evaporation was somewhat greater at the inland edge of the bare beach strand than on the front slope of the barrier dune, with evaporation on the dune crest being somewhat greater than that at the edge of the beach, and the rear slope of the barrier dune having an evaporation rate only slightly (perhaps negligibly so) greater than that of the dune crest. On September 8, 1979, evaporation was greatest on the crest of the barrier dune, with the rate at the edge of the beach strand being slightly greater than that on the front slope of the dune, and evaporation on the rear slope of the dune being equal to that at the edge of the beach strand.

Evaporation measured in the different dune zones (Tables 17 and 18) showed two slightly different patterns. During an eight-hour run on October 13, 1979, the sea oats zone had the greatest evaporation rate, with the shrub zone rate being somewhat less than the sea oats zone rate, and the rate in the bluestem zone being only slightly less than that of the shrub zone. During a 24-hour run on March 14-15, 1980, the sea oats zone again had the greatest evaporation rate, but this time the evaporation rate of the bluestem zone was somewhat greater than that of the shrub zone.

Pine Forest. On three occasions measurements at station 8, deep within the pine forest, revealed that the evaporation rate at this

Table 16

Amounts of Water Evaporated
from Atmometers Exposed for 8 Hours
in the Sea Oats Zone
Santa Rosa Island, Florida

Station	Aug. 29, 1979 (ml/hr)	Sep. 8, 1979 (ml/hr)
Edge of Beach (1)	3.60	5.27
Front Slope of Dune (2)	3.46	5.08
Crest of Dune (3)	3.85	5.40
Rear Slope of Dune (4)	3.90	5.27

Table 17

Amounts of Water Evaporated
from Atmometers Exposed for 8 Hours
in the Different Vegetation Zones
Santa Rosa Island, Florida
October 13, 1979

Zone	ml/hr
Sea Oats	3.59
Shrub	3.44
Pine Forest	2.16
Bluestem	3.43

Table 18

Amounts of Water Evaporated
from Atmometers Exposed for 24 Hours
in the Different Vegetation Zones
Santa Rosa Island, Florida
March 14-15, 1980

Zone	ml/hr
Sea Oats	3.11
Shrub	2.10
Pine Forest	1.40
Bluestem	2.57

Table 19

Amounts of Water Evaporated
from Atmometers Exposed for 24 Hours
in the Pine Forest and
at Adjacent Stations
Santa Rosa Island, Florida
June 19-20, 1982

Station	ml/hr
6	1.77
7	1.64
8	0.95
9	2.08

station was consistently less than that observed at stations in exposed sites in the sea oats, shrub, and bluestem zones, and that evaporation at station 8 was also considerably less than that observed at station 7 near the south edge of the pine forest (Tables 17, 18, and 19). The evaporation rate at station 7, however, was approximately the same as that at station 6, located in an open area in the shrub zone to the south of the pine forest.

Sand Movement

Observations concerning sand movement were made during the course of the present study. Wooden stakes were driven into the ground to mark stations 1 through 10. The tops of these stakes were allowed to protrude approximately 14 cm above the soil surface. After more than two years of exposure the tops of the stakes at stations 1 through 4 were still visible. At substitute salt spray stations 2, 3, and 4 glass soft drink bottles were used to mark the station locations. These were buried upside down in the sand with approximately 1 to 2 cm of the bottle protruding above the surface of the sand. After more than two years of exposure these bottles had not been buried by accumulated sand. These observations suggested that sand was not building up rapidly on these barrier dunes and that the dunes were well stabilized and apparently in a state of equilibrium with regards to sand accumulation.

Wind Direction and Velocity

Data concerning wind direction and velocity was obtained from readings made by the U.S. Coast Guard at its station located on Santa Rosa Island 1.7 km east of the main study area (Tables 20 and 21). Although readings for only the period from December 1, 1978, to

Table 20

Summary of Wind Direction* Data
Recorded by U.S. Coast Guard Station
Santa Rosa Island, Florida

Wind Direction	1978 Dec	1979 Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep†
N	19.4	13.8	9.0	11.6	7.2	6.7	2.2	7.0	2.9	7.0
NNE	6.9	8.3	9.7	6.6	4.3	3.8	5.4	2.1	7.3	17.5
NE	16.0	13.8	16.4	4.1	9.4	6.7	5.4	4.2	5.1	10.5
ENE	10.4	22.9	8.2	1.7	4.3	2.9	3.3	4.9	8.8	24.6
E	9.7	4.6	6.0	5.8	2.2	0.9	4.3	2.8	4.4	7.0
ESE	6.2	11.0	10.4	10.7	4.3	2.9	3.3	4.2	9.5	10.5
SE	6.9	0.9	3.7	9.1	19.6	18.1	9.8	7.0	5.8	3.5
SSE	2.8	3.7	4.5	9.1	12.3	7.6	8.7	7.0	8.8	0.0
S	4.2	3.7	6.0	9.1	8.0	17.1	5.4	19.6	7.3	3.5
SSW	2.1	1.8	3.7	3.3	3.6	5.7	12.0	4.2	5.8	0.0
SW	4.2	2.7	4.5	7.4	4.3	9.5	8.7	5.6	8.0	3.5
WSW	1.4	2.7	4.5	2.5	3.6	6.7	13.0	14.7	5.1	5.3
W	3.5	1.8	3.0	9.1	10.9	7.6	10.9	11.2	10.2	1.8
WNW	2.8	0.9	3.0	3.3	1.4	0.9	5.4	2.8	7.3	1.8
NW	1.4	2.7	3.7	3.3	1.4	0.9	2.2	2.1	2.9	3.5
NNW	2.1	4.6	3.7	3.3	2.9	1.9	0.0	0.7	0.7	0.0
Total Readings:	144	109	134	121	138	105	92	143	137	57

* Expressed as percent of total readings for each month.
† Readings available only up to September 12, on which date Hurricane Frederic struck and the U.S. Coast Guard weather station on Santa Rosa Island was discontinued.

Table 21

Summary of Wind Velocity (m/sec) Data
Recorded by U.S. Coast Guard Station
Santa Rosa Island, Florida

	1978 Dec	1979 Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep*
Monthly Maximum:	11.3	15.4	12.9	18.0	10.3	9.8	9.3	20.6	7.7	12.9
Monthly Minimum:	1.5	1.5	1.5	0.5	0.5	1.0	0.5	0.5	0.5	0.5
Monthly Mean of All Readings:	5.6	5.9	5.2	5.5	5.4	4.7	4.3	4.9	3.9	5.1
Monthly Mean of Daily Maxima:	7.2	7.4	7.2	7.5	6.5	5.8	5.6	6.4	5.3	7.3
Total Readings:	144	110	133	124	138	107	95	143	137	58

* Readings available only up to September 12, on which date Hurricane Frederic struck and the U.S. Coast Guard weather station on Santa Rosa Island was discontinued.

September 12, 1979, were available, even this scanty information provided indications of seasonal trends.

The wind direction pattern of Santa Rosa Island may be summarized as follows: winds came primarily from the south, west-southwest, and west in summer and primarily from the north and northeast in winter; the spring and autumn months were somewhat erratic transitional periods in which predominating winds came from directions intermediate between the prevailing directions of summer and winter but were restricted primarily to directions on the eastern half of the compass.

The wind velocity trend for western Santa Rosa Island may be summarized as follows: winds of greatest velocity occurred in winter, with a general increase in velocity starting in autumn (September) and apparently continuing till January, which exhibited winds of the highest velocity; wind velocities tended to decrease in spring, as compared with winter values, and continued to decrease until late summer, with August experiencing the year's weakest winds.

Wind-borne Salt Spray

General. Results of the four long-term salt spray collection runs are presented in Tables 22 through 25. The following information is given for each run: (1) the chloride (Cl^-) concentration (ppm) in the 500 ml elutriate from each collector; (2) the amount of chloride (in mg) received at each station; (3) the calculated amount of chloride which would be received per hectare at each station in one year's time at the observed rate of deposition; (4) the amount of chloride received per square decimeter per day at each station during the exposure period; (5) the calculated amount of ocean-derived sodium (Na^+) which would be received per hectare at each station in one year's time at the observed

Table 22

Results of Salt Spray Study
Santa Rosa Island, Florida
60 Days Exposure
Sep 19-Nov 18, 1980

Station	Cl Conc. (ppm)	Cl Received (mg)	Cl Received (kg/ha/yr)	Cl Received ($mg/dm^2/day$)	Na Received (kg/ha/yr)	Total Salts Received ($mg/dm^2/day$)	Percent of Total Input Received
1	*	*	*	*	*	*	*
2	32.4	16.2	502	1.38	279	2.48	49.5
3	11.9	6.0	186	0.50	103	0.91	18.2
4	10.9	5.4	167	0.46	93	0.84	16.6
5	*	*	*	*	*	*	*
6	2.0	1.0	31	0.08	17	0.15	3.0
7	---	---	--	----	--	----	---
8	---	---	--	----	--	----	---
9	1.8	0.9	28	0.08	16	0.14	2.7
10	6.5	3.2	99	0.28	55	0.50	9.9

* Sampler stolen

Table 23

Results of Salt Spray Study

Santa Rosa Island, Florida

60 Days Exposure

Apr 2-Jun 1, 1981

Station	Cl Conc. (ppm)	Cl Received (mg)	Cl Received (kg/ha/yr)	Cl Received ($mg/dm^2/day$)	Na Received (kg/ha/yr)	Total Salts Received ($mg/dm^2/day$)	Percent of Total Input Received
1	*	*	*	*	*	*	*
2	23.8	11.9	369	1.01	205	1.82	39.1
3	19.8	9.9	307	0.84	170	1.52	32.5
4	11.8	5.9	183	0.50	102	0.90	19.4
5	*	*	*	*	*	*	*
6	3.2	1.6	50	0.14	28	0.24	5.2
7	---	---	--	----	--	----	---
8	---	---	--	----	--	----	---
9	2.3	1.2	37	0.10	20	0.18	3.8
10	*	*	*	*	*	*	*

* Sampler stolen

Table 24

Results of Salt Spray Study
Santa Rosa Island, Florida
100 Days Exposure
Nov 28, 1980-Mar 9, 1981

Station	Cl Conc. (ppm)	Cl Received (mg)	Cl Received (kg/ha/yr)	Cl Received ($mg/dm^2/day$)	Na Received (kg/ha/yr)	Total Salts Received ($mg/dm^2/day$)	Percent of Total Input Received
1	*	*	*	*	*	*	*
2	37.5	18.8	349	0.96	194	1.72	54.3
3	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-
5	10.0	5.0	93	0.25	52	0.46	14.5
6	7.0	3.5	65	0.18	36	0.32	10.1
7	---	---	--	----	--	----	----
8	---	---	--	----	--	----	----
9	5.0	2.5	46	0.13	26	0.23	7.2
10	9.6	4.8	89	0.24	50	0.44	13.9

* Sampler stolen

- Sampler disturbed; aberrant data point rejected

Table 25

Results of Salt Spray Study
Santa Rosa Island, Florida
65 Days Exposure
Jul 10-Sep 13, 1981

Station	Cl Conc. (ppm)	Cl Received (mg)	Cl Received (kg/ha/yr)	Cl Received ($mg/dm^2/day$)	Na Received (kg/ha/yr)	Total Salts Received ($mg/dm^2/day$)	Percent of Total Input Received
1	*	*	*	*	*	*	*
2	13.6	6.8	193	0.53	107	0.96	34.5
3	8.7	4.4	124	0.34	69	0.62	22.1
4	6.2	3.1	88	0.24	49	0.44	15.7
5	3.1	1.6	44	0.12	24	0.22	7.9
6	2.3	1.2	33	0.09	18	0.16	5.8
7	---	---	--	----	--	----	---
8	---	---	--	----	--	----	---
9	5.5	2.8	80	0.22	44	0.39	14.0
10	*	*	*	*	*	*	*

* Sampler stolen

rate of deposition (this is based on the Cl^-/Na^+ ratio (1.8) in sea water stated by Gambell and Fisher (1966)); (6) the calculated amount of total sea salts received per square decimeter per day at each station (based on the following formula: Salinity = 1.80655 Chlorinity (Ingmanson and Wallace, 1973)); (7) the relative amount of salt spray deposited at each station expressed as the percentage of chloride received at that station in relation to the total amount of chloride received at all stations for which collections were recorded. The percentages given in the last column are thus only approximations, since data is missing for four stations of the 60- and 65-day runs and for five stations of the 100-day run.

Although a number of data points are missing (due to vandalism to collectors and rejection of aberrant results), the data obtained is sufficient to show the general pattern of salt spray deposition and its influence upon vegetation of Santa Rosa Island.

Dunes. The average amounts of salt spray (measured as chloride) received at the dune stations during the four runs were as follows: station 2, 13.4 mg; station 3, 6.7 mg; station 4, 4.8 mg; station 5, 3.3 mg; station 6, 1.8 mg; station 9, 1.8 mg; station 10, 4.0 mg. Thus, most of the salt spray was deposited on the front (south) slope of the barrier dune, with considerably less (approximately one-half as much) deposited on the crest, and somewhat less on the back slope than on the crest. Of all salt spray received on the barrier dune (stations 2, 3, and 4 only), 53.7 percent was deposited on the front of the dune, 27.0 percent on the crest, and 19.3 percent on the back of the dune. The amount of salt spray deposited decreased progressively at stations farther inland, with station 5 receiving less salt spray than the rear

slope of the barrier dune, and station 6 receiving less than station 5. Station 9 averaged a salt spray input approximately equal to that at station 6, with three runs showing less input at station 9 than at station 6 and one run showing greater input at station 9 than at station 6. The amount of salt spray then increased considerably at station 10, which received slightly more than did station 5 but not as much as did station 4.

Pine Forest. The quantities of salt spray (measured as chloride) determined for samples from stations 7 and 8 during the four runs were unexpectedly high (see the Discussion section for elucidation of this idea). For example, for the first 60-day run (September 19-November 18, 1980) the reading for the sample from station 7 was slightly higher than the reading for the sample from station 9, and the reading for the sample from station 8 was nearly twice as great as the reading for the sample from station 9. Results for the other runs were similar. Hence, the salt spray data for the pine forest obtained during this study was rejected because it was considered to be aberrant, and does not appear on Tables 22 through 25.

DISCUSSION

VEGETATION

DUNES

Based on quantitative data, reconnaissance observations, and a review of the literature, the vegetation at the present study site may be considered as typical northwest Florida coastal strand vegetation, except for the absence there of five species which occur to the east on Santa Rosa Island, namely, *Lupinus westianus*, *Chrysopsis cruiseana*, *Croton punctatus*, *Ipomoea pes-caprae*, and *Cenchrus tribuloides*. Two of these (*L. westianus* and *C. cruiseana*) are endemic to the northwest Florida coastal strand and consitute major floristic components of it, adding an element of uniqueness to this flora.

Calculation of Sorensen's Index values (Carlton, 1977) provided numerical expression of the similarity between strand vegetation at the present study site and vegetation at other coastal sites along the northern Gulf of Mexico, the eastern seaboard of the United States, and northern Mexico (Table 26). The values presented in Table 26 were determined by using the plant list for the sea oats zone of the present study and plant lists for the equivalent community published in the references cited with the various geographic locations listed, except as noted for comparisons with vegetation on Ocracoke Island, North

Table 26

Index of Similarity Values for Coastal Strand Vegetation of Santa Rosa Island, Florida, Compared with Coastal Strand Vegetation of Selected Sites along the Atlantic and Gulf Coasts of the United States and Mexico

Study Site	SI	Similarity Classification
FLORIDA		
Santa Rosa Island (Carlton, 1977)	59.1	Moderate
W. T. Stone State Park (Carlton, 1977)	38.1	Low
St. George Island (Carlton, 1977)	33.3	Low
Ft. Clinch State Park (Carlton, 1977)	37.2	Low
Ft. Matanzas Nat. Monument (Carlton, 1977)	34.8	Low
Apollo State Park (Carlton, 1977)	18.2	Very Low
Sanibel Island (Cooley, 1955)	13.6*	Very Low
SOUTH CAROLINA		
Edisto Island (Pinson, 1973)	26.1	Low
Kiawah Island (Pinson, 1973)	30.4	Low
Kiawah Island (Hosier, 1975)	38.1	Low
Isle of Palms (Pinson, 1973)	32.8	Low
Isle of Palms (Stalter, 1975)	31.8	Low
North Island (Pinson, 1973)	32.6	Low
Waiter Island (Pinson, 1973)	29.2	Low

Table 26
(Continued)

Study Site	SI	Similarity Classification
Huntington Beach State Park (Stalter, 1976)	28.6	Low
NORTH CAROLINA		
Shackleford Bank (Au, 1974)	23.8	Very Low
Cape Lookout Nat. Seashore (Godfrey and Godfrey, 1976)	20.5	Very Low
Ocracoke Island (van der Valk, 1975)	31.6**	Low
Portsmouth Island (Burk, 1961a)	21.6	Very Low
Outer Banks (Burk, 1962)	25.0	Very Low
VIRGINIA		
Smith Island (Clovis, 1968)	0.0	No
Parramore Island (Harvill, 1965)	6.2	Almost No
VIRGINIA-MARYLAND		
Assateague Island (Harvill, 1967)	15.8	Very Low
Assateague Island (Higgins et al., 1971)	19.5	Very Low
MASSACHUSETTS		
Cape Cod (Boyce, 1954)	0.0	No
ALABAMA		
Dauphin Island (Deramus, 1970)	41.0*	Low
MISSISSIPPI		
Horn Island (Eleuterius, 1979)	37.7	Low
Ship Island (Miller and Jones, 1967)	6.9	Almost No

Table 26
(Continued)

Study Site	SI	Similarity Classification
Cat Island (Penfound and O'Neill, 1934)	27.0	Low
LOUISIANA		
Breton Island (Gould and Ewan, 1975)	19.2	Very Low
TEXAS		
South Padre Island (Lonard et al., 1978)	27.0	Low
MEXICO		
Isla Aguada (Sauer, 1967)	11.8*	Very Low

SI Sorenson's Index of Similarity

* Plant lists for sea oats zone and shrub zone from the present study used for this calculation

** Plant list for front slope of barrier dune from the present study used for this calculation

Carolina, Sanibel Island, Florida, Dauphin Island, Alabama, and Isla Aguada, Mexico.

