Vegetation and Ecological Processes on SHACKLEFORD BANK, North Carolina

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SHU-FUN AU

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Duke University
Durham, North Carolina
May 1972

W. Dwight Billings

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Shu-fun Au

Summary

Shackleford Bank was selected for this study because of: (a) a pressing need of ecological information before the island is developed as a part of the Cape Lookout National Seashore; and (b) it is a convenient site for investigating ecological processes of the maritime vegetation.

The objectives of the present study are: (a) to know the present status of the vegetation on the island; and (b) to understand the ecological factors determining the existence of such vegetation.

A classification of the plant communities on the island is proposed, with a general description for each community and a vegetation map. The successional relationship of major vegetation types is also discussed.

Geologic factors determine the unstable nature of the island and the characteristics of the substratum. Historical factors, mainly human activities, inflicted serious damage upon the vegetation in the past.

The general climate of the island is milder than corresponding inland areas. Because of adequate rainfall and the even distribution of rainy days throughout the year, no prolonged drought exists.

Although the general climate on the island is favorable for plant growth, the microclimate of the dune environment is extreme in many aspects: high temperature in the air as well as on the ground surface, wide temperature fluctuation, high light intensity due to the reflective sand, low vapor pressure deficit in the atmosphere during daytime, and active air turbulence caused by a prevailing southwest sea breeze in summer. For these reasons, only a few species with special adaptions can grow well in such harsh dune environments.

The southwest sea wind dominates in summer, but the prevailing wind shifts to the northwest or to the north in winter. The maximum wind velocity is considerable and varies little in a year. More accumulated air movement is recorded in summer than in winter on the island, possibly due to the constant southwest winds.

The wind has manifold influences on the vegetation: (a) wind-borne salt spray kills susceptible species growing close to the ocean; (b) abrasive sand blast created by strong winds causes tissue wounds on plants, which enhance the toxic effect of salt spray; (c) constant and excessive wind may induce desiccation of leaves; (d) strong wind inflicts mechanical injury on plants such as breaking branches or defoliation; (e) winter storms cause salt-water erosion and flooding to the strand vegetation; and (f) shifting sands caused by wind bury and destroy all vegetation in their way.

Although measurable sand movement was detected after a year on a

dune transect, sand encroachment upon the forest has subsided and is not an imminent threat to the forest in a normal year. The amount of sand movement depends on the vegetational cover rather than the distance from the ocean.

The soils on the island have developed from medium to coarse sand and thus are well drained. The soil surface dries quickly after a rain, but ample water is always present in the subsurface layers. The soil developed on the fore dunes is characterized by coarser texture and a large amount of shell fragments. No appreciable amount of salt can be detected in dune soils. However, there is a trend of decrease in pH further away from the ocean.

The organic matter in soils varies from a rich 5% by oven-dry weight of maritime forest to less than 0.01% on the fore dunes. Dune soils are also low in nitrogen and phosphorus components. The accumulation of humus in such sandy soils is extremely slow, with no improvement in the soil structure.

A comparison between the soils on the island and inland Sandhills soils reveals a richer calcium and magnesium content in the former, possibly due to the marine origin of the coastal soils. The discrepancy in chemical properties of soils is suggested as an explanation for the absence of the Sandhills species and the disjunct distribution of red cedar *(Juniperus virginiana)* which is absent from the Sandhills.

Topography is regarded as an important environmental factor because of its effects on the gradients of other factors.

Livestock have done considerable damage to the vegetation on the island.

Measurements of water potential of 16 species show that they do not develop as high a water stress as that of either xerophytes or halophytes. A lower water potential is generally detected among tree species in the afternoon. Dune species under study also show some drought resistance.

The xeromorphic characteristics among dune species are due to the high stress of evapotranspiration in the air rather than the lack of water supply in the soil. Coastal dune species thus should not be considered as xerophytes in the same sense as those occurring in deserts.

Plants of dune species growing close to the ocean are generally tolerant to salt spray, but not to salt water in the soil. Hence, they cannot be classified as halophytes.

Complete nutrient solution greatly enhances the growth of dune plants. Low fertility of dune soil may be a limiting factor and explain the open vegetation on the dunes.

In addition to salt spray, the chemical properties of soil and lower limit of temperature are proposed to be effective in determining the distribution of live oak *(Quercus virginiana)*.

It is concluded that no single factor can explain satisfactorily the occurrence of coastal vegetation. The present status of such diversified maritime vegetation on the island is the result of the interactions among various environmental, biotic, geologic, and historic factors.

1 Introduction

Shackleford Bank, located approximately at mid-point of the North Carolina coast (Fig. 1), is one small section of a chain of barrier islands (Price 1951) bordering the southeastern United States. These barrier islands or offshore sand bars, separated from the mainland by shallow sounds and extending from Cape Henry, Va., to Bogue Inlet, N.C., are locally called Outer Banks.

Shackleford Bank is east-west oriented, almost 9 miles (14.5 km) long, 0.20-0.65 mile (0.3-1.0 km) in width, and has a total area of 2280 acres [923 hectares (ha)]. It is separated from Cape Lookout at its eastern end by Barden Inlet and from Bogue Banks at the western end by Beaufort Inlet and is bounded by Back Sound on the north and the Atlantic Ocean on the south.

The island has been relatively undisturbed by people during the last 60 years due to its geographical isolation. Two miles of water (Back Sound) separate the island from the nearest residential areas, Harkers Island and the town of Beaufort. All means of public transportation are lacking. The prevailing onshore wind and occasional hurricanes produce a unique and peculiarly insular vegetation. For as long as it retains its remoteness and wilderness, Shackleford Bank will provide ecologists with an extremely valuable location for continued study of maritime vegetation.

A half century ago the vegetation of Shackleford Bank was described in detail by Lewis (1917). Since then, except for a brief description of Engels (1952), no vegetational survey has been done, to say nothing about the inquiry of ecological processes on the island. Since the vegetation could have changed a great deal in the ensuing 50 years due to its unstable environment, a new appraisal of the vegetation and the flora seemed desirable. Moreover, since it is planned for Shackleford Bank to be a part of a National Seashore Recreation Area in the near future, it could be subject to extensive use by the public. Therefore, there is a pressing need for a comprehensive ecological survey before the possibility of an acute disturbance. Accordingly, the objectives of the present study are, first, to investigate the structure of the vegetation as well as the flora on the island; second, to measure several of the most important environmental factors; and, finally, to measure plant responses both in the field and by controlled experiments.

To provide a predevelopment record of Shackleford Bank, a detailed vegetation map was prepared with: (1) a classification of plant communities; (2) a list of vascular plants, bryophytes, and lichens collected on the island; and (3) a description of plant communities. To understand the environment-vegetation complex, the general climate of the