According to the similarity limits, or rankings, presented by Carlton (1977), the sea oats community at the present study site had only moderate similarity to the strand vegetation which was examined by Carlton (1977) only 2.3 km to the west on Santa Rosa Island. The Sorensen's Index value (59.1 percent) for these two sites was much lower than expected, since the two sites were fairly close to each other. This low value was probably due to the use of different sampling techniques at the two sites (viz. Carlton used only a single 76 m line-intercept transect).

As indicated by the similarity index values, vegetation along the Florida coast becomes increasingly dissimilar in comparison with that of the present study site as sites farther and farther to the east and south are considered. For example, coastal strand vegetation at Apollo State Park and Sanibel Island had very low similarity (in the range of 11-25 percent) to that of the present study site according to Carlton's classification. The same trend of decreasing similarity was seen when vegetation at the present study site was compared with sites progressively farther to the north along the Atlantic coast of the United States. For example, coastal vegetation of Parramore Island, Virginia, had almost no similarity to that of the present study site, and coastal vegetation at Smith Island, Virginia, and Cape Cod, Massachusetts--with similarity index values of 0.0 for both sites--had no simiarity at all to that of the present study site.

Coastal strand vegetation on Dauphin Island, Alabama, had low similarity to that of the present study site, with the similarity index

value for the two locations being only 41.0. Similarity between vegetation at the present study site and other sites farther west and south in Mississippi, Louisiana, Texas, and northern Mexico, was even less, with the similarity index value for Ship Island, Mississippi, being only 6.9, for Breton Island, Louisiana, being only 19.2, for South Padre Island, Texas, being only 27.0, and for Isla Aguada, Mexico, being only 11.8.

Of the 32 comparisons made between the plant communities at the present study site and other coastal sites of the Gulf and Atlantic United States and Mexico, only one produced a rating of moderate similarity, seventeen produced a rating of low similarity, ten produced a rating of very low similarity, and the four remaining comparisons yielded ratings of almost no or no similarity (Table 26). This indicated that the floristic composition of the present study site can generally be considered as not very similar to that of other coastal areas to the east and west in the southeastern and eastern United States and northern Mexico.

It should be noted that 26 of the comparison sites shared Uniola paniculata with the present study site (and that it was dominant at many of them), 25 sites shared Oenothera humifusa, 23 sites shared Panicum amarum, 17 sites shared Conyza canadensis, 17 sites shared Heterotheca subaxillaris, 16 sites shared Hydrocotyle bonariensis, and 14 sites shared Iva imbricata (Table 27). It thus appeared that a certain physiognomic similarity existed among many coastal strand sites in the southeastern and eastern United States--a similarity which was not strictly reflected in the mathematical calculation of Sorenson's Index of similarity.

Table 27

Occurrence of Species at Selected Coastal Strand Sites along the Atlantic and Gulf Coasts of the United States and Mexico

Species	Santa Rosa Island, FL (Carlton, 1977)	W. T. Stone St. Pk., FL (Carlton, 1977)	St. George Island, FL (Carlton, 1977)	Ft. Clinch St. Pk., FL (Carlton, 1977)	Ft. Matanzas Nat. Mon., FL (Carlton, 1977)	Apollo St. Pk., FL (Carlton, 1977)	Sanibel Island, FL (Cooley, 1955)	Edisto Island, SC (Pinson, 1973)	Kiawah Island, SC (Pinson, 1973)	Kiawah Island, SC (Hosier, 1975)	Isle of Palms, SC (Pinson, 1973)	Isle of Palms, SC (Stalter, 1975)	North Island, SC (Pinson, 1973)	Waiter Island, SC (Pinson, 1973)	Huntington Bch. St. Pk., SC (Stalter, 1976)
Uniola paniculata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Oenothera humifusa	X		X	X	X	X	X	X	X	X	X	X	X	X	X
Panicum amarum	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Heterotheca subaxillaris	X	X		X	X	X		X	X	X	X	X	X	X	X
Conyza canadensis	X	X		X				X	X	X	X	X	X	X	X
Hydrocotyle bonariensis	X	X	X	X	X					X	X	X		X	X
Iva imbricata							X		X	X	X	X	X	X	X
Ipomoea stolonifera				X	X	X					X				
Smilax auriculata	X	X			X			X	X		X		X		
Sesuvium portulacastrum					X		X				X				
Schizachyrium maritimum	X	X	X	X											
Cakile constricta															
Chamaesyce ammannioides	X						X								
Chrysoma pauciflosculosa	X	X													
Cuscuta pentagona							X								
Opuntia humifusa										X					
Balduina angustifolia	X														
Ceratiola ericoides															
Chrysopsis godfreyi	X														
Galium hispidulum							X								
Helianthemum corymbosum	X														
Panicum portoricense															
Paronychia erecta															
Polygonella gracilis															
Polypremum procumbens															

Table 27
(Continued)

Species	Shackleford Bank, NC (Au, 1974)	Cape Lookout Nat. Ssh., NC (Godfrey & Godfrey, 1976)	Ocracoke Island, NC (van der Valk, 1975)	Portsmouth Island, NC (Burk, 1961a)	Outer Banks, NC (Burk, 1962)	Parramore Island, VA (Harvill, 1965)	Assateague Island, VA-MD (Harvill, 1967)	Assateague Island, VA-MD (Higgins et al., 1971)	Dauphin Island, AL (Deramus, 1970)	Horn Island, MS (Eleuterius, 1979)	Ship Island, MS (Miller & Jones, 1967)	Cat Island, MS (Penfound & O'Neil, 1934)	Breton Island, LA (Gould & Ewan, 1975)	South Padre Island, TX (Leonard et al., 1978)	Isla Aguada, MX (Sauer, 1967)
Uniola paniculata	X	X	X	X	X				X	X	X	X		X	
Oenothera humifusa	X	X	X	X	X		X						X		
Panicum amarum			X			X									
Heterotheca subaxillaris					X				X	X				X	
Conyza canadensis	X	X	X	X	X		X								
Hydrocotyle bonariensis	X	X	X	X				X	X				X		
Iva imbricata	X		X		X				X	X	X				
Ipomoea stolonifera									X	X					
Smilax auriculata									X	X	X				
Sesuvium portulacastrum									X	X					
Schizachyrium maritimum												X			
Cakile constricta									X		X	X	X		
Chamaesyce ammannioides										X		X			
Chrysoma pauciflosculosa									X						
Cuscuta pentagona									X						
Opuntia humifusa									X						
Balduina angustifolia															X
Ceratiola ericoides															X
Chrysopsis godfreyi															X
Galium hispidulum															X
Helianthemum corymbosum															X
Panicum portoricense															X
Paronychia erecta															X
Polygonella gracilis															X
Polypremum procumbens															X

X indicates the presence of a species at the site shown and also at the present study site.

It was interesting to note that many of the plants found in the three dune strand zones examined in the present study also commonly occurred at inland sites well removed from the coastal strand. These included such well-known plants as Ceratiola ericoides, Chrysoma pauciflosculosa, Conradina canescens, Conyza canadensis var. pusillus, Heterotheca subaxillaris, Hydrocotyle bonariensis, Opuntia humifusa, Polygonella gracilis, and Smilax auriculata. However, Uniola paniculata and Schizachyrium maritimum--the two most outstanding dunal species--were restricted to the coastal strand and did not grow at inland sites; the same was true for Panicum amarum.

Uniola paniculata, of course, dominates the zone just inland from the bare beach strip. Its various xeromorphic characters, its ability to withstand sand burial, its resistance to salt spray, and its low soil moisture requirements, make U. paniculata ideally suited for survival in this harsh environment of continuous wind, strong sunlight, shifting sand, and intense wind-borne salt spray. In fact, U. paniculata succeeds in this environment as does no other plant and seems to thrive there to such an extent that its coverage at the crest of the barrier dune (41.5 percent) is greater than that of any other dune strand species at any point in the three dune zones. The success of U. paniculata on the barrier dune is particularly noticeable when it flowers in summer, covering the dune with a dense array of innumerable tall inflorescences.

The ecology of U. paniculata is well known, and has been elucidated by Wagner (1964), Kurz (1942), Godfrey (1977), and Dahl et al. (1975), among others. This species is, without doubt, the primary dune-stabilizing element of the coastal strand flora in the southeastern

United States, and serves this function from the southern part of Virginia southward to Florida's east coast down to the keys, and along Florida's northwest coast westward to Texas and south into Mexico. It is the ability of this grass to produce abundant horizontal rhizomes, and to do so in tiers as sand builds up around its main axis, which allows it to have its pre-eminent dune-building role. Uniola is the main pioneer species responsible for the genesis of barrier dunes by trapping wind-borne sand around its base. As sand accumulates and the dune builds up, the main axis of Uniola grows upward through the accumulated sand, producing horizontal rhizomes from each subterranean node--which, in turn, produce upright shoots at their nodes--forming a network of tiered rhizomes within the mound of sand which is the dune (for a diagram which illustrates this see Dahl et al., 1975). Uniola thus creates the dune, then holds it together and prevents it from being blown away. When the dune has become thus stabilized, other species of plants (e.g. Galactia microphylla) become established and, with their roots and stems, add to the stability of the dune.

Panicum amarum is another grass which occurs on the front of the barrier dune and participates in the process of sand entrapment and dune building. The autecology of this plant has been discussed by Dahl et al. (1975). On Santa Rosa Island this species occurs primarily as remotely scattered clumps. It does not seem to reproduce vegetatively as vigorously as does U. paniculata and does not form the large interconnected clones characteristic of Uniola. These clumps of P. amarum, however, do entrap wind-borne sand and can withstand considerable sand burial, and thus a small hummock of sand in the immediate area of each plant results.

Oosting and Billings (1942) observed that Uniola paniculata was dominant where salt spray intensity was greatest. Data from the present study showed that this observation also applied to the Santa Rosa Island coastal strand, for more salt spray was clearly received at stations where Uniola was dominant than at dune stations where it was not. Oosting and Billings (1942) also noted that Schizachyrium littorale (to which they referred by the old name Andropogon littoralis) was dominant where the salt spray intensity was less than at sites dominated by U. paniculata. For northwest Florida Schizachyrium maritimum is apparently the ecological equivalent of S. littorale (and is a species closely related to it). At the present study site S. maritimum was clearly dominant over U. paniculata in the zone along the north side of Santa Rosa Island, where less salt spray was received than in the sea oats zone. This distribution pattern was similar to that observed by Oosting and Billings (1942) for S. littorale in North Carolina.

Oosting and Billings (1942), among others, concluded that wind-borne salt spray was the main environmental factor producing and maintaining the zonation of coastal strand vegetation. The same conclusion applies at the present study site (cf. the discussion of wind-borne salt spray in this report for additional information). It may also be concluded that the floristic composition of the plant communities of the zones is determined by salt spray intensity, since in each zone grow only those plants which can tolerate the amount of wind-borne salt spray deposited there. As long as the salt spray input remains constant for a given zone (and it will remain so as long as the distance of the zone from the ocean and the wind regime remain unchanged), species

composition and dominance of the vegetation in that zone should remain unchanged, once vegetation becomes established there.

If the pioneer community for a particular coastal strand zone remains unchanged in composition and dominance for a protracted period of time, thus constituting a stable community, it may be concluded that succession as it is generally perceived by ecologists and botanists (i.e. autogenic or biotic succession) does not take place there, and that the pioneer community is also the climax community. This appears to be the situation for the coastal strand zones of extreme northwest Florida. A study of the coastal strand of Perdido Key recently conducted by Dr. M. I. Cousens (pers. comm.) revealed that the pioneer community of a dunal area there which was denuded by Hurricane Frederic had the same species composition as the apparently stable community of the sea oats zone examined on Santa Rosa Island during the present study, and Uniola paniculata was the most abundant plant colonizing the bare sites there. This suggests that in the sea oats zone, at least, succession does not occur.

Wells (1942) stated that each of the zones along a stable coastline are climax communities and are "stabilized by different salt intensities." Oosting (1954) considered coastal strand succession in great detail and concluded that the dominants in each zone "are there because of physiographic position, which in turn determines exposure to wind and salt spray, and depth to water table," and that "The zones are then stable, too, with little or no evidence of succession" and "there is no reason to believe that a shrub zone would invariably develop on a Uniola-dominated zone, and it is highly improbable that live oak forest could ever grow there." Martin (1959) stated that the herbaceous zones

of coastal vegetation at Island Beach, New Jersey, were "structurally and compositionally stable under the environmental conditions which characterize them," and that "The herbaceous, shrubby, and arborescent zones do not necessarily represent seral stages in biotic (autogenic) succession." Daubenmire (1968) considered the matter and recognized that near seacoasts the zones of terrestrial vegetation were relatively per-manent and did not show successional trends. Tyndall and Levy (1978) concurred with the conclusions of Wells (1942) and Martin (1959) and stated that "Foredune-grass, shrub, and tree zones are not progressive seral stages on stable or degrading coasts."

Of course, it can be seen that if something, such as shoreline migration, should cause the salt spray deposition pattern to change, then the zones of vegetation would shift accordingly, but their positions relative to one another and their community compositions would remain unchanged. Boyce (1954) stated the same idea as follows: "Succession in the salt spray community is actually an oscillation in space of the physiognomic zone, which is controlled by the long-period fluctuation of salt spray intensity." Daubenmire (1968) also elucidated a similar point: "Should the course of physiographic development, or manipulation by man, bring about a progressive change in the intensity of the factors controlling the belts [zones], the latter must migrate in an appropriate direction" and "The mere juxtaposition of communities on a gradient, then, is only an indication of possible successional relationships that may proceed in either of two directions."

Only if a physiographic change would produce an area sheltered from salt spray, could autogenic or biotic succession take place in the dune strand. An apparent example of such a situation was seen just west of

the Dunes Motel on Santa Rosa Island, where a large high sand dune apparently had a sheltered area on its leeward slope. In this sheltered spot an unusual assemblage of plants had developed, including the following species, most of which are usually associated with mesic habitats: Magnolia grandiflora, Toxicodendron radicans, Lonicera sempervirens, and Erythrina herbacea. Such small areas of plant communities showing autogenic succession in a habitat (the dune strand) which is generally in a state of stabilized dysclimax due to salt spray cannot be interpreted as the monoclimax that will eventually be achieved in the sea oats, shrub, and bluestem zones. These protected associations are probably best interpreted as ectopic communities which owe their existence in this unusual setting (the leeward dune slope) to a fortuitous quirk of nature, namely, being sheltered from salt spray impact.

PINE FOREST

The well-developed pine forest on the western end of Santa Rosa Island is a heterogeneous community and all of its major species also occur at inland sites on the mainland. It is clearly dominated by Pinus elliottii (slash pine), with the next most abundant species being Quercus virginiana var. geminata (sand live oak). Similar Pinus-Quercus forests have been described for barrier islands off the coast of Mississippi (Penfound and O'Neill, 1934; Pessin and Burleigh, 1941). Pessin and Burleigh (1941) noted that there were fewer live oaks than slash pines on Horn Island, but they could not explain why, and that "Most of the vegetation on Horn Island does not differ appreciably from that on the mainland."

The present study has been unable to demonstrate that salt spray is the factor which restricts the pine forest to the interior part of the island between the shrub and bluestem zones, but it is still postulated that such is the case. In other words, it is postulated that salt spray intensity is too great at the sites occupied by exposed dune communities (sea oats zone, shrub zone, and bluestem zone) for pine forest to exist there, and that it is actually the low intensity of salt spray near the interior of the island which permits pine forest to exist there. The species composition of the forest, however, may be influenced by other environmental factors as well, and considering the ecology of the two major trees (Pinus elliottii and Quercus virginiana var. geminata) provides hypotheses which may account for the species composition. These conjectures, which are discussed below, will require further investigation to be verified for the pine forest on Santa Rosa Island's western end.

Pinus elliottii seems to prefer sites that have a shallow water table. It is found in "wet flatwoods, branch-swamps, areas bordering shallow ponds, and along lagoons and bays near the coasts" (Kurz and Godfrey, 1962), hence its alternate common name "swamp pine." It is also occasionally seen along eroded banks of bayous and bays with its roots exposed and extending into the water to the substrate below, thus presenting a peculiar and precarious mangrove-like appearance. At the present study site, the water table was generally shallow where P. elliottii occurred. This was particularly evident near Blackbird Marsh where the largest pines grew. In fact, the presence of a relatively deep water table (>3.0 m) in the dredge spoil area (bluestem zone) north of the pine forest may explain--at least partially--why slash pines have

not become established there since deposition of the spoil in 1958-59. In contrast, Pinus clausa prefers well-drained sites, and thus would not do well at the sites occupied by P. elliottii on Santa Rosa Island. The other pines native to northwest Florida (P. echinata, P. glabra, P. palustris, P. serotina, P. taeda), as well as P. clausa, are apparently less tolerant to wind-borne salt spray than is P. elliottii (cf. Wells, 1942), and this might explain their absence from the study area.

Even though P. elliottii is quite resistant to salt spray, it could not withstand the extreme onslaught of salt spray and sea water inundation experienced during the night of September 12-13, 1979, when Hurricane Frederic struck. Many trees at the study site were killed, particularly those near the south side of the forest, but also some at the interior (near station 8) as well. It is interesting to note here that Stoneburner (1978) has shown that on barrier islands off the Mississippi coast, in areas where live oak forests (Q. virginiana var. geminata) are expected, pure slash pine forests (P. elliottii) were maintained by hurricane effects. He stated that hurricane-generated overwash destroyed the sand live oak seedlings in the understory, leaving only the mature oak trees, and that this destruction of the competitive understory permitted the germination and growth of slash pine seedlings. Stoneburner (1978) also observed that hurricane overwash appeared to temporarily stimulate the growth of established slash pines which survived, and that this was clearly shown in the annual ring patterns of tree trunk increment cores.

It appears that salt spray intensity south of the pine forest is too great for even Pinus elliottii to grow, and that at the interior of the island the salt spray input is much reduced, but is still great

enough to exclude many sensitive plants. If salt spray is indeed the environmental factor which determines the limits of the pine forest, this would explain why pine forest exists only on the wider parts of Santa Rosa Island. On the narrower parts of the island, salt spray intensity would be so great at all points across the width of the island as to prevent the establishment of pine trees.

In general, the woody species composition of the pine forest was not greatly different from that of an inland slash pine flatwoods, as determined from reconnaissance observations. This was particularly noticeable in areas where Ilex glabra dominated the understory vegetation at the study site--a situation which is common at inland flatwoods forests.

One outstanding plant which occurs in this pine forest, but is not found in inland flatwoods, is the sand live oak, Quercus virginiana var. geminata. This species is one of the most salt spray-resistant trees of the southeastern United States, and, as Wells (1939) pointed out, in coastal areas where it is dominant, its presence may be interpreted as constituting a "salt spray climax." Its occurrence as a salt-spray-formed shrub in the shrub zone on Santa Rosa Island is indicative of this resistance. In the pine forest Q. virginiana var. geminata occurs on the old dune ridges (which usually rise less than two meters above the lower, moister areas), where some specimens have achieved considerable dimensions. Interestingly, Oosting (1954) has observed that in Florida coastal strands sand live oak (Q. virginiana var. geminata) dominated on sterile acid sites, such as those found at the present study area, while live oak (Q. virginiana) occurred on less-acid and probably geologically older sites.

The pine forest at the study site thus is dominated by two of the most salt spray-resistant trees of northwest Florida. In addition to salt spray resistance, P. elliottii and Q. virginiana var. geminata appear to be able to grow, and even thrive, in soils of very low fertility, and this ability may also be an important factor in explaining the composition of the Santa Rosa Island pine forest.

Data from the present study showed that seedlings of Q. virginiana var. geminata greatly outnumbered those of P. elliottii, the dominant species of the forest canopy. This predominance of Quercus seedlings may indicate that a type of succession is taking place in which slash pine will eventually be supplanted in dominance by sand live oak. A similar type of succession (in which Quercus virginiana and other hardwoods succeeded Pinus caribaea (= P. elliottii)) was described by Alexander (1953) for a site on northern Key Largo, Florida. Alexander considered the slash pine to be a pioneer species at the site he studied. However, it seems unlikely that sand live oak will ever completely displace slash pine at the present study site, since the low areas where the slash pine thrives are not suitable for live oak development. Also, it is possible that some of the Quercus seedlings tallied may actually have been root sprouts, thus producing a misleading count. Furthermore, if the observations made by Stoneburner (1978) also apply to the present study site, the occurrence of periodic hurricane-generated overwash can be expected to prevent the sand live oak from becoming dominant.

THE ENVIRONMENT

SOIL FACTORS

Organic Matter, Moisture, Nutrients, and Other Chemical Factors

Dunes. Organic content of dune soils at the present study site was very low (less than 1.0 percent at all dune stations and less than 0.1 percent at four (1, 2, 3, and 4) of the five sea oats zone stations). In fact, it was uniformly so low at all dune stations that no pattern of coincidence between soil organic content and vegetational zonation was indicated by the data.

Wagner (1964) measured organic content of coastal strand soils on Bogue Bank, North Carolina. Of seven sites sampled, five had virtually no soil organic matter (0.0 percent), and the other two had soil organic matter of 0.1 percent and 0.2 percent. Au (1974) reported similarly low organic content for the dune strand soils he examined on Shackleford Bank, North Carolina.

Olson (1958), in the United States, and Scott (1965), in England, concluded that succession of plant communities in the sandy soil of an inland dune (near Lake Michigan) and of a shingle beach habitat, respectively, was dependent upon the accumulation of organic matter from dead plant remains in the soil. Since the harsh environment of the coastal strand apparently prevents the accumulation of any considerable amount of humus in the dune soil, it can be hypothesized that the type of autogenic succession described by Olson (1958) and Scott (1965) does not take place in such a habitat.

The dune soils in the present study area were composed primarily of white, coarse, siliceous sands mixed with various amounts of

ocean-derived shell fragments. The shell fragments were most abundant at the southern and northern edges of the island near the Gulf of Mexico and Santa Rosa Sound shorelines and at stations 9 and 10 in the bluestem zone.

The coarse sandy nature of these soils allows water to percolate very rapidly. Therefore, above the water table the moisture content of these soils is not great--a fact which makes the area studied an inhospitable site for most plant species. Au (1974) observed that in a North Carolina coastal strand area the water table was usually 30 to 60 cm below the surface and was not infrequently 1 m or so from the surface. He also noted that one day after a rain, water had moved down to a depth of 15-30 cm below the soil surface, and that after three days of percolation following a rainstorm the water had moved down to a stable depth in the soil profile which remained unchanged after three weeks.

With the exception of station 1, dune soil moisture content for the present study, measured several days after rainfall, was uniformly low in the upper 20 cm, ranging from 1.0 to 2.8 percent. Station 1 showed somewhat higher soil moisture content (3.5 to 3.6 percent), presumably due to ocean spray inputs.

Au (1974) found that three days after a rain, foredune and reardune soil moisture to a depth of 5 cm did not exceed 1 percent, was almost 0 percent at the very surface, was between 2 and 3 percent at a depth of 18 cm, and did not exceed 4 percent at a depth of 48 cm. He also reported that two weeks after a rain foredune soil moisture to a depth of 5 cm did not exceed 1 percent, was nearly 0 percent at the very surface, was between 1 and 2 percent at a depth of 18 cm, did not exceed 2 percent at a depth of 48 cm, and was between 2 and 3 percent at a

depth of 63 cm. Soil moisture results of the present study for all dune stations, except station 1, were within the same range as those reported by Au (1974). However, van der Valk (1974a) reported somewhat higher results for samples from 20, 40, and 60 cm depths on foredunes at Bodie and Ocracoke Islands, North Carolina, with soil moisture ranging from 3.1 to 4.5 percent.

Oosting and Billings (1942) also measured dune soil moisture at depths of 10 cm and 20 cm. Their results (excluding one station (3A) which was located in a dune swale) ranged from a low value of 1.7 percent of dry weight to a high value of 4.8 percent for samples collected at 10 cm depth along one transect. Their samples from 20 cm depth had somewhat greater soil moisture content than did the 10 cm samples, containing up to 8.6 percent for the two transects studied. This pattern of somewhat greater soil moisture content at 20 cm than at 10 cm depth was the same as that observed in the present study, and was similar to results reported by Au (1974), who also observed that the uppermost 15 cm of dune strand soil dries rapidly after rain and that the dry surface layer probably acts as a mulch contributing to preservation of moisture at lower soil levels.

Oosting and Billings (1942) observed that soil moisture requirements of Uniola paniculata were less than those of Schizachyrium littorale (referred to under its old name of Andropogon littoralis), the second most important plant in the coastal dunes of North Carolina. Although Oosting and Billings (1942) stated that soil moisture values for the upper 20 cm of their various stations seemed not to be significantly different from each other--a statement which may also be made for soil moisture results from the present study--and that "no correlation

is apparent between the vegetational zonation and any soil moisture factor between the surface and 20 cm," they also observed that U. paniculata predominated on higher, drier sites, such as the crest of the barrier dune, and that S. littorale predominated in habitats nearer the water table, such as at the base of the leeward slope of the barrier dune. An apparently similar distribution pattern was observed for U. paniculata and Schizachyrium maritimum in the present study. Schizachyrium maritimum is supposedly the ecological equivalent of, and a closely-related species to, S. littorale. On Santa Rosa Island S. maritimum was found to be dominant at station 5, which was located inland from the barrier dune ridge and at which soil moisture was slightly greater than at stations 2, 3, and 4, where U. paniculata was dominant. At stations 9 and 10 the soil moisture content was about the same as at station 5, and at these two stations S. maritimum was also dominant. It is possible that soil moisture content or proximity to the water table may be a factor in the distributional zonation of Uniola paniculata and Schizachyrium maritimum; however, the distribution of these two grasses in relation to water table depth on Santa Rosa Island seemed to be contrary to the hypothesis stated by Oosting and Billings (1942). The water table depth at station 5, where S. maritimum was dominant, was the same as at station 1, where U. paniculata was dominant, and the water table depth at stations 9 and 10, where S. maritimum also dominated, was three times as great as that at station 5 (cf. Table 6).

Tyndall and Levy (1978) studied soil moisture in relation to plant distribution in a barrier dune system in southern Virginia. They concluded that soil moisture was an important factor influencing the distribution of the grass Spartina patens and stated that "the paucity of

S. patens on the foredune is controlled, at least in part, by insufficient soil moisture." At the present study site S. patens was not observed in the foredune plant community, but was observed in some dune swales.

Soil pH values for dune stations of the present study did not vary greatly, ranging from 5.9 to 7.1, with most readings being between 6.0 and 6.9. The soil pH differences from zone to zone were not striking and did not appear to correspond with the vegetational zonation.

Soil pH readings from the present study were not greatly different from those reported by other investigators. Oosting and Billings (1942) reported that all soil pH readings at their dune study site on Bogue Bank, North Carolina, ranged from 7.4 to 7.9 and that no consistent differences between stations or depths were apparent. Gooding (1947) recorded pH for the coastal strand sands of Barbados, and all of his readings were between 7.5 and 8.5, with 85.7 percent of the readings being 8.0 or 8.5. Boyce (1954) reported that soil pH values for the coastal sands of Cape Fear, North Carolina varied between 7.0 and 8.0. Readings of pH for coastal strand sands on Bogue Bank made by Wagner (1964) all ranged from 7.7 to 8.0, with most readings being between 7.7 and 7.9. All of the soil pH values reported by Higgins et al. (1971) for the dunegrass community of Assateague Island ranged from 6.0 to 8.1, with most being between 7.0 and 7.8. Soil pH readings made by Au (1974) in the dune strand of Shackleford Bank ranged from 7.44 to 8.90, and those recorded by van der Valk (1975) for the Cape Hatteras foredune ranged from 6.7 to 6.9.

Soil calcium concentrations for samples from dune stations south of the pine forest in the present study were extremely low (with many

samples having only a trace of calcium), but the samples from the two stations (9 and 10) north of the pine forest were many times greater in calcium content. The higher values for stations 9 and 10 can be explained by the greater abundance of seashell fragments observed at those stations. Presumably these fragments yielded considerable amounts of calcium to soil of the bluestem zone via leaching. The higher content of soil calcium in the bluestem zone of the present study showed that this macronutrient was not responsible for the observed vegetational zonation, since Schizachyrium maritimum was dominant over Uniola paniculata also at station 5 where there was only a trace of soil calcium.

Wagner's (1964) calcium data for the dune sands of Bogue Bank ranged from 7.6 meq/100 g (1,520 ppm) to 8.0 meq/100 g (1,600 ppm). These figures were many times greater than the soil calcium concentrations for dune stations in the sea oats and shrub zones of the present study, but were of the same order of magnitude as soil calcium concentrations reported from the bluestem zone of the present study.

Au (1974) reported soil calcium concentrations for dunes on Shackleford Bank which ranged from a low value of 4,620 ppm to 38,100 ppm. In view of these figures, the sands of the Santa Rosa Island dune strand were remarkably low in calcium content (being at least an order of magnitude less in calcium concentration than the dune sands examined by Au), with even the front slope of the barrier dune registering only a trace of soil calcium. Au (1974) also found that the calcium content of his dune soil samples was considerably greater than the soil calcium content reported for an inland sandhills habitat (19 ppm), and attributed this difference to contributions from sea shell fragments near the

coast. Soil calcium concentrations from the present study were lower than that reported by Au (1974) for a sandhill habitat. However, van der Valk (1974a) reported foredune soil calcium concentrations for Bodie Island which were of the same order of magnitude as those observed for the foredune of the present study, with results for his surface samples and samples from 20 cm depth ranging from 4.4 kg/ha (2.0 ppm) to 7.0 kg/ha (3.1 ppm). For additional comparison, various soils for six stands of longleaf pine in Santa Rosa County, Florida, had calcium concentrations for the upper 30 cm which ranged from 0.0 meq/100 g (0 ppm) to 0. 5 meq/100 g (100 ppm), with most samples having 0.2 meq/100 g or less of calcium (Carlisle et al., 1978).

Soil magnesium content of the dune stations may be described as exceedingly low, especially when compared with the findings of Au (1974), who reported foredune soil magnesium concentrations which were 60 to 70 times greater than those of the present study! Higgins et al. (1971) reported soil magnesium concentrations for the dunegrass community of Assateague Island which averaged 21.3 ppm for the surface and 20.5 ppm for a depth of 20 cm. These figures were several times greater than those recorded in the present study. Van der Valk (1974b), however, reported soil magnesium concentrations for the foredunes of Bodie and Ocracoke Islands which were similar to those of the present study, being, in fact, somewhat less; his concentrations for the surface and 20 cm depth ranged from 2.0 kg/ha (0.9 ppm) to 4.4 kg/ha (2.0 ppm). Although in the present study soil magnesium concentrations were considerably greater in the bluestem zone than in the sea oats and shrub zones, soil magnesium did not appear to coincide with the vegetational zonation for the following reasons: the floristic composition of the

sea oats and bluestem zones were almost the same, even though the soil magnesium concentrations were different; and Schizachyrium maritimum was dominant at both stations 5 and 10, although soil magnesium concentrations were three times as great at station 10 as at station 5.