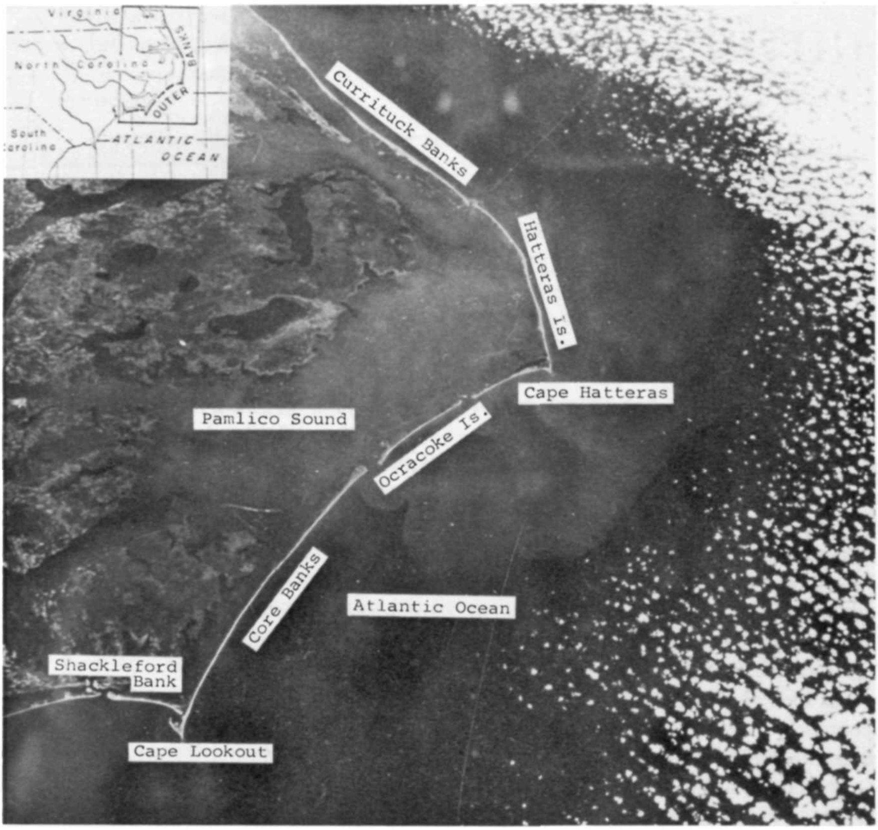

Fig. 1. Outer Banks photographed from Apollo 9 showing the location of Shackleford Bank, with inserted index map from Fisher (1967).

area, the striking wind, and edaphic factors were investigated in detail. Also, plant response to drought stress, to salt water and salt spray, and to the nutrients in the substratum were investigated. Hopefully, we will gain a better ecological understanding of the island, one that will be useful in any land management plan. Furthermore, we may acquire some knowledge of how complex environmental factors operate together to define the characteristics of plant communities on the coast. Since the interaction of the various factors is exceedingly complex, this study can only draw attention to several of the principal environmental factors influencing maritime vegetation and thereby provide a basis for future studies.

2
Literature Review

Though a large number of publications concerning the sand-strand vegetation and maritime forest of the eastern United States has been published, Oosting's (1954) excellent review summarized our knowledge of coastal ecology up to that time. Thus, this information need not be duplicated here. This book is confined principally to more recent developments, particularly those concerning North Carolina.

Just a year after Cowles' (1899) classic papers on sand-dune ecology at Lake Michigan, Kearney (1900) published a detailed account of the strand vegetation on Ocracoke Island. He presented a system for classifying strand vegetation, discussions of environmental parameters, and notes on the anatomy of some strand species. Johnson (1900) described briefly the flora in the vicinity of Beaufort and Lewis (1917) gave a comprehensive description of the vegetation on Shackleford Bank. Coker (1918) visited Smith Island and noted the northernmost limit of cabbage palmetto *(Sabal palmetto)*.

Wells and Shunk (1937) recognized that the flag form of seaside shrubs and trees is due to the killing effect of wind-borne salt spray to the growing shoots. They (1938) further emphasized that the salt spray is the most important factor in determining the distinctive composition and succession of the dune community. Wells (1939) explained the live oak forest of Smith Island on the basis of tolerance to salt spray and called the forest the "salt spray climax."

By means of cheese-cloth traps, Oosting and Billings (1942) measured wind-borne salt spray on the dunes at Fort Macon and noticed the correlation between the intensity of salt spray and the zonation of dune grasses. This was checked experimentally by spraying potted plants of these grasses with sea water. No significant correlations could be detected with regard to soil moisture, soil temperature, soil pH, air temperature, relative humidity, evaporation, and soil salinity. Oosting (1945) further tested the tolerance of strand plants with artificial salt spray and observed again that they are relatively tolerant to salt spray. Boyce (1954) demonstrated clearly the source, the distribution, and the physiological effects of salt spray on some species. By that time, salt spray as the most effective factor for limiting the distribution of strand plants growing close to the ocean was well established and commonly accepted. However, it has not been demonstrated that salt spray is equally important in limiting the distribution of tree species in the maritime forest.

Engels, in the course of investigating the vertebrate fauna of Ocracoke Island (1942) and Shackleford Bank (1952), described briefly the vegetation of those two areas. He (1952) discussed the paths of hurricanes and their damaging aftermath on Shackleford Bank. Rondthaler (1952) also studied the vegetation and flora of Ocracoke Island. More recently, the vegetation and flora of the Outer Banks were described by Brown (1959). Bourdeau and Oosting (1959) carried out a phytosociological study of live oak forest in North Carolina with description and measurements of edaphic factors. Burk (1962) collected specimens extensively on the northern sections of the Outer Banks. The only comprehensive autecology of sea oats *(Uniola paniculata)* was studied by Wagner (1964), who investigated its life cycle and determined how the species is instrumental in the formation and maintenance of dunes.

Other papers dealing with the strand vegetation outside North Carolina but on the East Coast were published by Davis (1942), by Kurz (1942) and Laessle and Monk (1961) for Florida, by Martin (1959) for New Jersey, and by Egler (1942) for Cape Henry, Va. As a whole, more coastal studies have been done in North Carolina than in any other eastern state. Also, far more papers have been published concerning coastal vegetation on the East Coast than on the West Coast of the United States. Of the latter, the investigations of Olsson-Seffer (1908, 1909a, b), Ramaley (1918), and Purer (1936) are representative.

Early research on dune communities in Britain was carried out by Oliver (1912), Farrow (1919), Salisbury (1922, 1925), and Rempel (1936). After World War II, the dune community received much attention from British ecologists, notably Gimingham (1951), Robertson and Gimingham (1951), Salisbury (1952), Gillham (1953, 1957), Gorham (1958, 1961), Ranwell (1958, 1959, 1960), Willis et al. (1959a, b), Wilson (1960), Willis and Yemm (1961), Willis (1963, 1965), Scott (1965), and Etherington (1967). They commonly emphasized the important roles of edaphic factors and sand movement. Until recently, only one paper concerning the effects of salt spray on the vegetation in Britain has been published (Edwards and Holmes 1968), although the measurement of salt spray was reported by Edwards and Claxton (1964) and Rutter and Edwards (1968).

A large amount of research on dunes and maritime forest has been done by Japanese ecologists such as Numata et al. (1948), Numata and Nobuhara (1952), Tsuda (1961), Nobuhara et al. (1962), Nobuhara and Toyohara (1964), Saito et al. (1965), and Mitsudera et al. (1965). Their approaches generally followed those of American ecologists in attention paid to the damaging effects of salt spray and sand movement on the dune community.

3
Description of the Area

Geology

The geological origin of Shackleford Bank is a relatively recent one. Milliman and Emery (1968) stated that the sea level was approximately at the present level about 30,000 to 35,000 years ago during the last interglacial stage. Due to the subsequent growth of the glaciers, the mean sea level was lowered to about −130 m at the climax of the Wisconsin regression which occurred about 16,000 years ago. According to Richards (1950), the shoreline was then some 90 miles east of the present beach. Milliman and Emery (1968) suggested that Holocene transgression probably began about 14,000 years ago. For the next 7000 years the sea level rose rapidly as the ice sheets melted. Thereafter, the rise was more gradual and the shoreline advanced to its present position. From the evidence of old sod and stumps along the coast, Richards (1950) believed that the sea level is probably still rising but at an almost imperceptible rate.

Johnson (1919) proposed a classical theory concerning the formation of the Outer Banks in terms of two stages. In the early stage, sea-water encroachment eroded the sea bottom by means of onshore waves. These eroded materials were deposited locally to form offshore submarine sand bars. Subsequently, through deposition of materials by longshore currents, a chain of barrier islands was built, largely of loose sand and, of course, totally barren on emergence. The theory has been questioned by recent coastal geologists. Fisher (1967) discussed in detail the arguments against the submarine origin of the Outer Banks. However, Johnson (1956) and Shepard (1963) indicated the possibility of an offshore supply of beach sand due to wave action.