Soil potassium concentrations from the present study were uniformly very low for all dune stations and thus did not show any correspondence with the vegetational zonation. Wagner (1964) reported dune sand potassium concentrations for Bogue Bank, North Carolina, as ranging from 0.03 meq/100 g (11.7 ppm) to 0.05 meq/100 g (19.5 ppm)--figures which were approximately three to five times as great as most of the dune soil potassium concentrations for the present study. Higgins et al. (1971) reported soil potassium concentrations (as lbs/acre K_2O) for the dunegrass community of Assateague Island as averaging 4.3 ppm for the surface and 4.7 ppm for 20 cm depth--results which were similar to those from the present study. Au (1974) reported soil potassium concentrations for the foredunes and rear dunes of Shackleford Bank as ranging from 35.2 ppm to 44.0 ppm for the upper 30 cm of the soil profile--values which were several times greater than those of the present study. For Bodie and Ocracoke Islands van der Valk (1974b) reported foredune soil potassium concentrations ranging from 1.6 kg/ha (0.7 ppm) to 4.5 kg/ha (2.0 ppm) for the surface and 20 cm depth--concentrations which were less than those of the present study. For additional comparison, Carlisle et al. (1978) reported soil potassium concentrations for various soil types at six stands of longleaf pine forest in Santa Rosa County, Florida, as ranging from a mere trace to 0.69 meq/100 g (269.1 ppm) for the upper 30 cm of the soil profile.

Soil phosphorus concentrations for the present study were extremely low for dune stations south of the pine forest, indicating the infertility of the soil at those stations. The soil phosphorus concentration did not differ between the sea oats zone and the shrub zone, indicating that this nutrient was not causally related to the zonation of the vegetation. The somewhat higher soil phosphorus concentrations found in the bluestem zone did not show a pattern of coincidence with the vegetational zonation, since Schizachyrium maritimum was also dominant at station 5 where the soil phosphorus concentration was the same as those for the other stations of the sea oats and shrub zones.

Wagner (1964) reported dune sand phosphorus concentrations for Bogue Bank which ranged from 73.0 ppm to 128.0 ppm--figures which were many times greater than the dune soil phosphorus concentrations of the present study. Higgins et al. (1971) reported soil phosphorus concentrations (as lbs/acre P_2O_5) for the dunegrass community of Assateague Island which were in approximately the same range as those found in the sea oats zone of the present study. Their results, converted to ppm of P, yield an average value of 1.09 ppm for surface samples and an average value of 1.02 ppm for samples from 20 cm depth. Au (1974) similarly reported very low soil phosphorus concentrations for Shackleford Bank, with samples from the foredunes having virtually no measurable phosphorus and the rear dunes averaging 5.0 ppm for the upper 30 cm. Wright (1956) also reported extremely low soil phosphate content for an English dune.

Soil nitrate concentrations for dune stations of the present study were very low, and no coincidence between this factor and vegetational zonation was evident. Although nitrogen is generally considered to be

an important nutrient for all higher vascular plants, few investigations or measurements of it have been made in coastal strand habitats. Au (1974) reported dune soil nitrogen concentrations which ranged from 20 ppm to 30 ppm for the upper 30 cm of the soil profile. This was several times greater than the soil nitrogen content of the present study, and underscored how low in nitrogen the Santa Rosa Island dune sands were. For additional comparison, soils from two inland sites had nitrogen concentrations of 470 ppm and 290 ppm (Au, 1974).

Au (1974) also performed phytometric studies in which transplanted dune species were watered with liquid fertilizers containing nitrogen, phosphorus, and potassium. His results showed that potassium alone was not a limiting factor for the growth of dune species, but that nitrogen and phosphorus were extremely important in this regard. He concluded that "dune soils are conspicuously low in nitrogen and phosphorus, and thus the supply of these elements may be a limiting factor for many species," so that "only a few low-nutrient-requiring species . . . can survive in such environments" and that "competition for meager nutrition in the soil may explain to some degree the open vegetation in the dune environments." Since the dune soil nitrogen and phosphorus concentrations from the present study were lower than those found by Au (1974), the same conclusions may legitimately be applied to the Santa Rosa Island dune strand species.

Along the same lines, Boyce (1954) stated that "sea water apparently contains all of the necessary mineral ions in sufficient quantity for normal growth of land plants except nitrogen and phosphorus." Accordingly, he examined the effects of phosphate and nitrate fertilizers upon Uniola paniculata, Panicum amarum, Triplasis purpurea, Croton

punctatus, Physalis maritima, Oenothera humifusa, and Cakile edentula by adding them to selected plots in natural stands of these plants. Boyce found that phosphate-treated plants showed slightly better growth than untreated plants and that the susceptibility to salt spray of the treated plants was not different from that of untreated plants. Plants treated with nitrate fertilizer, however, showed better growth than untreated plants, but were also much more susceptible to salt spray damage than the untreated plants due to the fact that they developed thinner leaf cuticles which allowed more chloride to enter their leaves. Boyce concluded that low "available nitrogen in the dune environment operates as a conditioning factor," resulting "in an increase in the tolerance of dune species to salt spray," and that if the available soil nitrogen of the dunes were somehow increased, the pattern of plant zonation and distribution would change so that many species would become restricted to areas of lower salt spray intensity. Since several of the species considered by Boyce (1954) also occur on Santa Rosa Island at the present study site, the same observations and suggestions may also be applied there.

Oosting and Billings (1942) reported the NaCl content of dune soils, and found the greatest concentration to be 1.81 mg/100 g, which is equivalent to 1.10 mg Cl^-/100 g (11.0 ppm Cl^-). This amount of soil chloride was approximately two to ten times as great as results from dune soil samples of the present study; but Oosting and Billings still concluded that such "minute quantities of salt" as they observed in their soil samples could not affect the growth or distribution of plants on the dunes.

Boyce (1954) measured soil chloride content of the upper 1 cm layer and at a depth of 15 cm on the dunes at Long Beach, Brunswick County, North Carolina. He found that the surface layer had a much greater chloride content (averaging 36.8 ppm) than did the lower soil stratum (averaging 8.0 ppm). This was the same situation reported by a number of other investigators cited in his discussion. A similar result was observed during the present study for soil samples collected at the very surface and at depths of 5 cm and 10 cm near substitute salt spray dune station 3: after a prolonged dry period the soil surface chloride concentration was found to be several times greater than that at 5 cm and 10 cm depths. Boyce (1954) also found that immediately after a rain the soil chloride content at a depth of 15 cm remained almost unchanged (averaging 7.75 ppm), but the surface chloride content decreased to a concentration (averaging 7.5 ppm) approximately equal to that of the 15 cm stratum. He concluded that "most of the chlorides are leached from the sands by the frequent rains" and that, since salts deposited as salt spray remained at the soil surface and were then rapidly leached through the sand by rains, "a negligible quantity of chloride is absorbed by the roots of dune plants."

Au (1974) investigated soil salinity in the dune strand of Shackleford Bank, North Carolina, and reported the amount of salt in his samples as ranging from 3.3×10^{-4} N to 6.1×10^{-4} N. Au's soil samples were approximately 50 g in weight, and the aqueous extract for each sample for the salinity analysis was 100 ml in volume. The extracts were read with a conductivity bridge, and salinity was established from a standard curve prepared with known concentrations of sodium chloride. Based on this information, Au's figures (expressed as normality of the

soil extract) may be converted to the following approximate concentrations of NaCl in the soil samples: 38.6 ppm to 71.4 ppm; and these converted figures further yield soil chloride concentrations of 23.4 ppm to 43.3 ppm, respectively, which were several times greater than the soil chloride concentrations reported in the present study. However, it should be noted that Au's results for soil salinity analyses were not entirely reliable due to the analytical method which he employed. Au's readings were produced by the conductivity of all soluble salts from a soil sample, not just NaCl. Applying such conductivity readings to a standard curve based on known concentrations of NaCl would yield concentrations for NaCl which were erroneously greater than the actual NaCl concentration of the solution which was measured. However, since NaCl probably comprises a considerable percentage of total soluble salts in coastal strand soils, Au's figures, which were similar to concentrations reported by Boyce (1954), were probably not greatly erroneous. Nevertheless, Au considered the amounts of salt in all of his soil samples to be minuscule, and, although he did not measure the uppermost 5 cm of the dune sand, he stated that due to the low water content, this soil layer would have higher relative salinity than deeper strata. Au also observed that "continuous leaching by rainwater results in little salt accumulation in soil"--an observation similar to that made earlier by Boyce (1954).

Stalter (1976) measured soil chloride for the dune strand of Huntington Beach State Park, South Carolina. His results showed that the uppermost layer of dune soil had a greater chloride concentration (and hence, greater salinity) than did the deeper soil strata, with results for samples from 1 cm depth ranging in chloride content from 5

ppm to 160 ppm (average: 38.8 ppm). For soil depths of 15 cm and 37.5 cm Stalter's results ranged from 2 ppm to 8 ppm chloride (average: 3.6 ppm), with 60 percent of his samples having a chloride content of 2 ppm. Stalter's results for the deeper soil samples compared very closely to results of the present study, even though different depths were considered in the two studies.

Higgins et al. (1971) measured soil salinity of the dunegrass zone on Assateague Island using a conductivity bridge and a method which was probably similar to that of Au (1974). For surface samples their results averaged 0.14 ppt (140 ppm), for samples from 20 cm depth the mean was 0.26 ppt (260 ppm), and for samples collected at the top of the water table (range: 45 cm to 190 cm depth) the mean was 0.36 ppt (360 ppm). The results observed by Higgins et al. (1971) were most unusual for two reasons. First, they reported increasing soil salinity with increasing depth in the soil profile, which was contrary to what other investigators have observed. Secondly, the concentrations they reported were much greater (as much as one order of magnitude greater) than soil salinities reported by other investigators for Atlantic coast sites of the United States and for the present study site. It is possible that these results were erroneously too high due to the analytical method employed; but it is also possible that the wind, salt spray, and precipitation regimes of Assateague Island were such as to produce these apparently excessive amounts of soil salinity or that salt water intrusion (or a similar phenomenon) was evidenced.

Higgins et al. (1971) also measured salinity of groundwater collected at the upper surface of the water table, and reported an average of 3.19 ppt for samples from the dunegrass community. This figure was

in the same concentration range as results reported for soil water samples from Island Beach State Park, New Jersey, by Martin (1959), who considered as "a negligible amount" the concentrations (which did not exceed 2 ppt) of soil water salinity which he found.

Barbour and DeJong (1977) reported soil salinity values for beach sites all along the Pacific coast of the United States. Their results ranged from 75 ppm to 2,800 ppm for samples collected at 10 cm depth from 34 different locations. These results were many times greater than the concentrations (extrapolated from chloride readings) reported for the present study, and the higher concentrations were at least ten times as great as values reported by Higgins et al. (1971). Barbour and DeJong's collection loci were apparently very close to the ocean shoreline, and this may account for their high beach soil salinity values.

The low concentrations of soil chloride observed in the present study, and similarly low concentrations of soil chloride and/or soil salinity reported by most other investigators of coastal strand habitats, tended to support the findings of Kearney (1904) and Barbour (1970d) that dune strand species are not edaphic halophytes. The observation made by Oosting and Billings (1942), Boyce (1954), Clayton (1972), Au (1974), and van der Valk (1974b) that rapid leaching by frequent rains prevents the buildup of dune soil salinity contributed by wind-borne salt spray also appears to be true for the coastal strand of Santa Rosa Island, Florida.

Sodium was generally the most abundant cation found in dune soil samples from the present study site, with the exception that at stations 4 and 6 some calcium concentrations slightly exceeded the corresponding sodium concentrations, and at stations 9 and 10 the soil calcium

concentrations were much greater than the sodium concentrations. Nevertheless, soil sodium concentrations for the dune stations of the present study were not unusually high (with the highest reading being only 48 ppm) and did not demonstrate a pattern which coincided with the vegetational zonation.

Dune soil sodium concentrations from the present study were much less than those reported by Au (1974), who recorded dune soil sodium concentrations which ranged from 337 ppm to 1,165 ppm for samples collected on Shackleford Bank.

However, Clayton (1972) reported soil sodium concentrations for the California coast which ranged from 39.1 ppm to 57.5 ppm--results which were not much greater than those reported in the present study. Van der Valk (1974b) also reported dune soil sodium values for Bodie and Ocracoke Islands which were very similar to those of the present study. His results ranged from 17 kg/ha (7.6 ppm) to 80 kg/ha (35.8 ppm) for surface soil samples, and from 5.0 kg/ha (2.2 ppm) to 24 kg/ha (10.7 ppm) for samples collected at 20 cm depth.

For further comparison, various sandy soils at six stands of longleaf pine in Santa Rosa County, Florida, had sodium concentrations which ranged from 0.00 meq/100 g (0.0 ppm) to 0.05 meq/100 g (11.5 ppm) for the upper 43 cm of the soil profile (Carlisle et al., 1978). This indicates that coastal strand sands are generally higher in sodium content than are inland sandy sites, presumably due to greater sodium inputs from ocean spray.

Soluble salts concentrations were low in all dune soil samples, particularly so in the samples from stations 3, 4, 5, and 6. No relationship was evident between total soluble salts concentrations of the

dune soil and the vegetational zonation. Total soluble salts results from the present study showed that the dune soil on Santa Rosa Island was very infertile in regards to plant growth and overall plant nutrition--an observation which was verified by the low concentrations observed for the individual cations and anions in the soil samples.

No other American investigator has measured the soluble salts content of dune soils. However, Boyce (1954) did comment on this aspect of his coastal study sites when he wrote that "silicate sands of coastal dunes furnish little or no available mineral ions to dune plants."

Higgins et al. (1971) and Au (1974) supposedly measured soil salinity, but an examination of their methods shows that the conductivity readings which they measured were actually indicative of all soluble salts in their soil samples, not just NaCl or total sea salts present. But since their results were not expressed as soluble salts, the concentrations which they presented probably only approximated the soluble salts content of their samples.

Cation exchange capacity values for soil samples from dune stations of the present study were extremely low, with values less than 1 meq/100 g predominating. As with the soluble salts analysis and the other soil nutrient analyses, this indicated that the dune soil of Santa Rosa Island was extremely infertile. No other investigators have considered the cation exchange capacity of coastal strand soils in the United States. For comparison, however, the cation exchange capacity values for various soils at six longleaf pine stands in Santa Rosa County, Florida, cited by Carlisle et al. (1978) may be considered. They reported values which ranged from 2.47 meq/100 g to 20.81 meq/100 g for the top 30 cm of the soil profile. Although the sandy upland sites on

which longleaf pine dominates are generally considered to not be very fertile, it can be seen that the cation exchange capacity values for soils from these sites were considerably greater than those for dune strand soils of the present study, thus emphasizing the infertility of dune soil at the present study site.

In summary, the dune strand soil at the present study site was very low in nutrient content and in all cations and anions which were measured, with the exception of sodium. It was particularly low in organic matter content and in nitrate, phosphorus, potassium, and calcium. The sodium concentration of the dune strand soil was somewhat greater than that of inland sandy sites vegetated by longleaf pine (cf. Carlisle et al., 1978). The results of pH measurements showed that the dune soil was somewhat acidic at all stations. Analyses for chloride content showed that the dune soil was low in salinity, apparently due to rapid leaching of salt spray inputs (cf. Boyce, 1954; Au, 1974). Moisture content of the upper portion of the soil profile was not great in the dune strand, but other authors have reported that there was no lack of moisture available to plants in subsurface soil layers (usually at a depth of 30-60 cm) in the coastal strand (Kearney, 1900; Au, 1974). Measurements of soluble salts and cation exchange capacity also demonstrated that the dune strand soil of the present study site was very infertile. No relationship between any of the soil parameters and the vegetational zonation in the dunes was evident at the present study site--an observation which has also been made by other authors (Oosting and Billings, 1942; Au, 1974).

Pine Forest. Soil parameters measured for samples from the pine forest showed distinct differences between station 7 (at the southern edge of the forest) and station 8 (located deep inside the forest).

For most soil factors, results for samples from station 7 did not differ greatly from corresponding results for dune station samples. This was particularly noticeable for comparisons with results from station 6, which was located not far to the south of station 7 within the dune shrub zone. Station 7 may thus represent the edaphic limits which can be tolerated by Pinus elliottii; that is, apparently P. elliottii can grow satisfactorily in soil which is almost identical to that found in the treeless dune strand zones dominated by Uniola and Schizachyrium. The fact that P. elliottii is absent from the treeless dune zones obviously cannot be explained on the basis of soil factors; therefore, some other environmental factor (or factors) must be determining its distribution on Santa Rosa Island.