The beach erosion study (U.S. Congress 1948) reported that 6 miles of the shoreline of Shackleford Bank has retrograded an average of 1.55 ft (45 cm) per year and another mile has prograded 0.24 ft (7 cm) per year. Engels (1952), from the comparison of the U.S. Coast and Geodetic Survey maps of 1851-53 and 1949, discerned that the ocean beach of Shackleford Bank has moved northward (landward) from 40 to 150 yards (37-137 m) along virtually its entire length. However, the inner beach did not have a comparable landward movement as Johnson (1919) had proposed. Similarly, Pierce (1964), from a comparison of the U.S. Coast and Geodetic Survey charts of Core Banks from 1856 to 1957, found a general shoreward movement of the coastline and he confirmed such long-term coastal changes with data obtained from borings. He also discovered that most of the sediment supplied to the barrier islands is coming from the north as longshore drift.

Recently, a new hypothesis concerning the origin of the Outer Banks was proposed by

Fisher (1967). The Outer Banks are considered to have developed primarily as distal prograding spits beginning 5000-7000 years ago when the sea level was stillstand. Since that time, the sea level has fluctuated no more than 6 m around mean high tide. The fluctuation even diminished to less than 1 m about 3750 years ago. The migration and growth of these coast-parallel spits were the result of a dominant longshore movement from north to south and the reworking of the near-shore bottom material. No new offshore material is now available and barriers are undergoing worldwide erosion. Fisher (1967) further suggested that the age of Cape Hatteras is about 1200 years and the age of the Outer Banks is probably double that, i.e., about 2400 years. Since this recent hypothesis is based on intensive field studies, it probably represents a more accurate account of the formation of the Outer Banks.

Recent History

During the past century, Shackleford Bank has received more than its share of both biological and physical abuse. The island was almost completely covered by forest until at least 1853, according to the U.S. Coast and Geodetic Survey map. It was quite suitable for human habitation and hence was one of the earliest settled areas on the Outer Banks. According to Lewis (1917), former inhabitants remembered that it was "possible to sit in a tree and cast a fishing line into the water," demonstrating the closeness of the forest to the ocean. According to Stick (1958), the first permanent house was built in the 1760s. By 1885, about 600 people lived on the island. There were 500 residents of Diamond City, which is situated at the eastern end of the Bank near Cape Lookout on Core Banks. The population made its livelihood primarily from whaling and fishing. However, due to the intrinsic nature of human inhabitancy, such as cutting trees for homes and ship building, burning for cultivation, and raising livestock, the once luxuriant woodland vegetation gradually degenerated and dwindled away.

In August 1899, a severe hurricane struck the island. The sea level rose so high that the sea covered most of the island and killed most of the remaining forest. Having found the island to be unsafe, the islanders emigrated and most of them settled on Harkers Island across Back Sound. Within 3 years, Shackleford Bank was completely deserted. Because of the lack of vegetational cover, successive storms moved the loose sand from the ocean side across the island. As the sand moved, it covered dead and live trees in its path, and only dead trees remained when the sand dunes moved on. Lewis (1917) estimated that the sand wall was advancing at a rate of 4-12 ft (1.2-4.0 m) per year. Uncovered tree skeletons make up a unique scenery—"ghost trees" or "graveyard forest"—on the Outer Banks. Today, there are no permanent residents and less than 5% of the island is covered by forest.

Physiography

Although Shackleford Bank scarcely exceeds 2000 acres (810 ha), considerable diversity in plant habitats can be found — from the driest dunes to the wettest fresh marshes and ponds — depending on the closeness of ground surface to the water table. Nevertheless, only three major types of vegetation are here recognized: the woodland, the grassland, and the marshland.

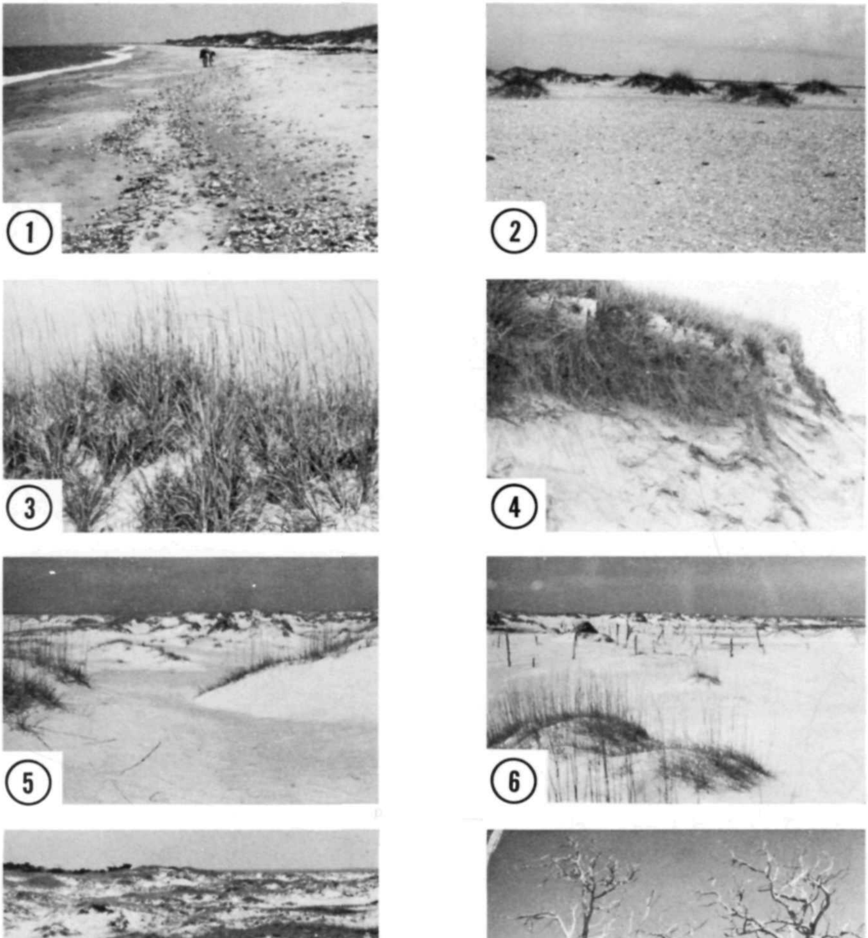

Plate I

(*1*) Outer beach: wide and barren, with abundant shell fragments; (*2*) Embryonic dunes developed on newly deposited land at the western end of the island; (*3*) Heavy salt spray moistening the leaves of sea oats at the windward side of fore dunes (visible as reflective white area on leaves); (*4*) Massive root system of sea oats is an excellent sand binder; (*5*) Sorting effect of wind on sand particles. Notice darker colored (coarser) particles in the trough and white (finer) particles on the slopes of the fore dunes; (*6*) Uncovered formerly buried forest, south of Mullet Pond; (*7*) Grassy dunes on the western half of the island; (*8*) "Ghost trees"—remaining skeletons of red cedar.

Plate II

(*9*) A dune marsh (formed by "blow-outs") during dry period; (*10*) Same dune marsh with a temporary freshwater pond, formed after prolonged rain; (*11*) Sand wall, a contact zone of the grassy dunes and maritime forest, is actually the lee slopes of the rear dunes; (*12*) Another view of the sand wall; (*13*) Goats, the most destructive mammal on the island, roaming along the sand wall; (*14*) Sheep grazing on the back of the rear dunes; (*15*) Animal path extending from the sand wall to the forest. The activities of goats and sheep apparently accelerate sand invasion to the forest; (*16*) Inner beach at low tide.

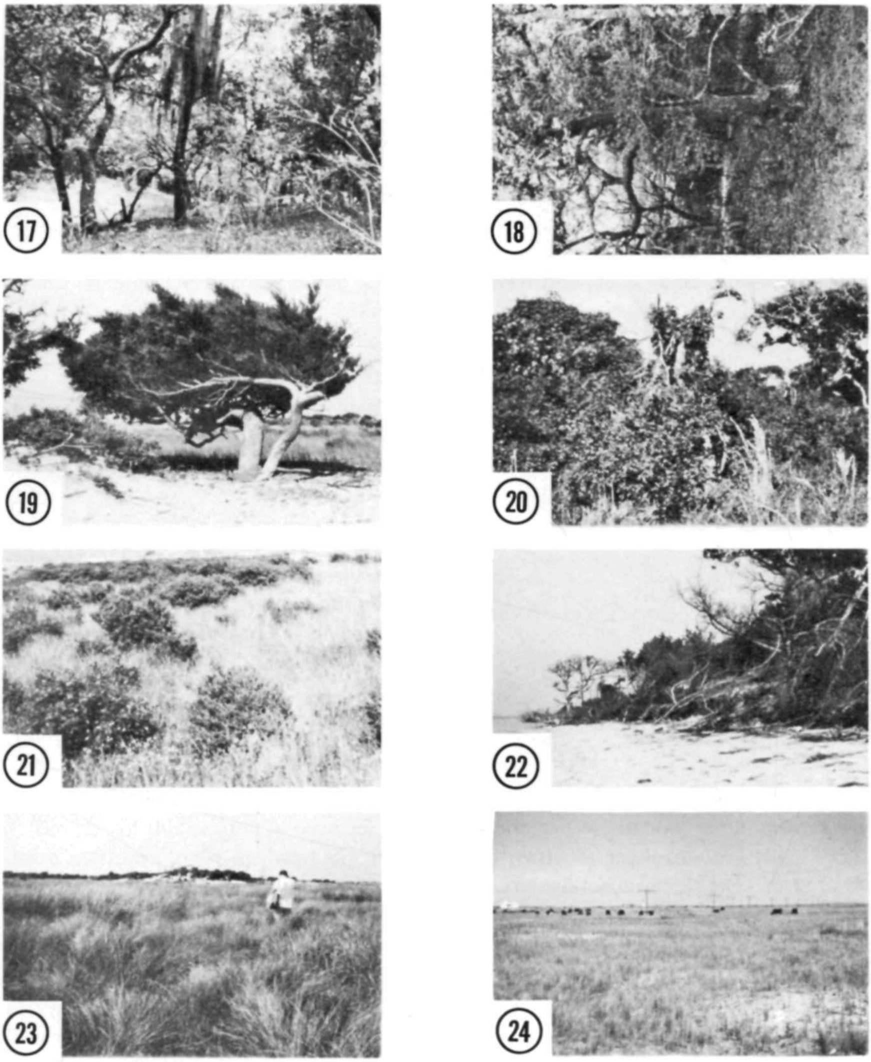

Plate III

(*17*) Maritime forest, with Spanish moss hanging on the branches of live oak; (*18*) Another view of maritime forest (the picture is orientated sideways); (*19*) A flag-form red cedar, caused by wind-borne salt spray as well as sand blasting; (*20*) A wet thicket behind rear dunes, with abundant climbing vines; (*21*) *Juniperus-Myrica* scrub flat, a successional stage leading to maritime forest; (*22*) Inner beach. At this particular location, 10 ft of maritime forest have been undercut by wave erosion in the winter of 1967-1968. The standing dead tree in the distance was killed by sea water; (*23*) A stand of *Juncus roemerianus* on the grassy sand flat; (*24*) The winter aspect of grassy sand flat with *Spartina patens* as dominant. Cows graze on the grasses in the distance.

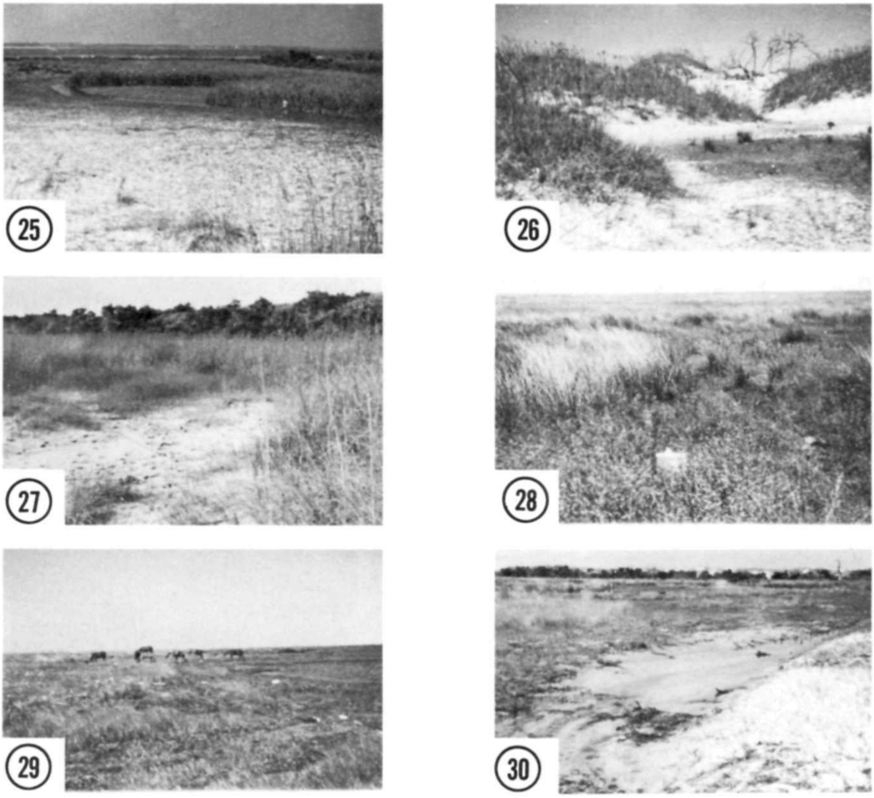

Plate IV

(*25*) Mullet Pond, the largest freshwater pond on the island, with *Typha* marsh on the far side and *Hydrocotyle bonariensis* covering the foreground; (*26*) Dune marsh in close-up; (*27*) *Cladium* stand of a freshwater marsh; (*28*) A wet depression on grassy sand flat with many hydrophytic species; (*29*) Horses grazing on salt marsh (*Spartina alterniflora*) at the sound side of the island; (*30*) Creek marsh, with *Distichlis spicata* at the right foreground, *Spartina alterniflora* on left midground, and *Juncus roemerianus* in front of maritime forest in the distance.

The general features of the vegetation and topography of the island are illustrated by two transects in Fig. 2.

At the western third of the island, as depicted in the upper transect, the sequence of physiographic pictures from ocean to sound is: a wide and bare outer beach (Pl. I-1); fore dunes; occasional patches of grassy flat; dunes proper (Pl. I-7); rear dunes; a narrow belt of marsh-like depressions; maritime forest (Pl. III-17, 18) with intra- or inter-forest marshes; and a narrow inner beach (Pl. II-16). There is generally a fairly sharp transition from one type of vegetation to another.

The outer beach and possibly the fore dunes are subject to occasional inundation during storms. Behind the fore dunes, occasionally one can find small depression areas called "slacks" or "swales" where the ground water approaches the surface of the sand and often forms a temporary shallow pond after heavy rains. Storm waves also find their way between the fore dunes to the rear "slacks," which are flooded in times of heavy storms.