Organic matter content of soil at station 7 was slightly greater than at station 6, but slightly less than the soil organic matter content for dune stations 9 and 10. This indicated that the low organic content of the coastal strand soil would not preclude growth of P. elliottii. In contrast to the organic matter content, soil moisture for station 7 was considerably greater than that of all dune stations for both depths measured. The greater soil moisture was obviously due to the shallowness of the water table, which was observed to be higher at station 7 than at any of the dune stations (cf. Table 6) and was often less than 40 cm from the soil surface.

For soil samples from station 7, concentrations of calcium, magnesium, potassium, sodium, phosphorus, and nitrate were approximately the

same as, and in some cases were less than, corresponding concentrations for soil samples from dune stations to the south and north of the pine forest. Soil pH readings for station 7 were almost the same as those for station 6.

Soluble salts concentration for soil from station 7 was considerably greater than corresponding concentrations at dune stations 3, 4, 5, and 6 for samples taken at 5 cm depth, but was considerably less than corresponding results from dune stations 1, 2, 9, and 10. For soil samples from 10 cm depth station 7 had a soluble salts content that was approximately the same as that of most dune stations, but was considerably less than corresponding results for samples from dune stations 1, 9, and 10.

Station 8, which was located in a low area typical of the interior of the pine forest near Blackbird Marsh, had considerably more organic matter in the soil than did station 7 or any of the dune stations. The higher organic content and the shallowness of the water table, which was usually less than 30 cm from the soil surface, contributed to considerably greater soil moisture content at station 8 than was found at station 7 or at any of the dune stations. Presumably also due to the high humus content, the soil at station 8 had a lower pH value than did any other station.

The soil at station 8 was higher in concentrations of magnesium, potassium, and sodium than was soil at all other stations, and also had a greater cation exchange capacity and soluble salts content than did the soil at all other stations. In fact, the cation exchange capacity of the soil at station 8 was in approximately the same range of values reported by Carlisle et al. (1978) for inland soils at six stands of

longleaf pine in Santa Rosa County, Florida. Soil magnesium concentrations for station 8 were similar in magnitude to those reported by Au (1974) for forest soil on Shackleford Bank, but the station 8 soil potassium and sodium values were many times lower than those observed by Au (1974) for Shackleford Bank forest soil samples.

Surprisingly, the soil phosphorus and nitrate concentrations for station 8 were very low, being about the same as corresponding values for soil from station 7. Concentrations of these two soil nutrients at station 8 were less than corresponding values for soil samples from the bluestem zone, but were about the same as corresponding values reported for soil samples from the other dune stations. This was contrary to the findings of Au (1974), who reported slightly higher phosphorus concentrations for the forest soils he examined than for the dune soils and also reported high levels of nitrogen in the forest soils on Shackleford Bank. The low concentrations of these two nutrients at the pine forest stations in the present study indicated that the pine forest soil was probably not much more fertile than the dune station soils and further underscored the lack of any relationship between vegetational zonation and the soil concentrations of these two nutrients.

Calcium content of the soil at station 8 was many times greater than corresponding concentrations at station 7 and at all dune stations south of the pine forest, and also exceeded soil calcium values reported for stands of longleaf pine in Santa Rosa County, Florida, by Carlisle et al. (1978). This high calcium concentration obviously contributed to the higher cation exchange capacity of the soil at station 8. Soil calcium concentrations at stations 9 and 10 exceeded those of station 8; however, the fact that the values for cation exchange capacity of the

soil at stations 9 and 10 were much lower than the corresponding value for station 8 added evidence to the hypothesis that the shell fragments at these two stations contributed to the analyzed soil calcium value and that this high calcium value did not reflect a high soluble calcium content in the soil at dune stations 9 and 10.

The chloride content of the 10 cm soil samples from station 7 of the present study was greater than the corresponding concentrations for all dune stations except station 1, for which soil chloride concentration exceeded that of station 7 only slightly; and the chloride content of the 20 cm soil sample from station 7 was nearly twice as great as the corresponding concentration for the 20 cm sample from station 1. The chloride content of the soil at station 8 was much higher than that of all other stations, being five times as great as the soil chloride content at station 1 for a depth of 10 cm.

The higher soil chloride concentrations in the pine forest indicated that the soil there, with its greater organic content, was acting as a chloride trap. This is not to say that chloride was being chemically bound in the soil matrix, but that since the pine forest soil retained more moisture than did dune soil, an increased chloride level was probably produced simply because the chloride was not leached out as rapidly as it was at the exposed dune stations, where the soil was almost pure sand without organic matter.

Furthermore, a water sample collected near the edge of Blackbird Marsh (less than 2 m south of station 8) on September 13, 1981, was analyzed (using a Dionex Model IC 10 ion chromatograph) and was found to have a chloride concentration of 50.0 ppm. This additionally indicated that the pine forest substrate was a chloride trap; however, salt water

intrusion from the nearby bay and Gulf of Mexico may also have contributed to the pine forest chloride pool.

Although the soil chloride level in the pine forest was considerably greater than that found at most of the dune stations, it cannot be considered unusually great. The highest soil chloride value recorded during the present study (27.0 ppm, station 8) was much less than 0.01 percent.

Temperature

Dunes. Dune soil temperature data from the present study showed trends similar to those for dune soil temperature values observed by Oosting and Billings (1942). The actual temperatures reported by Oosting and Billings (1942) also compared favorably to readings from the present study. For example, they reported maximum soil surface temperatures of 125 ^{o}F (51.6 ^{o}C) to 127 ^{o}F (52.7 ^{o}C), maximum temperature at a depth of 4 inches (10 cm) of 95 ^{o}F (35.0 ^{o}C), and a maximum temperature at a depth of 10 inches (25 cm) of 89 ^{o}F (31.7 ^{o}C), while the respective maxima for the same three depths recorded in the present study were as follows: surface--54.0 ^{o}C, 10 cm--38.0 ^{o}C, and 25 cm--34.0 ^{o}C. Oosting and Billings (1942) stated that the temperature conditions which they observed for North Carolina dunes were similar to those reported for English dunes by Salisbury (1934), and they concluded that "No soil temperature variations were noted which can be interpreted as factors in the zonal distribution of a species."

Oosting (1956) also reported the results of a study which measured soil temperatures on a sand dune at Beaufort, North Carolina, in August, 1947. The maximum soil surface temperature recorded was 133 ^{o}F (56.1 ^{o}C), the maximum temperature at a depth of 4 inches (10 cm) was 98 ^{o}F

(36.7 °C), and the maximum temperature at a depth of 18 inches (46 cm) was 86 °F (30.0 °C). These readings were similar to the respective maxima stated above for the surface and depths of 10 cm and 25 cm in the present study.

Au (1974) did not study soil temperature in great detail in his study of dunes on Shackleford Bank, but he did state that in the summer the surface of the bare sand reached a temperature of 51-52 °C, which was very close to the surface temperature maxima observed in the present study.

Van der Valk (1974a) measured soil temperatures in upper (5-10 cm depth) and lower (20-25 cm depth) levels on the front, top, and back of a foredune on Bodie Island, North Carolina. His results for the front slope compared very well with the temperatures recorded in the present study at station 2, located on the front slope of the barrier dune. For example, van der Valk recorded an average maximum upper soil temperature of 13 °C for the month of February, compared with a maximum soil temperature of 13.0 °C for 10 cm depth at station 2 of the present study in February; and for the month of September van der Valk recorded an average minimum upper soil temperature of 25 °C and an average maximum upper soil temperature of 34 °C, compared with corresponding minimum and maximum readings of 27.0 °C and 33.0 °C for soil temperatures at 10 cm depth for station 2 of the present study in September. Van der Valk also concluded that soil temperature differences between zones "are not great enough to have any influence on the establishment or survival of dune plants."

Oosting and Billings (1942) and van der Valk (1974a) both expressed the idea that soil temperatures in coastal dunes did not show

differences between vegetation zones which could be interpreted as a causal factor in producing or maintaining the vegetational zonation. Results from the present study led to the same conclusion. The following observations serve to illustrate this point: (1) on one occasion soil temperature readings at all dune stations for a given depth and run were the same; (2) the highest and lowest soil temperatures for a given depth and run were both observed in the sea oats zone on thirteen occasions, with the lowest temperature for the same depth and run also recorded in the bluestem zone on four of those occasions, the highest and lowest temperatures for the same depth and run also recorded in the bluestem zone on one of those occasions, the highest temperature for the same depth and run also recorded in the bluestem zone on three of those occasions, and the highest temperature for the same depth and run also recorded in the shrub zone on five of those occasions; (3) the highest soil temperature for a given depth and run was recorded in the sea oats zone, and the lowest temperature for the same depth and run was recorded in the bluestem zone, on two occasions, with the highest temperature for the same depth and run also recorded in the shrub zone on one of those occasions; (4) the lowest soil temperature for a given depth and run was recorded in the sea oats zone, and the highest temperature for the same depth and run was recorded in the bluestem zone, on thirteen occasions, with the highest temperature for the same depth and run also recorded in the shrub zone on two of those occasions, and the lowest temperature for the same depth and run also recorded in the shrub zone on one of those occasions; (5) the highest soil temperature for a given depth and run was recorded in the shrub zone, and the lowest temperature for the same depth and run was recorded in the sea oats zone, on two occasions; and

(6) the highest soil temperature for a given depth and run was recorded in the shrub zone, and the lowest temperature for the same depth and run was recorded in the bluestem zone, on one occasion.

Pine Forest. Not surprisingly, soil temperature patterns for the present study at the two pine forest stations (7 and 8) were distinctly different from each other.

Soil temperatures at station 7, located at the south edge of the pine forest, showed a pattern which was generally similar to the soil temperature pattern for station 6, the nearest dune station located not far from it to the south. This fact underscored the observation that soil temperature was not a deciding factor in vegetational zonation at the present study site, and showed that, as far as this environmental factor was concerned, slash pines would be able to grow at dune stations, where only herbaceous species and shrubs are actually found, if some other environmental factor were not acting to preclude them from the nonarboreous dune zones.

Generally, soil temperature readings at station 8 during the present study showed a more moderate pattern than did soil temperature at the dune stations and at station 7. Soil temperature fluctuations were less extreme, and temperature differences from one depth to another were not as great at station 8 as they were at the dune stations and at station 7.

Generally, soil temperature readings at station 8 were slightly less at all depths than were corresponding readings at dune stations and at station 7 in spring, summer, and autumn, and the same was true for winter readings taken at midday and in the early evening. These slightly lower soil temperatures at station 8 were presumably due to a

shading effect of the forest canopy which prevented the sun from warming up the soil as much as it did at the more exposed stations. In the winter, early morning surface soil temperature at station 8 was slightly greater than corresponding surface temperature at the dune stations and at station 7. This was presumably due to the fact that the protection of the forest canopy at station 8 caused less heat loss than at the more exposed stations, and that before sunrise the exposed sites did not have an opportunity for the sun to heat up the soil there. The early morning winter soil temperatures at the lower depths at station 8 were generally slightly less than the corresponding temperatures at the dune stations and at station 7, indicating that, due to forest canopy shading, the station 8 soil at lower depths had not warmed up as much the previous afternoon as did the soil at the more exposed stations.

ATMOSPHERIC FACTORS

Air Temperature

Dunes. Air temperature measured at dune stations (Tables 7, 8, 9, and 10) in conjunction with soil temperature also did not show a pattern which appeared to coincide with the zonation of the vegetation. Differences in air temperature from station to station and from zone to zone were common, and fluctuations at a given station during a single 24-hour period were as great as 19.0 ^{o}C. The following observations illustrate the absence of a coherent pattern in the air temperature data of the present study and the absence of any relationship between air temperature and vegetational zonation: (1) on one occasion air temperature readings at all dune stations for a given run were the same; (2) the highest and lowest dune station air temperatures for a given run

were both observed in the sea oats zone on three occasions, with the highest air temperature for the same run also recorded in the bluestem zone on one of those occasions, and the lowest air temperature for the same run also recorded in the bluestem zone on one of those occasions; (3) the highest dune station air temperature for a given run was recorded in the sea oats zone, and the lowest dune station air temperature during the same run was recorded in the bluestem zone, on three occasions, with the highest air temperature for the same run also recorded in the shrub zone on one of those occasions; (4) the lowest dune station air temperature for a given run was recorded in the sea oats zone, and the highest air temperature for the same run was recorded in the bluestem zone, on four occasions, with the lowest air temperature also recorded in the shrub zone on three of those occasions; and (5) on one occasion the highest dune station air temperature for a given run was recorded in the shrub zone, and the lowest air temperature for the same run was recorded in the sea oats zone.

Oosting and Billings (1942) measured air temperature simultaneously at ten stations on two transects in the dunes at Fort Macon, North Carolina, taking readings hourly during a 24-hour period, and also made similar simultaneous air temperature measurements at other isolated times during the months of July and August. They did not report their actual readings, but stated that much variation was observed and that maximum temperatures did not exceed 100 ^{o}F (37.8 ^{o}C). They concluded that no correlation was apparent between air temperature in the dunes and vegetational zonation, and that no correlation existed between air temperature and topography in the dunes. The same observations may be made concerning dune air temperature readings from the present study.

Oosting (1956) also reported the results of a study which measured air temperature on a sand dune at Beaufort, North Carolina, in August, 1947. The maximum air temperature recorded was 104 ^{o}F (40.0 ^{o}C), which compared closely to the maximum air temperature (43.5 ^{o}C) for the present study.

Au (1974) recorded air temperature continuously during a one-year period at a single station in the coastal strand of Shackleford Bank, North Carolina. Although he reported only weekly and monthly averages, his results showed some similarity to figures from the present study. Au reported that the highest air temperatures observed were "35 ^{o}C or more," and in the present study 43.5 ^{o}C was the highest recorded dune air temperature. Au also observed that air temperature readings at his single station varied as much as 20 ^{o}C in a single day or week, while for the present study the greatest range of air temperature variation within a single day at a given station was 19.0 ^{o}C.

Van der Valk (1974a) measured air temperature approximately 35 cm above the sand surface on the front slope of a barrier dune at Bodie Island, North Carolina for a one-year period. His results were reported as monthly averages for daily minimum and maximum readings and an average for all readings during each month. Van der Valk's average maximum air temperature of 12 ^{o}C for the month of February compared favorably with the maximum air temperature of 14.0 ^{o}C recorded at station 2 (the front slope of the barrier dune) on February 17, 1979, during the present study; and his average maximum air temperature of 31 ^{o}C for the month of July was not greatly different from the maximum air temperature of 34.5 ^{o}C recorded at station 2 on July 7, 1979, during the present study. However, van der Valk's average maximum air temperatures for the

months of April and September, which were, respectively, 18 °C and 28 °C, did not compare well with the maximum air temperatures (32.0 °C and 36.0 °C) recorded at station 2 during the present study on April 14, 1979, and September 16, 1978, respectively. The higher temperatures recorded in the present study may be a result of the fact that the present study site was located approximately 720 km farther south than was van der Valk's study site.

Oosting and Billings (1942) observed that during the summer, air temperature in the dunes near Fort Macon, North Carolina, was less than soil surface temperature (usually 11 °C to 14 °C less) measured at the same time during the day, but was greater than the soil surface temperature at night. Data collected in the present study during the months of April, July, and September, showed a similar trend for air temperature in the dunes of Santa Rosa Island.

Oosting and Billings (1942) also observed that, as in all soils, the highest and lowest dune soil temperatures did not occur simultaneously with high and low air temperatures, but lagged considerably. Hourly air temperature readings from the present study (Tables 11 and 12) indicated that in the dunes of Santa Rosa Island maximum air temperature occured at 2 PM to 3 PM on a given day. From this information, as well as from the soil temperature data, it may be inferred that maximum dune soil temperatures on Santa Rosa Island normally occured between 3 PM and 6 PM on a given day.

Pine Forest. Pine forest air temperatures measured at stations 7 and 8 in the present study did not differ greatly in magnitude from corresponding air temperatures measured at dune stations immediately to the north and south of the pine forest. This was particularly true for

air temperatures at station 7 (where the forest canopy was not very dense) in relation to air temperatures at dune station 6, which was located not far to the south of station 7.

Air temperatures recorded at station 8 showed less fluctuation within a 24-hour period than did corresponding air temperatures measured at station 7, with the noon air temperature at station 8 always being less than the corresponding noon air temperature at station 7. The cooler midday air temperatures and the smaller range of daily air temperatures at station 8 (deep inside the pine forest) may be attributed to the sheltering and moderating effects of the forest canopy, which was considerably denser at station 8 than at station 7.

Relative Humidity

Dunes. Relative humidity values for dune stations on Santa Rosa Island during the present study showed considerable variation and fluctuation with respect to time and from station to station. No discernible pattern of relative humidity values during the present study showed a relationship with the zonation of the vegetation. The following observations about the relative humidity data serve to underscore this point: (1) the relative humidity at all dune stations was the same for a single run on one occasion; (2) the highest and lowest dune station relative humidity values for a single run both occurred in the sea oats zone on three occasions; (3) the highest dune station relative humidity value for a given run was recorded in the sea oats zone, and the lowest dune station relative humidity value for the same run was recorded in the bluestem zone, on four occasions; and (4) the lowest dune station relative humidity value for a given run occurred in the sea oats zone,

and the highest relative humidity value for the same run occurred in the bluestem zone, on four occasions.

Oosting and Billings (1942) measured relative humidity in the dune strand of Bogue Bank, North Carolina. Measurements were made simultaneously at ten stations on different occasions, and simultaneously at hourly intervals throughout one day, during the months of July and August. They reported wide variations and fluctuations from hour to hour and from station to station, with a range of as much as 30 percent (high: 84 percent; low: 54 percent) for simultaneous readings taken at five stations on a single transect. This compared to 21 percent for the maximum range of readings taken at approximately the same time at all dune stations (March 11, 1979) in the present study. On one occasion Oosting and Billings found that the relative humidity was identical at every station; the same observation was made in the present study for readings taken at 6 AM on March 11, 1979.

The highest relative humidity value recorded by Oosting and Billings (1942) was 88 percent, and the lowest was 54 percent. In the present study the highest dune station reading was 94 percent (6 AM, August 4, 1979), which was close to the maximum reading reported by Oosting and Billings. The lowest dune station relative humidity value reported from the present study was 35 percent (12 N, March 11, 1979), which varied considerably from the lowest reading reported by Oosting and Billings. The great difference in low readings between the two studies may be attributed to the fact that readings were taken at different seasons of the year in the present study (not just during the summer, as was done by Oosting and Billings), and the low reading

observed in March may represent a seasonal phenomenon produced by winter weather conditions.

Oosting and Billings (1942) also concluded that their data did not suggest a strong relationship between the distribution of vegetation and relative humidity on the dunes.

Pine Forest. Relative humidity values for the pine forest (stations 7 and 8) in the present study showed no pattern or outstanding characteristics which distinguished them from relative humidity values for the dune stations. Values for stations 7 and 8 were surprisingly similar to relative humidity values for the dune stations, not differing by more than 2 or 3 percent from corresponding values for dune stations, and were often the same as a corresponding dune station relative humidity value. These findings added support to the idea that relative humidity was not a causative factor in the distribution of vegetation in the coastal strand of Santa Rosa Island, and indicated that Pinus elliottii, the dominant forest tree at the western end of Santa Rosa Island, could exist under the same relative humidity conditions experienced by the dune vegetation communities.

Evaporation

Dunes. Averaging the results of evaporation rate measurements on the barrier dune (stations 1 through 4) for the two runs made during the present study revealed the following pattern: evaporation was greatest on the crest of the dune (station 3), being somewhat greater there than on the front slope (station 2) and slightly greater there than at the edge of the beach (station 1) (where the rate was intermediate between the rates for the front slope and the crest); and evaporation on the

rear slope of the barrier dune slightly exceeded that at the edge of the beach and was slightly less than the rate at the dune crest.

Oosting and Billings (1942) measured evaporation rates on North Carolina dunes for a total of 217 hours during an 18-day period in the months of July and August. The pattern of evaporation rates they observed on a barrier dune closely paralleled the pattern observed for the barrier dune in the present study; however, the results of the present study for the months of August and September averaged approximately 2 ml/hr more than the results reported by Oosting and Billings.

Although evaporation rate data for the different vegetation zones in the present study was not extensive, it clearly showed that evaporation was greatest in the sea oats zone. Oosting and Billings (1942) also observed that evaporation was greatest in the dunes where sea oats were dominant and was not as great at stations where Andropogon littoralis (= Schizachyrium littorale) dominated. This led them to conclude that "greater daytime evaporation in the exposed situations may contribute to the presence of Uniola and the absence of Andropogon in such places." The evaporation data of the present study appeared to add support to this hypothesis, since the evaporation rate where U. paniculata dominated (sea oats zone) was greater than where Schizachyrium maritimum was dominant (bluestem zone).

Davis (1942) (as recounted by Oosting, 1954) exposed Livingston atmometers for two periods of 15 days each in three zones on the Florida keys: near the beach, in scrub, and in a mangrove mangal. The average daily amount of water evaporated for the station located near the beach was 30.1 cc. This computes to an average of 1.25 ml/hr (assuming that the 30.1 cc was evaporated in a 24-hour period), an evaporation rate

which was less than one-third of the dune station averages of the present study. The data from the present study showed that Davis's assumption that evaporation rates on the keys must be greater than at points farther north (because of greater exposure and the nearness of the continuous tradewinds) was false. Data reported by Oosting and Billings (1942) also demonstrated that Davis's assumption was not correct.

Evaporation rates are generally believed to be directly correlated with transpiration rates of dune plants; however, Oosting (1954) found that this assumption was not always true. His studies using Uniola paniculata, Andropogon scoparius var. littoralis, Spartina patens, Cakile edentula, and Heterotheca subaxillaris, and plotting daily water losses from atmometers with daily transpiration losses for the five dune species, showed marked discrepencies on enough occasions that he concluded that factors other than those of the atmosphere sometimes influenced the loss of water by transpiration from dune species. He stated that "Physiological and structural peculiarities of the plants must at times have a controlling effect which exceeds those conditions determining evaporation rates." Oosting (1954) also pointed out that an earlier study (Bowman, 1918) in the Tortugas showed that several coastal strand species transpired more in the shade than when they were exposed to intense sunlight and became overheated and partially wilted.

Pine Forest. Data from the present study (although not extensive) clearly showed that evaporation deep inside the pine forest (station 8) was considerably less than at the exposed dune stations. This was assumed to be due to the sheltering effects of the forest canopy. Although verification measurements were not made, reconnaissance observations indicated that wind velocity and incident solar radiation were

less within the pine forest than at the treeless dune stations. Oosting (1954) also pointed out that evaporation was much greater in positions exposed to the wind than in protected sites, and the evaporation data from the present study tended to support this observation.

At station 7, however, evaporation was approximately equal to that at station 6 in the shrub zone. Presumably this was due to the fact that the forest canopy was not as dense at station 7 as at station 8, and apparently wind and incident radiation conditions there were not greatly different from those at station 6, which was only 40 m to the south. The evaporation rate at station 7 indicated that Pinus elliottii can withstand evaporation stress similar to that experienced by vegetation in the shrub zone to the south. Since P. elliottii did not actually occur as far south as the shrub zone, it may be inferred that some factor other than evaporation stress determined the distribution of this species at the present study site.

Wind Direction and Velocity

The wind direction pattern for Santa Rosa Island, based upon U. S. Coast Guard data (Table 20), showed that winds measured there came primarily from the south, west-southwest, and west in summer, and primarily from the north and northeast in winter, with the spring and autumn months being somewhat erratic transitional periods in which predominating winds came from directions intermediate between the summer and winter prevailing directions, but were primarily from directions on the eastern half of the compass. This was slightly different from the general pattern for western Florida stated by Gorsline (1966): "During the spring, winds come from the east; during summer, winds are southerly; during winter, they approach from the northwest."

Nix (1976) presented the wind direction pattern for Pensacola Naval Air Station, which was located directly north of the present study site across the mouth of Pensacola Bay, giving percentages of annual wind direction as follows: north--16.0 percent, northeast--10.5 percent, east--11.5 percent, southeast--11.5 percent, south--13.0 percent, southwest--10.5 percent, west--8.0 percent, northwest--9.0 percent. It was not easy to compare this data with the wind direction pattern for Santa Rosa Island, since the Coast Guard recognized eight more wind directions than were shown on Nix's diagram; however, some differences did seem to be indicated by the Coast Guard wind direction data cited in the present study, for which the following percentages of total readings were from the north, south, and east, respectively: 9.0 percent, 8.7 percent, 4.7 percent.

Oosting and Billings (1942) reported that at Beaufort, North Carolina (which is located on the coast north of Shackleford Bank), winds were prevailingly from the southwest during all months except September, October, and November. This pattern was quite different from that reported for Santa Rosa Island in the present study. However, somewhat farther to the north at Hatteras, North Carolina (which is located on Hatteras Island southwest of Cape Hatteras), prevailing winds were reported to be from the southwest in spring and summer, and from the northeast in autumn (Oosting, 1954)--a pattern which was not greatly different from the wind direction regime noted for Santa Rosa Island. Au (1974) reported that the wind direction pattern at Morehead City, North Carolina (which is located on the coast north of Bogue Bank), was the same as that at Hatteras. The similarity in wind direction patterns at Santa Rosa Island, Hatteras, and Morehead City may be due to the

orientation of the coastlines, which is basically the same at the three sites, namely, in a primarily east-west direction. In contrast to this, prevailing winds at Key West were from the west (Oosting, 1954).

Wind velocity data from the Santa Rosa Island Coast Guard Station (Table 21) showed that the strongest winds generally occurred in the winter months of December, January, February, and March, although an unusually strong wind (20.6 m/sec) was recorded in the middle of summer (July). Average wind velocities for the months of December through April exceeded the averages for the remaining months, but by no more than 2 m/sec for any given month and usually by no more than 1 m/sec.

The wind velocity pattern at Morehead City, North Carolina, differed from that at Santa Rosa Island, with the strongest winds generally occurring in March, April, May, June, and July (Au, 1974). The average monthly maximum wind velocity for winter and spring months at Morehead City was approximately 5 mph (2 m/sec) less than that of the summer months, but stronger winds were occasionally recorded in winter months than in summer (Au, 1974). The maximum monthly wind velocity values for Morehead City were of approximately the same magnitude as those recorded at Santa Rosa Island and ranged from 12.0 m/sec (September) to 25.6 m/sec (December). The monthly means for daily maximum wind velocity for Morehead City were also of similar magnitude to corresponding means for Santa Rosa Island, ranging from approximately 6.0 m/sec (December) to approximately 8.4 m/sec (April).

The average wind velocity for all available Coast Guard readings on Santa Rosa Island (Table 21) was 5.0 m/sec. This compared closely to the average wind velocity of 13.4 mph (5.4 m/sec) reported for Hatteras, North Carolina (Oosting and Billings, 1942; Oosting, 1954), but was

somewhat greater than the average wind velocity of 9.6 mph (3.8 m/sec) reported for Key West, Florida (Oosting, 1954). In contrast to this, van der Valk (1974a) reported that the average annual wind velocity at Cape Hatteras was 2.6 m/sec.

Boyce (1954) investigated the relationship of wind velocity and the production of wind-borne salt spray in coastal strand areas. He found that at lower wind velocities only slight amounts of salt spray were produced, but that at wind velocities between 5.5 and 7.5 m/sec there was a dramatic increase (at least two- to three-fold) in the amount of salt spray deposited in the coastal strand. Boyce presented his findings in a striking diagram and also pointed out that his findings agreed with the previous finding by Munk (1947) that 7.0 m/sec was a critical wind velocity for air-sea boundary processes at which a number of such processes underwent abrupt changes.

The critical wind velocity for the movement and transport of sand grains was stated by Ranwell (1972) as being approximately 4.5 m/sec, apparently based upon formulas given by Bagnold (1965). Similarly, Godfrey (1977) gave the critical wind velocity as approximately 4.0 m/sec for sand movement along the Atlantic coast of the United States. It is assumed that these two figures apply generally to sand grains in the range of 0.08-0.5 mm diameter, which is the size range for dune sands. Since the size of dune sand on Santa Rosa Island is 0.29-0.35 mm diameter (van Wyk, 1973), which is larger than coastal sand of most areas in the southeastern United States (Martens, 1931), the higher critical wind velocity of 4.5 m/sec probably applies to Santa Rosa Island. It should be noted, however, that critical wind velocity for sand movement can only be approximated for purposes of general

ecological discussion, since the critical velocity at any specific time and place is also determined by cohesion of the sand grains, which is greatly influenced by moisture in the sand and in the air.

On Santa Rosa Island every month of the year from December to September (and also probably October and November) had some wind velocities which exceeded the critical wind velocity (ca. 4.5 m/sec) for transport of sand particles and which also exceeded the critical velocity (ca. 7.0 m/sec) for the production and transport of considerable amounts of salt spray, as indicated by monthly maximum wind velocity values. However, the average wind velocity for every month, except June and August, exceeded the critical wind velocity for sand transport, but it was less than the critical wind velocity for salt spray transport during all months.

A different picture presented itself when the monthly mean values of daily maximum wind velocity were examined: for every month of the year, the mean of daily maxima exceeded the critical wind velocity for sand movement (with the highest means occurring in January, February, March, September, and December); but, only for the months of January, February, March, September, and December (and probably for October and November as well) did the monthly mean of daily maxima exceed the critical wind velocity for salt spray transport. Thus, winds sufficiently forceful to transport considerable amounts of salt spray occurred on most days of the months just stated, with the opposite being true for the months of April through August, during which the averages of the daily maxima did not exceed the critical transport velocity for salt spray. This indicated that the salt spray regime of Santa Rosa Island was a seasonal phenomenon; with most of the salt spray activity

occurring in late autumn and winter months through early spring, since the greatest wind velocities occured during that period.

Wind velocity data indicated that salt spray on Santa Rosa Island was a generally moderate process, with small amounts of salt spray being deposited continuously on most days, and, as was observed by Au (1974), it apparently builds up as a soil surface deposit and on vegetation surfaces during nonpluvious periods, only to be washed off and leached away when rains occur. Wind velocity data also seemed to indicate that Santa Rosa Island experiences only small amounts of sand movement on most days.

Au (1974) discussed the importance of wind in the coastal strand environment and reviewed the literature regarding it. He stated that "of all physical environmental factors influencing coastal vegetation, wind seems to be the most important," and he summarized the impact of the wind on vegetation in the following six statements: "(1) wind-borne salt spray kills susceptible species growing close to the ocean; (2) abrasive sand blast created by strong winds causes tissue wounds which enhance the toxic effect of salt spray on plants; (3) constant and excessive wind may induce desiccation of leaves; (4) strong wind inflicts mechanical injury on plants such as breaking branches or defoliation; (5) winter storms cause salt-water erosion and flood the strand vegetation; and (6) wind causes shifting sands which in turn bury and destroy all vegetation in their path." It is reasonable to assume that all of the six points made by Au probably apply, in various degrees, to wind-induced phenomena in the coastal strand of Santa Rosa Island, but the present study was not designed to identify or quantify all the effects stated by Au.

Sand Movement

Not much sand movement or accumulation was noted in the coastal strand of Santa Rosa Island during the present study. In part, this was probably due to the fact that at the primary study site the barrier dune was well-stabilized by vegetation. However, reasons for the accumulation of such a small quantity of sand (less than 14 cm) at the primary study site were not readily apparent. It is possible that a type of equilibrium existed there (determined by the prevailing meteorological and sand budget regimes) such that the stabilized dune could not accumulate additional sand because it had reached its maximum possible size. It is also possible that not much sand was being deposited by wave action on the south side of the island, and that whatever quantity of sand was made available in this manner was remaining in the exposed bare beach strip. Perhaps winds from the south were transporting this sand only as far inland as the northern edge of the beach during the summer months, and winter winds from the north were blowing the sand back to the south edge of the beach and even back into the Gulf of Mexico.

Au (1974) investigated sand movement in the coastal dunes of Shackleford Bank, North Carolina. He found that sand was being removed from the ocean side (prevailing windward slope) of the foredune and being deposited on the leeward slope. Vegetational cover determined the amount of sand movement, and the accretion rate was relatively small, not exceeding 20 cm/yr and being less than 10 cm in a normal year. He stated that maximum sand movement in the dunes "seems to occur in winter (November to March)," and concluded that during the winter, sand movement was the most important factor affecting the vegetation since

"herbaceous plants are either dormant or dead and thus nothing can prevent the movement of sand."

Van der Valk (1974a) investigated sand movement on barrier dunes at Bodie and Ocracoke Islands, North Carolina, in Cape Hatteras National Seashore. He found that most sand movement occurred during winter months, as had Au (1974). Van der Valk also found that on the barrier dune at Bodie Island, which was over 2.5 m high, sand accumulation occurred primarily on the front of the dune; whereas at Ocracoke Island, where the barrier dune was less than 2.5 m high, sand accumulation took place on the front, top, and back of the dune. He further observed that the annual sand deposition rate at his study sites was 20 to 30 cm (similar to what Au noted) and that sand could also be removed from the front of barrier dunes by wind action.