The dunes proper are a series of irregular grassy ridges running soundward (northward) with increasing elevation, primarily colonized by sea oats. Here and there appear "ghost trees" (Pl. I-8) — the uncovered skeletons of red cedar. The dunes, under the constant impact of wind, are continually changing their shape, particularly in areas lacking vegetational cover. Hollows or "blow-outs" are produced by wind erosion and some of these depressions become dune marshes (Pl. IV-26) while others are just exposed, bare sand flats. As a result of heavy rainfall, the hollows become temporary ponds (Pl. II-9, 10). The topography becomes more stable as one approaches the rear dunes.

The highest land on the island is represented by the rear dunes, usually about 30-40 ft (10-13 m) above sea level. The soundward slope of the rear dunes is called the "sand wall" (Pl. II-11, 12), occasionally possessing a 20-30° inclination on some steeper slopes. The sand wall is slowly advancing in a few places, mainly along the larger animal trails (Pl. II-15) where tongues of sand advance from the sand wall to the forest. Behind the rear dunes in this portion of the island, there is a marshy belt about 10-30 ft (3-10 m) wide.

The rest of this section is covered partly by woodland vegetation, varying from very dense maritime forest to dwarf dry thickets, and partly by fresh marshes (Pl. IV-25), brackish marshes, and creek marshes (Pl. IV-30). Though the original forest cover of the island has been largely destroyed, the forest remnant confined here represents a good example of the distinctive maritime forest of the southern Atlantic coast. Marshes are distributed between thickets or on the soundward side of the forest. Also, wherever the ground surface approaches or is lower than the water table inside the forest, wet thicket (Pl. III-20) or fresh marsh (Pl. IV-27) is formed. As a result, maritime forest, thickets, and marshes compose an intricate vegetational pattern.

The inner beach is much narrower than the outer beach. Although the water of Back Sound is generally calm during the summer, the north to northeastern winds in winter create forceful waves which undercut the beach at places and wash out dead trees killed by salt water (Pl. III-22). This erosion process apparently occurs every winter and consequently produces an unstable inner beach in certain locations. During the winter of 1967-68, I observed that 10 ft (3 m) of maritime forest at one location were lost through wave erosion.

Another area deserving specific mention is the western end of the island to which 150 acres (60 ha) of land have been added in the past 10 years (1956-66). The newly added portion is basically a loose, sandy waste but small dunes have recently appeared (Pl. I-2).

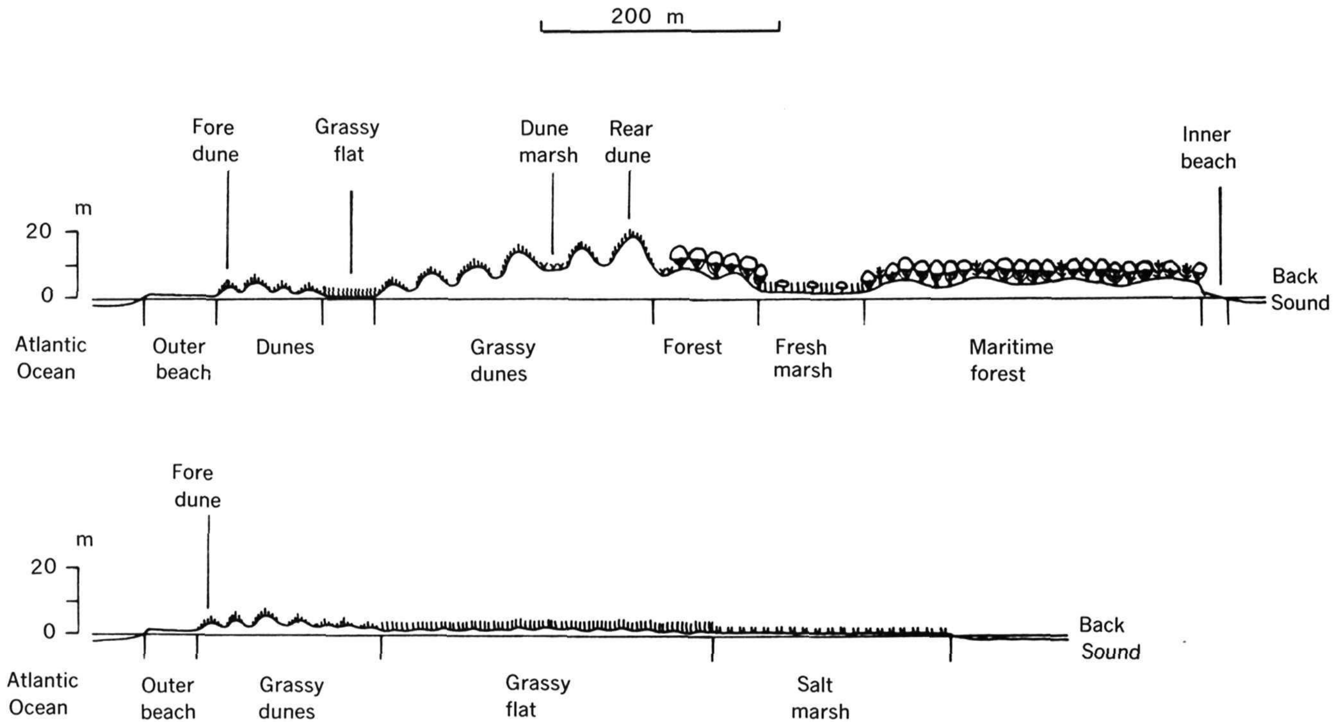

Fig. 2. Transects showing general physiography of Shackleford Bank.

The physiographic appearance of the eastern two-thirds of the island is much simpler, as shown in the lower transect of Fig. 2. Here, salt marsh (Pl. IV-29) substitutes for inner beach bordering the sound. A slightly elevated, grassy sand flat (Pl. III-23, 24) or meadow occupies most of the area instead of woodland or dunes, and low grassy dunes less than 10 ft (3 m) in height rise along the ocean front. Scattered on the grassy flat behind the low fore dunes are a few shallow depressed areas (Pl. IV-28) on which numerous hydrophytic species thrive. Except for several stumps in one small area, all traces of the previous forest have vanished from the eastern two-thirds of the island.

4
Flora and Vegetation

Flora

A full list of all plants collected on the island by me as well as by W. R. Anderson and R. L. Wilbur is appended. The specimens are deposited in the herbarium of Duke University.

For vascular plants, the nomenclature of *Guide to the Vascular Flora of the Carolinas* (Radford et al. 1964) is followed except where another authority is cited. The nomenclature for mosses, liverworts, and lichens is based on *A List of the Mosses of North America* (Crum et al. 1965), *List of Hepaticae Found in the United States, Canada, and Arctic America* (Evans 1940), and *A Third Checklist of the Lichens of the Continental United States and Canada* (Hale and Culberson 1966), respectively.

The scientific-common name index was compiled from *Gray's Manual of Botany* (Fernald 1950), the author's list appended, and *The Lichen Book* (Nearing 1962).

Due to diverse physiographic features, 281 species and varieties of vascular plants belonging to 83 families, 14 species of mosses, 2 species of liverworts, and 21 species of lichens (foliose and fruticose) have been collected on the island. The number of vascular plants is relatively large as compared with other areas on the Outer Banks; Kearney (1900) recognized 135 species on Ocracoke, N.C., and Harshberger (1900) observed 228 species in the New Jersey strand flora. Small and Martin (1958) reported 267 species of vascular plants representing 63 families at Island Beach State Park, N.J. — a peninsula of almost the same size (2300 acres) as Shackleford Bank (2280 acres).

Lewis (1917) listed 241 species of vascular plants in his paper. In the present checklist there are 87 species of vascular plants not found or recognized by Lewis, while 47 species in Lewis' list were not found in this study. By applying Jaccard's (1912) formula for the community coefficient ($\frac{2w}{a+B} = 100$, w is the number of species on both checklists, a is the number of species in the old checklist, and b is the number of species in the present checklist), a coefficient of 74.3 is obtained. In other words, there is about 74% similarity between these two checklists. Some species listed in Lewis' paper appear to be misidentified, and the present checklist is based on a more thorough opportunity for collecting specimens. Nevertheless, the coefficient of 74 may indicate that the flora of the island has undergone some change in the past 50 years under relatively unstable environmental conditions. Consequently, the appended checklist will serve as a background against which future changes may be viewed.

Vegetation

Vegetation map

The base map was obtained by tracing the outline of a series of serial photographs of 1:7920 scale taken in 1964. Though major vegetation types could be recognized from the aerial photographs, the validity of lines from tracing and various plant communities were checked and defined by personal reconnaissance in the field as well as color aerial photographs taken by the author.

Classification of plant communities

Detailed classifications of strand vegetation on the Outer Banks of North Carolina have been proposed by Kearney (1900) on Ocracoke, by Lewis (1917) on Shackleford Bank, by Rondthaler (1952) on Ocracoke, and by Brown (1959) on the Outer Banks in general. Their systems of classification are listed as follows in comparison with a new system that I proposed.

Kearney (1900):

I. Sand strand vegetation
  1. Treeless (open)
    a) Beach formation
    b) Dune formation
  2. Evergreen trees and shrubs
    a) Tree formation
    b) Thicket formation

II. Salt marsh vegetation
  1. Creek marsh (close) formation
  2. Dune marsh formation
  3. Tidal flat (open) formation

III. Pastures and ruderal plants

IV. Cultivated plants

Lewis (1917)

I. Sand strand vegetation
  1. Treeless (open)
    a) Inner beach formation
    b) Outer beach formation
    c) Dune formation
  2. Trees and shrubs (closed)
    a) Thicket formation
    b) Thicket woodland formation
    c) Woodland formation

II. Marsh vegetation
  1. Salt marsh formation (closed)

2. Creek marsh formation (closed)
3. Dune marsh formation
4. Tidal flat formation (closed)

Rondthaler (1952)

- I. Sand strand vegetation
  1. Fore dune
  2. Beach proper
  3. Back of the beach
  4. Dune
  5. Thicket and woodland
- II. Marsh vegetation
  1. Salt marsh
  2. Creek marsh
  3. Tidal marsh
- III. Roadside and field

Brown (1959)

- I. Sea beach
- II. Dunes
  1. Live dunes
  2. Grass-covered
  3. Wooded
- III. Sand flats
  1. Interdunal, restricted
  2. Open
     a. Dry
     b. Moist
        a. Freshwater
        b. Brackish to saline
- IV. Tidal marshes
- V. Ponds

Au (1968)

- I. Grassland vegetation
  1. Outer beach
  2. Inner beach
  3. Grassy dunes
  4. Grassy sand flat
- II. Woodland vegetation
  1. Forest
  2. Thicket
     a. Dry thicket

b. Wet thicket
3. Scrub flat
III. Marshland vegetation
1. Freshwater to brackish marsh
a. Dune marsh
b. Freshwater marsh
c. Brackish marsh (converted saline marsh)
2. Creek marsh
3. Salt marsh

Description of plant communities

Principal plant communities in each type of vegetation are named according to their dominant species. The number after each community indicates its locations on the vegetation map (Fig. 3, located at the back of the book). In fact, the plant communities which belong to the same vegetation type are alike in physiognomy, species composition, and habitats. The only difference among them is a shifting in importance of the dominant species.

I. Grassland vegetation

Outer beach: Spurge (*Euphorbia maculata*) and spike grass (*Uniola laxa*) community (1). It is typically a flat and barren sandy waste above the mean high-tide line (Pl. I-1), about 30 m wide, covered with an abundance of large shell fragments deposited by occasional floods during winter storms. Very little vegetation occurs on the drifting sands except for a few small clumps of sea oats which build up incipient dunelets, and sparsely scattered individuals of seaside spurge *(Euphorbia polygonifolia)*. The latter is, in fact, the species occurring nearest to the sea. It may be aided in its adaptation to salt spray by its prostrate growth form. Other species found here are sea rocket *(Cakile edentula)*, common saltwort *(Salsola kali)*, and seabeach amaranth *(Amaranthus pumilus)*. As a whole, the vegetation of the outer beach is exceedingly sparse.

Inner beach: Cordgrass *(Spartina)*, spike grass, and water pennywort *(Hydrocotyle)* community (2). Between the mean high-tide line and the grassy dunes or maritime forest on the sound side is a narrow strip of inner beach which is also largely barren (Pl. III-22). Here, the more common species are saltmeadow cordgrass *(Spartina patens)*, sea oats, silver-leaf croton *(Croton punctatus)*, and seaside pennywort *(Hydrocotyle bonariensis)*. Other species frequently found are seabeach evening primrose *(Oenothera humifusa)*, sandspur *(Cenchrus tribuloides)*, ground cherry *(Physalis maritima)*, horseweed *(Conyza canadensis)*, and smartweed *(Polygonum glaucum)*. Common saltwort grows occasionally in abundance along the upper edge of the inner beach. Very close to the water is sea beach orach *(Atriplex arenaria)*, a species which withstands temporary submergence and thus is one of the strand's most halophytic species.

Grassy dunes: Spike grass, beardgrass *(Andropogon)*, and croton *(Croton glandulosus)* community (5). The dune environment presents one of the most unstable plant habitats. Sea oats, a successful dune builder and stabilizer, occupies more than 90% of the vegetated dune area (Pl. I-7). Secondary components are dune bluestem *(Andropogon littoralis)*, silver-leaf croton, and seabeach evening primrose. Other herbs occurring on the dunes include horseweed, sandspur, sandgrass *(Triplasis purpurea)*, seaside spurge, seaside pennywort, and, on lower gentle dunes, saltmeadow cordgrass and ground cherry. A single shrubby species, seashore elder *(Iva imbricata)*, is rarely found on the dunes of Shackleford Bank, in contrast to its abundance on Bogue Banks or Bear Island to the west; nor has beach grass *(Ammophila breviligulata)* been found by the author though the species is widely planted at Fort Macon just across Beaufort Inlet. Several vines successively colonize the rear dunes: Virginia creeper *(Parthenocissus quinquefolia)*, poison ivy *(Rhus radicans)*, China brier *(Smilax bona-nox)*, wild bean *(Strophostyles helvola)*, pepper vine *(Ampelopsis arborea)*, and muscadine grape *(Vitis rotundifolia)*. On the sand wall, cudweed *(Gnaphalium purpureum)*, sea burdock *(Xanthium echinatum)*, goldenrod *(Solidago sempervirens)*, and red mulberry *(Morus rubra)* are to be found.

Spike grass, marsh elder *(Iva)*, and saltwort *(Salsola)* community (3). This community represents a stage in the development of the grassy dunes on loose sandy wastes. The dominants are sea oats, seashore elder, and goosefoot saltwort. Other species that occur frequently are sea rocket, seaside spurge, smartweed, seabeach amaranth, seaside pennywort, saltmeadow cordgrass, purple sand grass, and wild bean.

Croton, common thistle (*Cirsium*), and spike grass community (22). This community develops on dunes made up largely of shell fragments, a highly alkaline substratum. Silver-leaf croton is the dominant species and yellow thistle *(Cirsium horridulum)* grows in abundance. Beside the much-repressed sea oats, there are seaside pennywort, saltmeadow cordgrass, palmetto *(Sabal minor)*, and seaside spurge.