Van der Valk (1974a) also studied the effects of sand burial on seed germination and seedling growth of six species of dune strand forbs. He found that seeds of Erigeron canadensis and Solidago sempervirens can tolerate only 1 cm of burial, seeds of Physalis viscosa can tolerate 3 cm of burial, seeds of Iva imbricata can tolerate 4 cm of burial, seeds of Croton punctatus can tolerate 12 cm of burial, and seeds of Strophostyles helvola can tolerate 14 cm of burial. Thus the winter deposition of 20 to 30 cm of sand which he recorded would make it impossible for these plants to become established on the front of the barrier dune by means of seed germination. He observed that transplanted seedlings of E. canadensis and S. helvola could not withstand the salt spray conditions of the front slope of the foredune. Though seeds of I. imbricata could not survive much burial, the mature plants and seedlings readily grew up through accumulated sand; therefore, this

plant can only become established from germinating seeds during years of unusually low sand deposition. Van der Valk concluded that "Sand movement, then, is the major factor preventing the establishment of most forbs on the front of the foredune or any other area of shifting sand" and that "Salt spray plays only a secondary role in eliminating forbs from the front of the dune."

Even though sand movement at the present study site on Santa Rosa Island did not appear to be as great as that described by Au (1974) and van der Valk (1974a), it is possible that moving sand there plays a role similar to that reported by van der Valk in determining the composition of vegetation on the front of the barrier dune.

Wind-borne Salt Spray

General. The expected pattern for salt spray deposition (cf. Oosting and Billings, 1942; Martin, 1959; Randall, 1970; Au, 1974; van der Valk, 1974b; Stalter, 1976; Barbour, 1978; inter alia) during the present study was as follows for all stations, considering relative amount (or percentage) deposited at each station: station 1>station 2>station 3>station 4>station 5>station 6>station 7>station 8<station 9<station 10, with the amount deposited at station 9 approximately equaling the amount deposited at station 5. The reasons for expecting this pattern are stated here. (1) If the amount of salt spray received at a given point decreases with increasing distance from the Gulf of Mexico or from Pensacola Bay, the station nearest the ocean (station 1) should receive the greatest amount of salt spray, and other stations progressively farther inland should receive less and less, with station 8, being farthest inland, receiving the least salt spray. Station 10, because of its proximity to Pensacola Bay, would be expected to receive

more salt spray than station 9, which was farther inland from the bay. (2) If tolerance to salt spray determines the location of a plant species in the dune strand, then the vegetational zonation pattern should be indicative of the relative amount of salt spray received in each zone. It was expected that the sea oats zone would receive more salt spray than the shrub zone, and that, since there were no shrubs (such as Ceratiola ericoides, Chrysoma pauciflosculosa, Ilex vomitoria, etc.) in the bluestem zone (except for a few scattered individuals of Opuntia pusilla and Smilax auriculata), the bluestem zone would receive more than the shrub zone. Since the pine forest species were generally the least tolerant to salt spray of the plants encountered at the present study site, it was expected that the pine forest stations would receive the least amount of salt spray, certainly less than was received in the shrub and bluestem zones.

Since the salt spray collectors employed during the present study were open to the atmosphere, they received what is known as bulk precipitation (Gambell and Fisher, 1966), which consists of inputs from windborne salt spray, rainfall, and dry fallout. Near the ocean, dry fallout is negligible, and, as Gambell and Fisher (1966) further pointed out, sea salt is the only significant source of chloride in rainfall. Thus, there is no need here to consider individually the three components of bulk precipitation, since all chloride received in this study was from the ocean. The amount of chloride received at the various stations may then be considered as indicative of the total effect of ocean-derived salt aerosols upon the vegetation. Also, for purposes of later discussion, it must be stressed that the collectors employed in the

present study measured the amount of salt spray received at the soil surface.

Dunes. For dune stations 1 through 6 the observed pattern of salt spray deposition in the present study matched the expected pattern, with progressively less salt spray being received at stations farther and farther inland from the Gulf of Mexico.

If the barrier dune only is considered as a unit, the averaged percentages of salt spray received on the front (53.7 percent), top (27.0 percent), and back (19.3 percent) of the barrier dune in the present study are similar to the averages reported by van der Valk (1974b) for the front (53.0 percent), top (32.5 percent), and back (14.5 percent), respectively, of two dunes on Bodie and Ocracoke Islands, North Carolina. The barrier dune percentages of the present study were comparable to the findings of Oosting and Billings (1942), who reported the following percentages of salt spray deposition for two transects measured across barrier dunes at Bogue Bank, North Carolina (cf. van der Valk, 1973): Transect I--55 percent (front), 28 percent (top), 17 percent (back); Transect II--59 percent (front), 29 percent (top), 12 percent (back). Percentages from the present study also compared well with those reported by Stalter (1976) for a barrier dune at Huntington Beach State Park, South Carolina: 52.7 percent (front), 34.6 percent (top), 14.0 percent (back). Comparing the results of the present study with these averages showed that on the Santa Rosa Island barrier dune somewhat less salt spray was deposited on the front slope and crest, and that somewhat more was deposited on the back slope. Salt spray thus appeared to be more evenly distributed between the crest and rear slope

of the Santa Rosa Island barrier dune than on the Carolina dunes studied by other investigators.

This depositional difference may be attributed to differences in sampling techniques. Oosting and Billings (1942), van der Valk (1974b), and Stalter (1976) all used collectors which were mounted above the soil surface, and they placed the collector measuring salt spray deposition for the rear of the dune close to, or at, the base of the dune. In the present study the collector for the rear of the barrier dune was placed midway down the rear slope, and was thus much closer to the collector on the crest than was the case for the three other studies cited.

Considerably less salt spray was received in the bluestem zone than in the sea oats zone (as shown by results for samples from stations 9 and 10), and this may explain the dominance of Schizachyrium maritimum and the paucity of Uniola paniculata in this zone. Oosting and Billings (1942) observed that U. paniculata was dominant only where salt spray intensity was the greatest and that Andropogon littoralis (= Schizachyrium littorale), which is apparently the ecological equivalent of Schizachyrium maritimum and is a closely-related species, predominated in areas which received less salt spray. Their observations coincided exactly with those of the present study for the distribution of S. maritimum, which was dominant at stations 9 and 10, where less salt spray was received than at sea oats zone stations where U. paniculata was dominant.

To make comparisons of quantitative results from different coastal strand salt spray studies, it is of paramount importance to realize that the amount of salt spray received by a collector at or near the soil surface is considerably less than the amount received by a collector

mounted several centimeters above the soil surface and, obviously, is also less than the amount received by parts of plants not near the soil surface. This fact has been observed by Martin (1959), Randall (1970), and Barbour (1978), who placed collectors at various heights above the soil surface in their salt spray studies.

Martin (1959) found that traps placed 1 ft (30.5 cm) above the soil surface along the New Jersey coast received 32 percent less salt spray than did traps exposed 3 ft (91.4 cm) above the surface. Randall (1970) reported that traps at the soil surface in exposed coastal strand areas of Barbados received only 16.7 percent as much salt spray as traps 1 m above the soil surface. Barbour (1978), working along the California coast, found that traps placed 14 cm above the soil surface received 75 percent as much salt spray as traps mounted 25 cm above the surface, and that traps placed at the soil surface received only 14 percent as much salt spray as traps 25 cm above the surface. Interestingly, Barbour (1978) pointed out that Etherington (1967) and van der Valk (1973, 1974b) overlooked in their mineral cycling studies this phenomenon of salt spray deposition decreasing with proximity to the ground and, consequently, presented figures which were erroneously too high. Along the same lines, Malloch (1962), who used cylindrical collectors with openings near the soil surface, similar to those employed in the present study, reported that 5 percent to 15 percent less sodium was received by his salt spray collectors than was collected by rain gauges with rims placed 50 cm above ground level.

Martin (1959), Randall (1970), and Barbour (1978) used vertical pieces of cheesecloth, toweling, or filter paper placed at right angles to the wind for their above-ground-level traps and placed horizontally

at the soil surface. It does not seem unusual that such traps inserted into the moving stream of salt-laden air would collect considerably more salt spray than a trap placed horizontally at the soil surface, since the horizontal trap would collect mostly fallout from the moving air stream. In Malloch's study the salt spray collectors and rain gauges both collected bulk precipitation, and thus it is understandable that the difference he observed was less than that reported by investigators using laminar traps, though it reflected the same pattern in regards to the elevational gradient.

Randall (1970) and Barbour (1978) also observed that the difference between amounts of salt spray deposited at the soil surface and at loci above it decreased with increasing wind speed. It should additionally be noted that Boyce (1954) determined that cheesecloth traps situated above the soil surface did not collect as much salt spray as was deposited on leaves and twigs of coastal vegetation, but merely provided an indication of the relative intensity of spray at different stations.

Oosting and Billings (1942) reported the following averages for NaCl ($mg/dm^2/day$) received for the two barrier dune transects they studied: 20.2 (front), 10.4 (top), 5.2 (back). These figures were, respectively, 14.7, 13.0, and 9.1 times as great as the average amounts of NaCl received on the front, top, and back of the barrier dune in the present study (assuming that sea salt is 78.5 percent NaCl).

Boyce (1954) measured salt spray at Long Beach, North Carolina, at various distances inland from the tide line and under various prevailing wind speeds, and reported his results as $mg/dm^2/hr$ of total sea salts received. Expressing Boyce's figures for a wind speed of 5.5 m/sec (which was probably close to the approximate extrapolated average wind

speed for the time periods of the four salt spray runs of the present study) as mg/dm^2/day of total sea salts received, yields the following quantities for the stated distances from the tide line: 45 m--16.8, 95 m--12.0, 120 m--9.6. In the present study, stations 2, 4, and 5 were, respectively, 58 m, 72 m, and 120 m inland from the tide line of the Gulf of Mexico. Expressing the salt spray data from these stations as mg/dm^2/day of total sea salts, using Boyce's computational method (salinity = 1.805 chlorinity + 0.03), yields the following averaged figures: station 2--1.75, station 4--0.73, station 5--0.34. Comparing this data with Boyce's data shows that Boyce's concentrations were, respectively, 9.6, 16.4, and 28.2 times as great as those from the present study.

Martin (1959) measured salt spray at Island Beach State Park, New Jersey, using cheesecloth traps. He determined the chloride concentrations of his elutriated test solutions by titration with silver nitrate using the Knudson method and reported his results as mg/dm^2 of total sea salts received. For one run of 48 hours exposure during moderate winds with traps mounted 1 ft (30.5 cm) above the soil surface, Martin's results may be converted to mg/dm^2/day of total sea salts received at the following foredune locations: front--22.50, top--9.50, back--1.50. Expressing the barrier dune salt spray data from the present study as mg/dm^2/day of total sea salts, using the Knudson equation to determine salinity from chlorinity (salinity = 1.805 chlorinity + 0.03), yields the following averaged values: front--1.75, top--1.02, back--0.73. Martin's results were, respectively, 12.9, 9.3, and 2.0 times greater than results from the present study for the front, top, and back of the barrier dune.

Cartica and Quinn (1980) also measured wind-borne salt spray at Island Beach State Park, New Jersey, using cheesecloth traps mounted with centers 42 cm above the soil surface. During two 24-hour runs they reported the deposition of 5.1 mg/dm^2/day and 6.7 mg/dm^2/day of chloride at a station located approximately 25 m inland from the ocean. The average value (5.9 mg/dm^2/day) for these two runs was 6.1 times as great as the average amount of chloride (0.97 mg/dm^2/day) received at station 2 during the present study. This difference is understandable in view of the fact that Cartica and Quinn's traps were mounted several centimeters above ground level and were located much closer to the ocean. At a distance of 550 m inland from the ocean Cartica and Quinn (1980) collected 2.3 mg/dm^2/day and 2.6 mg/dm^2/day of chloride (approximately 2.5 times the amount recorded at station 2 in the present study), which indicated that the salt spray regime at their study site was considerably more intense than that of the present study site.

Clayton (1972) collected rain and salt spray along the coast of San Mateo County, California (approximately 100 km south of San Francisco), using a cylindrical plastic bottle 25 cm deep and with a cross-sectional area of 192 cm^2 located 40 m inland from the high tide line. After 86 days of exposure the collected water (2,380 ml) in his single bottle was analyzed for chloride, sodium, potassium, magnesium, and calcium. The concentration of chloride in the sample was 2.00 meq/L (70.91 mg/L). This figure converts to a deposition rate of 1.02 mg/dm^2/day, which was close to the amount of chloride received in the present study at station 2 (approximately 58 m inland from the high tide line). The amount of sodium received by Clayton's collector was also 2.00 meq/L (45.98 mg/L). This figure converts to an input of 241 kg/ha/yr, which was not much

greater than the average input (196 kg/ha/yr) of sodium received at station 2 in the present study.

Malloch (1972) collected salt spray on the Lizard Peninsula of England using collectors almost identical to those employed in the present study. His results for sodium received at various distances from the sea, expressed as kg/ha/day, were as follows: 50 m--4.92; 100 m--1.15. In the present study stations 2, 4, and 5 were, respectively, 58 m, 72 m, and 120 m from the high tide line of the Gulf of Mexico. If the average calculated sodium inputs for these stations are expressed as kg/ha/day the following figures result: station 2--0.54, station 4--0.22, station 5--0.10. Malloch's 50 m result was 9.1 times as great as the station 2 input from the present study, and his 100 m result was 5.2 times as great as the station 4 input from the present study and 11.5 times as great as the station 5 input. The greater inputs reported by Malloch (1972) were probably due to differences in the wind regimes of the two study sites.

Malloch (1972) also reported the inputs of sodium and chloride for a rain gauge (with its rim 50 cm above the soil surface) located 30 m from the ocean on the Lizard Peninsula. Sodium deposition at this point was 204 kg/ha/yr; chloride deposition was 366 kg/ha/yr. Assuming that the rain gauge collected 10 percent more sodium than the ground-level tube (as Malloch stated), it can be seen that the inputs in the present study were actually slightly greater than those reported by Malloch, averaging 196 kg/ha/yr sodium and 353 kg/ha/yr chloride at station 2 (58 m from the ocean).

Van der Valk (1974b) determined by flame photometry the cation content of the test solutions derived from his salt spray collections

(using traps composed of strips of plastic tape stretched across a frame) along the North Carolina coast, and expressed the results as kg/ha/yr received. His averaged results for sodium at two transects across the foredune on Bodie and Ocracoke Islands were as follows: front--1040, top--635, back--280. Averaged sodium input values (kg/ha/yr) for the four salt spray runs of the present study were as follows for the three stated barrier dune locations: front--196, top--132, back--94. Van der Valk's values were, respectively, 5.3, 4.8, and 3.0 times as great as corresponding results of the present study for the front, top, and back of the barrier dune. Values for the two studies compare favorably, in view of the fact that van der Valk's collectors were mounted several centimeters above the soil surface.

Stalter (1976) collected salt spray at Huntington Beach State Park, South Carolina, using pieces of paper toweling (10 cm x 15 cm) mounted with the lower edge 15 cm above the soil surface. His results were reported as ppm of chloride for the 100 ml solution which was used to elutriate the salt spray from the paper towel. If values from Stalter's 27 runs are expressed as $mg/dm^2/day$ of chloride received, the following averaged figures result for his barrier dune stations: front--2.37, top--1.58, back--0.90. These figures were amazingly similar to the barrier dune chloride averages ($mg/dm^2/day$) from the present study (front--0.97, top--0.56, back--0.40) and were, respectively, 2.4, 2.8, and 2.2 times as great as results from the present study for the front, top, and back of the barrier dune. The similarity of Stalter's data to that of the present study can be explained (at least partly) by the fact that his collectors were mounted relatively close to the ground surface.

Barbour and DeJong (1977) reported results of salt spray collections made at two California beaches with cheesecloth traps similar to those employed by Oosting and Billings (1942). Inputs ranged from less than 5 $mg/dm^2/day$ of total salts received to approximately 175 $mg/dm^2/day$ during a one-year period, depending upon the wind speed, with most figures being 50 $mg/dm^2/day$ or less. These results were much greater than those reported from the present study, but, since the collectors were laminar in construction and were mounted several centimeters above the soil surface, the disparity is understandable.

Barbour (1978) measured salt spray along the California coast using 5.5 cm-diameter circles of filter paper with their centers mounted 14 cm above the soil surface. These were arranged in 6 parallel rows spaced at 4 m intervals from 60 m to 80 m inland from the mean tide line. Barbour's averaged results for collectors at various distances from the tide line, expressed as $mg/dm^2/day$ of total sea salts, were approximately as follows: 60 m--20, 64 m--18, and 72 m--12. In the present study, stations 2, 3, and 4 were, respectively, approximately 58 m, 64 m, and 72 m from the high tide line of the Gulf of Mexico. The average salt spray loads for these stations, expressed as $mg/dm^2/day$ of total sea salts received, were as follows: station 2--1.75, station 3--1.02, and station 4--0.73. Comparing these values with Barbour's data showed that Barbour's concentrations were, respectively, 11.4, 17.6, and 16.4 times as great as those from the present study (station 2 compared with Barbour's 60 m concentration; station 3 compared with Barbour's 64 m concentration; station 4 compared with Barbour's 72 m concentration). The disparity between Barbour's results and those of the present study was probably caused by different wind regimes at the two study sites.