Grassy sand flat: Cordgrass, rush *(Juncus)*, and beardgrass community (19). This community covers the greatest area on the eastern part of the island (Pl. III-23, 24). It occurs also between salt marshes on the sound side and low dunes on the ocean side. The elevation of the gentle flat is generally no more than a meter above the high-tide level. Here and there are dark-green clumps of rush which usually occupy the moist sites on the meadow, often associated with small patches of fresh to brackish marshes. Characteristic species are saltmeadow cordgrass, rush, and hair grass *(Muhlenbergia capillaris)*, together with various grasses, sedges, and rushes. Other abundant species are broom sedge *(Andropogon virginicus)*, *Fimbristylis castanea*, chairmaker's rush *(Scirpus americanus)*, foxtail grass *(Setaria geniculata)*, sea pink *(Sabatia stellaris)*, cyperus *(Cyperus)*, and whitetop sedge *(Dichromena colorata)*. Seaside pennywort and finger grass *(Chloris petraea)* are dominant on slightly elevated dry sites. Secondary species are blanket flower *(Gaillardia pulchella)*, ground cherry, sandspur, purple sandgrass, nodding ladies' tresses *(Spiranthes vernalis)*, and horseweed. Scattered small, woody plants include shrubby marsh elder *(Iva frutescens)*, sea myrtle *(Baccharis halimifolia)*, wax myrtle *(Myrica cerifera)*, and red cedar.

Cordgrass, *Fimbristylis*, and Muhly *(Muhlenbergia)* community (23). Basically, this community is not very different from the community mentioned above except that the dominants are saltmeadow cordgrass, *Fimbristylis castanea*, and hair grass.

Cordgrass, rush, and beardgrass community (7). This community develops in interdunal slacks habitats where the water table comes close to the ground surface. Dominant species are saltmeadow cordgrass, rush *(Juncus coriaceus)*, and broom sedge. Secondary species are chairmaker's rush, rush, seaside pennywort, *Fimbristylis castanea*, sea pink, and foxtail grass. On areas with a frequent wet surface, hydrophilic species such as capeweed *(Lippia nodiflora)*, water pimpernel *(Samolus parviflorus)*, water hyssop *(Bacopa monnieri)*, whitetop sedge, and climbing hempweed *(Mikania scandens)* prevail.

II. Woodland vegetation

Forest: Oak *(Quercus)*, juniper *(Juniperus)*, and holly *(Ilex)* community (10). Live oak, red cedar, and American holly *(Ilex opaca)* are the three most important tree species of maritime forest (Pl. III-17, 18). As represented on Shackleford Bank, the forest is about 5-10 m high. Well-developed live oak trees may reach a diameter of 66 cm. The abundant woody vines and low shrubs often make it difficult to force a passage through the luxuriant forest. Common species of trees, in addition to the three important ones mentioned above, are willow oak *(Q. phellos)*, loblolly pine *(Pinus taeda)*, sweet bay *(Magnolia virginiana)*, red bay *(Persea borbonia)*, flowering dogwood *(Cornus florida)*, wild olive *(Osmanthus americanus)*, wax myrtle, and Hercules' club *(Zanthoxylum clava-herculis)*. Species of shrubs or smaller trees making up an understory include yaupon *(Ilex vomitoria)*, ironwood *(Carpinus caroliniana)*, beauty berry *(Callicarpa americana)*, red mulberry, and dwarf sumac *(Rhus copallina)*. Palmetto is occasionally present inside the forest but more abundant at the edge of maritime forest behind the rear dunes. The number of herbaceous species is small and the vegetational ground cover is scanty. The principal herbaceous species are spike grass, needle grass *(Stipa avenacea)*, partridge berry *(Mitchella repens)*, Spanish needles *(Bidens bipinnata)*, elephant's foot *(Elephantopus nudatus)*, pepper grass *(Lepidium virginicum)*, bullnettle *(Cnidoscolus stimulosus)*, and panic grass *(Panicum)*. Epiphytic species, mostly on live oak, are Spanish moss *(Tillandsia usneoides)* (Pl. III-17), mistletoe *(Phoradendron serotinum)*, and resurrection fern *(Polypodium polypodioides)*. Lichens are abundant on tree trunks and branches, especially on live oak where species of shield lichen *(Parmelia)*, blister lichen *(Physcia)*, twig lichen *(Ramalina)*, beard lichen *(Usnea)*, and shore lichen *(Teloschistes)* flourish. However, the most conspicuous lichen is wedding ring *(Lopadium leucoxanthum)*, a crustose which grows best on American holly and occasionally on yaupon. For this reason, one can recognize American holly at a distance by a bright red patch on the bark. At High Hill, a large quantity of several sod lichen *(Cladonia)* species covers the ground under the forest. Finally, there are numerous woody vines climbing into the canopy, such as greenbrier *(Smilax)*, muscadine grape, Virginia creeper, pepper vine, rattan vine *(Berchemia scandens)*, and poison ivy.

Thicket: a. Dry thicket — Holly, juniper, and oak community (11). This community is characterized by small shrubs usually no more than 5 m high which grow close together and are tangled with various woody vines. Behind dunes, the thicket is composed chiefly of yaupon which in some areas forms an almost pure stand. Four other important components are red cedar, live oak, Hercules' club, and beauty berry. Associated vines are summer grape *(Vitis aestivalis)*, muscadine grape, Virginia creeper, china brier, catbrier *(Smilax auriculata)*, pepper vine, and poison ivy. Portions of the dry thicket are not readily penetrable due to the dense growth of shrubs and vines. However, pure stands of dwarf yaupon usually have ample bare ground sparsely beset with such herbaceous species as frostweed *(Helianthemum georgianum)*, purple sand grass, finger grass, and prickly pear *(Opunita humifusa)*.

b. Wet thicket — Wax myrtle, juniper, and oak community (9). The physiognomy of this community is similar to that of the dry thicket but it occupies the wet sites. The dominants are wax myrtle, red cedar, live oak, and gallberry *(Ilex glabra)*. Secondary species are beauty berry, shrubby marsh elder, red mulberry, and, occasionally, dogwood *(Cornus stricta)*. Woody vines tangled on top of wet thicket (Pl. III-21) are china brier, bamboo *(Smilax laurifolia)*, muscadine grape, Virginia creeper,and rattan vine. Many herbaceous species typical of marshes find their niches on the wet ground here.

Scrub flat: Wax myrtle, juniper, and cordgrass community (6). This community is basically a grassy sand flat, but with a large number of saplings or small shrubs of red cedar and wax myrtle. From the trend of colonization by woody species, scrub flats may be regarded as a successional stage leading to the maritime forest. Other shrubs which are rather abundant are shrubby marsh elder and sea myrtle.

III. Marshland vegetation

Freshwater marsh: a. Dune marsh—*Fimbristylis,* water pennywort, and fogfruit *(Lippia)* community (24). This community is found in small depressions formed by "blow-outs" among grassy dunes (Pl. IV-29). Basically, it is a poorly developed fresh marsh. Its water is derived wholly from rainfall. These marshes may become small fresh-water ponds (Pl. II-9, 10) after a heavy rain, particularly in the spring, or dry up following a long drought. Consequently, the flora is far poorer than that of well-developed fresh-water marshes. Major species are sedges and rushes such as *Fimbristylis castanea,* chairmaker's rush, rush *(Juncus megacephalus)*, and whitetop sedge. Creeping on the ground, in large numbers, are seaside pennywort, capeweed, smartweed, and water hyssop. Nodding ladies'-tresses and saltmeadow cordgrass are occasionally present.

b. Freshwater marsh: Wherever the water table reaches the soil surface within the maritime forest or between wet thickets, and at the same time is isolated from the ocean, a fresh-water marsh possessing the richest flora of any of the bank's communities is formed. The fresh-water marsh is usually covered by a thin layer of water or is at least saturated and, thus, is difficult to traverse. In the spring and summer, it is often flooded and turns into a shallow swamp. Only late in the fall, when dry weather prevails, can one walk through it without sinking into the mud. Since numerous ticks thrive there in the summer and an appalling number of mosquitoes prosper in it from spring until late fall, the fresh-water marsh is the least comfortable place in which to work.