Tyndall and Levy (1978) used cheesecloth traps exactly like those of Oosting and Billings (1942) to measure salt spray input 10 cm above the herbaceous vegetation on a peninsular foredune at Back Bay National Wildlife Refuge near Virginia Beach, Virginia, during two runs of 105 hours and 26 hours. A single trap was exposed (apparently on the dune crest) during each run. The titration method described by Martin (1959), which employed the Knudson equation, was used to determine total sea salts received as mg/dm^2. Their results, expressed as $mg/dm^2/day$, yielded an average value of 1.84 for the two exposure periods. This figure was only 1.8 times as great as the average dune crest input of 1.02 $mg/dm^2/day$ total sea salts for the present study (as calculated according to the Knudson equation).

The comparisons just considered showed that, quantitatively, the salt spray results of the present study compared well with results reported by a number of other investigators, if allowances and adjustments were made for differences in collection techniques and wind regimes. The closest comparisons were between the results of the present study and those recorded on the South Carolina coast by Stalter (1976) and on the Virginia coast by Tyndall and Levy (1978).

In summary, the pattern of salt spray deposition across Santa Rosa Island observed in the present study at the dune stations was essentially the same pattern described by other investigators (Oosting and Billings, 1942; Martin, 1959; Randall, 1970; Stalter, 1976; Barbour, 1978; inter alia): salt spray intensity decreased with increasing distance inland from the ocean. This was particularly well-illustrated by the results from stations 2 through 6. And salt spray intensity also

decreased with increasing distance inland from Pensacola Bay, as shown by the results from stations 9 and 10.

The present study also showed that salt spray deposition on Santa Rosa Island did coincide with the zonation of the dune strand vegetation--an observation which has previously been made by other investigators (Oosting and Billings, 1942; Boyce, 1954; Stalter, 1976; inter alia) at dune strand sites in the eastern and southeastern United States. Clearly the sea oats zone received considerably more salt spray than was received by the shrub zone. However, the bluestem zone deviated somewhat from the expected salt spray pattern. Although station 10 received more salt spray than the shrub zone and less than the sea oats zone during all four runs, station 9 received slightly less salt spray than the shrub zone during three runs, but received more salt spray than the shrub zone during the fourth run. This suggests that, for at least a certain time of the year, salt spray intensity at station 9 may be sufficient to effectively preclude the establishment of shrubs there. Whether this situation of greater salt spray input at station 9 is a recurrent phenomenon (and, if so, at what intervals it occurs) can only be determined by further long-term studies. It seems possible that, in the long run (perhaps over a one-year period), station 9 receives more salt spray than does station 6.

For the four runs of the present study the average salt spray inputs at stations 6 and 9 were approximately equal. If this is indicative of long-term conditions, it suggests that some factor other than wind-borne salt spray is responsible for the absence at station 9 of shrub species that are abundant just south of the pine forest. Perhaps depth to the water table, which was considerably greater at station 9

than at station 6, is important here. Obviously, further study is needed to determine conclusively why common shrub zone shrubs are generally absent from the area of station 9. Nevertheless, since edaphic and other factors at station 9 were not greatly different from those at station 10 (where salt spray intensity was clearly great enough to preclude the establishment of shrubs), salt spray intensity was still assumed to be the most probable cause for the absence of shrubs at station 9.

Martin (1959) and Au (1974), among others, presented excellent discussions on the interactions of environmental factors in coastal strand habitats. Au (1974) stated that "it is difficult to evaluate accurately the relative importance of different factors to the coastal vegetation or to give preference to one factor" and that "There are interrelated, simultaneous, and compensative effects which cannot be dealt with separately." But he also stated that "A single factor may be predominant at a certain time and space" and concluded that "salt spray exerts a limiting effect on the strand plants within a short distance from the ocean." As Au also pointed out, however, maritime vegetation, just like any other plant community or association, was certainly "a biotic expression of the holocoenotic environment." Nevertheless, Oosting and Billings (1942), Boyce (1954), and Martin (1959), among others, have demonstrated beyond any doubt that wind-borne salt spray was the major factor determining the zonation of coastal strand vegetation. And the results from the present study showed that salt spray intensity was the only factor which had a clear pattern of variation that corresponded closely with the vegetational zonation in the coastal strand of Santa Rosa Island. Therefore, it is concluded that on the western end of Santa Rosa Island, wind-borne salt spray appears to be

the main environmental factor responsible for the zonation of the coastal strand vegetation.

Pine Forest. The chloride concentrations observed in elutriates from the salt spray collectors exposed in the pine forest on Santa Rosa Island were much greater than expected. Although the chloride concentrations for samples from stations 7 and 8 were consequently rejected, and thus were not reported, it should be noted that the sample from station 7 had a higher chloride concentration than the sample from station 6 for all four runs, and the sample from station 8 had a chloride concentration greater than that of the sample from station 6 for all four runs and greater than that of the sample from station 5 for two runs.

It might be asked if it were possible that the pine forest actually was receiving the amounts of salt spray indicated by the chloride concentrations observed in salt spray collectors during the present study. A simple biological indicator at the study site showed that this was not the case. For example, if the salt spray input at station 8 were actually as great as indicated by the chloride measurements for salt spray samples from that station, then one would expect that slash pines (Pinus elliottii), which were abundant at station 8, would also be found at least as far south as station 5 (since the chloride concentration of the station 8 sample was greater than that for station 5 in the 100-day run). Of course, no pine trees grew anywhere near station 5; in fact, they did not occur south of the vicinity of station 7.

As mentioned earlier, a water sample collected in the stand of Typha domingensis near station 8 was found to have a chloride concentration of 50.0 ppm. This was much higher than expected (particularly so in view of the data presented by Beal (1977), which showed that he did

not observe this cattail growing in water with a chloride concentration greater than 3.5 ppm). This relatively high chloride concentration in marsh water near station 8, as well as the relatively high soil chloride concentrations at stations 7 and 8 (Table 6), made it apparent that the pine forest soil, with its generally greater organic content, was acting as a chloride trap.

It was thus also evident that soil chloride contamination had produced the higher-than-expected chloride concentrations in the salt spray collectors at the pine forest stations. Since the upper end of the installed salt spray collector was only 1 cm above the soil surface, it can be seen that it was not difficult for soil particles to enter the collector (e.g. via rainwater splashing or wind action). This was verified by the brownish color (due to humus leachate) of the elutriates from the stations 7 and 8 salt spray collectors for every run and the presence of soil organic matter in the collectors from those stations. Furthermore, station 8 was observed to be completely inundated with water from nearby Blackbird Marsh to a depth of at least 15 cm on one occasion, and such inundation was undoubtedly a source of excessive chloride in the salt spray collector there.

Due to soil chloride contamination, it is probably not possible to obtain an accurate long-term salt spray sample in the Santa Rosa Island pine forest with the type of collector employed in the present study. Theoretically, a laminar collector mounted 30 cm above the soil surface would be suitable for salt spray collection in the pine forest, but such a collector is useful only during rainless periods, unless a rain shield similar to that described by Randall (1970) were to be employed.

Furthermore, at the present study site such a collector could only be exposed for a short period of time before it would be vandalized.

Therefore, the salt spray collections made in the pine forest during the present study were not reliable, and further study of salt spray in the pine forest is needed. However, the lack of pine forest salt spray data did not seriously affect the present study, since its primary focus was the exposed dune strand communities, and the pine forest was studied mainly for purposes of comparison.

It is believed, then, that stations 7 and 8 are actually receiving much less salt spray than was indicated by chloride concentrations recorded during the present study. It was expected, in fact, that almost no salt spray at all was being deposited deep inside the pine forest, and that only a small amount was being received at station 7.

S U M M A R Y

The coastal strand vegetation on the western end of Santa Rosa Island was studied quantitatively, and a number of environmental factors were examined to determine which ones might be responsible for the zonation of the dunal vegetation. The pine forest located at the interior of the island was studied to compare data collected there with data obtained in the nonforested dunal areas. The principle results are summarized below.

1. The coastal strand vegetation on the western end of Santa Rosa Island existed in distinct zones, as follows: (1) sea oats zone, where Uniola paniculata was the dominant species; (2) shrub zone, where Chrysoma pauciflosculosa and Ceratiola ericoides were co-dominant species; and (3) bluestem zone, where Schizachyrium maritimum was the dominant species. An extensive forest dominated by Pinus elliottii was located at the interior of the island between the shrub zone and bluestem zone.

2. Vegetation of the sea oats zone was generally not very similar to vegetation of the equivalent zone of other sites along the Atlantic and Gulf coasts of the United States and northern Mexico (based on Sorensen's index), even though some of the species (e.g. Uniola paniculata) were shared by several of the comparison sites.

3. Dune soil at the study site was low in calcium, magnesium, potassium, phosphorus, and nitrate, but was high in sodium.

4. Dune soil at the study site was low in organic matter and was slightly acidic.

5. Moisture content of the dune soil at the study site was not great in the upper 20 cm of the soil profile, averaging only 2.2 percent for all measurements.

6. Salinity of the dune soil at the study site was low, presumably due to rapid leaching of salt spray inputs.

7. No definite relationship was evident between any of the soil parameters and the vegetational zonation in the dunes at the present study site.

8. Soil at the southern edge of the pine forest was similar to that found in the dunes, but deep inside the forest the soil contained much more organic matter and moisture than was found in dune soil samples.

9. Dune soil temperatures generally showed considerable variation from station to station and at the various depths, but did not show differences between vegetation zones which could be interpreted as a causal factor in producing or maintaining the vegetational zonation.

10. Soil temperatures deep inside the pine forest were generally more moderate than those at dune stations (presumably due to forest canopy sheltering), but soil temperatures measured near the southern edge of the pine forest were similar to those observed at the exposed dune sites.

11. Dune station air temperatures did not show a pattern which appeared to coincide in any way with the zonation of the vegetation.

12. Air temperatures deep within the pine forest were more moderate than those observed at exposed dune stations (probably due to forest canopy sheltering), but at the southern edge of the pine forest, where the canopy was sparser, air temperatures were similar to those observed at dune stations.

13. Relative humidity values for dune stations showed considerable variation and did not correspond with the zonation of the vegetation.

14. Relative humidity values in the pine forest were similar to those of the exposed dune stations.

15. Evaporation was greater where Uniola paniculata dominated (sea oats zone) than where Schizachyrium maritimum was dominant (bluestem zone).

16. Evaporation at the southern edge of the pine forest was similar to that observed in the shrub zone, but evaporation deep inside the pine forest was considerably less than at the exposed dune stations and was also less than at the southern edge of the forest.

17. Winds measured on Santa Rosa Island came primarily from the south, west-southwest, and west in summer and primarily from the north and northeast in winter, with spring and autumn winds coming from directions intermediate between summer and winter prevailing directions.

18. The average wind velocity for Santa Rosa Island was 5.0 m/sec, which was slightly greater than the critical wind velocity of 4.5 m/sec for the transport of sand, but was less than the critical velocity of 7.0 m/sec for the transport of salt spray; however, for the months of January, February, March, September, and December the monthly averages for daily maximum wind velocity readings exceeded both of these critical velocities.

19. Salt spray and sand movement on Santa Rosa Island occurred in small amounts on most days throughout the year, with most of the salt spray and sand movement activity occurring in late autumn and winter months through early spring.

20. The pattern of wind-borne salt spray deposition in the dune strand of Santa Rosa Island was similar to that described by other investigators and appeared to coincide well with the zonation of the vegetation. More salt spray was deposited in the sea oats zone than in the other two dunal zones, and the bluestem zone generally received somewhat more salt spray than did the shrub zone.

21. Wind-borne salt spray appeared to be the main environmental factor responsible for the zonation of coastal strand vegetation on Santa Rosa Island.

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A P P E N D I X

ERRONEOUS REPORTS OF PLANT SPECIES IN THE DUNE STRAND OF SANTA ROSA ISLAND

A number of vascular plants have been erroneously reported in the literature as occurring in the dune strand of Santa Rosa Island.

Blair (1951) reported Uniola laxa as abundant in the dunes of his study area on the western end of Santa Rosa Island, but, interestingly, did not report the presence of U. paniculata. McFarlin (1941) and Carlton (1977) did not report U. laxa from Santa Rosa Island. Hitchcock (1950) stated that U. laxa occurs in "Moist woods, Coastal Plain, Long Island to Florida and Texas, extending to western North Carolina, Kentucky, Arkansas, and Oklahoma," and Wagner (1964) also described the habitat of this species as "rich woods in the southeastern United States." Uniola laxa was not observed in the coastal strand of Santa Rosa Island during the present study. It is believed that the plant which was actually observed by Blair (1951) was Uniola paniculata, which is the dominant dune species of the northwest Florida Gulf coast and is abundant on Santa Rosa Island.

Carlton (1977) presented a list (Table 23, p. 26) of species which he observed in the dunes near Ft. Pickens. Helenium amarum and Smilax laurifolia are included in this list. By examination of Carlton's voucher specimens it was determined that two misidentifications had occurred and that consequently H. amarum and S. laurifolia were listed erroneously. Carlton 50 (herbarium of Florida Department of Natural Resources Marine Research Laboratory, St. Petersburg), which was labeled as Smilax laurifolia L., is actually Smilax auriculata Walt.; Carlton 424 (herbarium of Florida Department of Natural Resources Marine Research Laboratory, St. Petersburg), which was labelled Helenium amarum (Raf.) H. Rock, is actually Balduina angustifolia (Pursh) Robins.

Balduina angustifolia and Smilax auriculata were found to be common in the dunes of Santa Rosa Island during the present study, whereas Helenium amarum and Smilax laurifolia were not observed there at all.

The plant listed by Carlton (1977) as Chrysopsis gossypina is really Chrysopsis godfreyi, a species recently named by Semple (1978). This golden aster is endemic to the Gulf coast barrier islands of west Florida and has two readily-distinguishable forms (forma godfreyi and forma viridis). It is the most abundant golden aster in the coastal strand of Santa Rosa Island and Perdido Key and is found in association with C. cruiseana where the distributions of the two species overlap. Chrysopsis gossypina does not occur on either of these islands.

The plant listed by Carlton (1977) as Cakile edentula is actually Cakile constricta, a species recently named by Rodman (1974). Cakile constricta is the only sea rocket which grows along the Gulf coast of Florida. Apparently the name Cakile edentula has been misapplied for many years by numerous authors and botanists to sea rocket specimens from Florida's northwest coast. C. constricta is common along the northwest coast of Florida and extends westward along the Gulf coast to eastern Texas.

The plant listed by Carlton (1977) as Conyza ramosissima is most probably Conyza canadensis var. pusilla, a plant that is common in Florida's northwest coastal strand. Conyza ramosissima resembles C. canadensis var. pusilla, and the two can be easily mistaken for each other in field observations. Conyza ramosissima, however, was not reported by Clewell (1980) for northwest Florida, and McFarlin (1941) did not record it for Santa Rosa Island.

The listing of Panicum adspersum by Carlton (1977) for the dune strand of Santa rosa Island is extremely doubtful and probably constitutes a misidentification. Panicum adspersum was not reported for all of the Florida panhandle by Clewell (1980), nor did McFarlin (1941) list it for Santa Rosa Island. Carlton's listing of Physalis viscosa var. maritima is possibly also the result of a misidentification, since this plant was not observed by McFarlin (1941), nor was it seen on Santa Rosa Island during the present study. Another species, Physalis angustifolia, is, however, quite abundant in the dunes of western Santa Rosa Island and may be the species which was actually observed by Carlton. Unfortunately, Carlton did not collect voucher specimens of the plants he listed as Panicum adspersum and Physalis viscosa var. maritima.

Table 26 in Carlton (1977) should, therefore, be corrected by removing the names Helenium amarum, Smilax laurifolia, Chrysopsis gossypina, and Cakile edentula, and replacing them with Balduina angustifolia, Smilax auriculata, Chrysopsis godfreyi, and Cakile constricta, respectively. Appendix I of Carlton (1977) should, then, also have Balduina angustifolia (Pursh) Robins. added to it and be corrected to include Chrysopsis godfreyi Semple and Cakile constricta Rodman.