Cattail-flag *(Typha)*, rush, and twig-rush *(Cladium)* community (8). In addition to the pure patches of common cattail *(Typha latifolia)*, saw grass *(Cladium jamaicense)* (Pl. IV-27), and rush, other common species are *Fimbristylis castanea,* broom sedge, rush, foxtail grass, whitetop sedge, morning glory *(Ipomoea sagittata)*, and seaside pennywort.

Rush, cattail-flag, and mallow *(Kosteletzkya)* community (13). This is an intraforest fresh-water marsh with the richest flora of all marsh communities. Dominants are rush, common cattail, and seashore mallow *(Kosteletzkya virginica)*. Secondary species are saw grass, rush, chairmaker's rush, cyperus, paspalum *(Paspalum floridanum)*, spike rush *(Eleocharis albida)*, and whitetop sedge. Other abundant species are false nettle *(Boehmeria cylindrica)*, marsh fleabane *(Pluchea)*, false loosestrife *(Ludwigia)*, water hemlock *(Cicuta maculata)*, knotweed *(Polygonum)*, morning glory, climbing hempweed, nodding ladies'-tresses, fleabane *(Erogeron quercifolius)*, duck potato *(Sagittaria latifolia)*, water pimpernel, ebony spleenwort *(Asplenium platyneuron)*, and bracken fern *(Pteridium aquilinum)*. Creeping on the ground are capeweed, seaside pennywort, pennywort *(Centella asiatica)*, and water hyssop.

c. Brackish marsh: Wherever a sandy beach or a low dune develops obstructing the passage of water in a creek marsh, a brackish marsh is formed. It is gradually transformed to a brackish or even to a fresh-water marsh, depending upon the thoroughness of leaching. Consequently, both salt marsh and fresh-water marsh species may grow in such a brackish habitat with their proportions depending upon the salinity of the substratum.

Rush, groundsel tree *(Baccharis)*, and beardgrass community (14). Dominants are rush, sea myrtle, and broom sedge. Secondary species include goldenrod and small shrubs of red cedar and wax myrtle.

Marsh elder, *Fimbristylis*, and water pennywort community (16). Dominants are shrubby marsh elder, *Fimbristylis castanea*, and seaside pennywort. Secondary species are rush, saltmeadow cordgrass, foxtail grass, broom sedge, and wax myrtle.

Cordgrass, rush, and water pennywort community (17). Dominants are saltmeadow cordgrass, rush, and seaside pennywort. Less abundant herbaceous species include *Fimbristylis castanea*, broom sedge, foxtail grass, and cyperus. Woody species include wax myrtle, sea myrtle, and red cedar.

Creek marsh: Along the sound side of the western part of the island, there are several creek marshes surrounded by higher ground, excepting the narrow creek which permits the twice daily passage of tidal water. Usually, several vegetational zones are distinguished by the distance from the entrance of a tidal stream. Each zone is dominated by one or two species. A typical situation is a cordgrass *(Spartina alterniflora, S. distichlis, S. spicata)* zone near the entrance of tidal creek (Pl. IV-30), a rush zone, and a common cattail zone, as the water changes from salty to brackish to nearly fresh.

Rush, twig rush, and cattail-flag community (12). Dominants include rush, saw grass, and common cattail, with each species occupying a distinctive zone. Other species frequently observed at the periphery are morning glory, climbing hempweed, seashore mallow, and *Fimbristylis castanea*.

Rush, cordgrass, and cattail-flag community (15). This subdivision is similar to the community mentioned above, except that the dominants are rush, saltwater cordgrass *(Spartina alterniflora)*, and common cattail.

Rush, cordgrass, and spike grass community (18). This is the typical creek marsh mentioned earlier. Dominants are rush, saltwater cordgrass, salt grass *(Distichlis spicata)*, and common cattail. Quite a few halophytic species occur at the entrance of the tidal creek, such as perennial saltwort *(Salicornia virginica)*, dwarf saltwort *(Salicornia bigelovii)*, sea lavender *(Limonium carolinianum)*, and sea ox-eye *(Borrichia frutescens)*. Other species observed at the periphery are *Fimbristylis castanea*, seaside pennywort, saltmeadow cordgrass. and silver-leaf croton.

Salt marsh: Cordgrass, rush, and glasswort *(Salicornia)* community (20). Spreading along the sound side of the eastern half of the island is a well-developed salt marsh (Pl. IV-29). It can be further subdivided into two categories: a low salt marsh and a high salt marsh. The low salt marsh is inundated daily by tidal water and its silty substratum is permanently moist, whereas the high salt marsh is only occasionally inundated by the highest tides and generally is less salty. Saltwater cordgrass, which can withstand temporary complete submergence, is the preponderant species of the low salt marsh. Associated with it, rather abundantly, are dwarf and perennial glasswort *(Salicornia bigelovii, S. virginica)*. Less important members are salt grass and sea lavender. In the high salt marsh, saltmeadow cordgrass and rush are dominants. Other species found in this community are *Fimbristylis castanea,* sea ox-eye, and sea beach orach. Small shrubs include sea myrtle, shrubby marsh elder, and sometimes wax myrtle growing at the higher fringe of the salt marsh.

Cordgrass, spike grass, and *Fimbristylis* community (4). This is the only salt marsh community at the western half of the island and its area is less than 1 acre (0.4 ha). The community is heavily grazed by livestock, especially by cows and horses. Dominants are saltwater cordgrass, salt grass, and *Fimbristylis castanea*. Secondary species are sea ox-eye, perennial saltwort, and sea beach orach.

Cordgrass community (21). This salt marsh community is separated from the island proper and consists of pure stands of saltwater cordgrass.

Succession

In the remnant forest, most of the live oak trees are probably less than 70 years old. Therefore, some of them might have been developed from seeds set by a few surviving old trees after the devastating hurricane of 1899. However, pure patches of live oak trees about the same size are often found in the forest. It is conceivable that they might have developed by vegetative propagation from an old tree half-buried by dune sands.

Due to the mild maritime climate, herbaceous plants can colonize the barren ground rapidly. Lewis (1917) described the eastern half of Shackleford Bank as follows: "From Wade's Shore to Cape Lookout, both forest and swamp have disappeared completely save for one or two small groves of live oak, which have been able to resist the advancing sand. Elsewhere this portion of the island is a sandy waste, with little or no vegetation, . . ." Today, a well-developed meadow covers that once sandy waste. Furthermore, young seedlings and small shrubs of red cedar and wax myrtle are found in abundance in some sections of the grassy flat (Pl. III-21). The recolonization of the newly formed sandy surface can also be seen at the western end of the island (Pl. I-2). Also, in situations where the sand wall of the rear dunes have been stabilized by herbaceous plants, a number of woody seedlings are established.

The speed of succession is relatively fast at the moist sites but rather slow on the dry sand of the dunes. Under favorable conditions, individuals of red cedar and wax myrtle will be the pioneer trees to appear on a grassy flat or a moist depression. Their important roles lie in the gradual improvement of soil fertility as well as soil physical properties by the accumulation of organic materials. On the other hand, yaupon is a successional species on dry sites, especially behind the sand dunes.

Three serial pathways leading to a maritime forest can be recognized (Fig. 4). On a protected sandy waste, herbaceous species need only a couple of years to colonize such barren ground. Afterwards, shrubby species and tree seedlings may develop on the grassy flat, providing that a seed source is available. A scrub flat is thus formed and will eventually progress to a maritime forest. On an unprotected sand barren, the interaction of prevailing

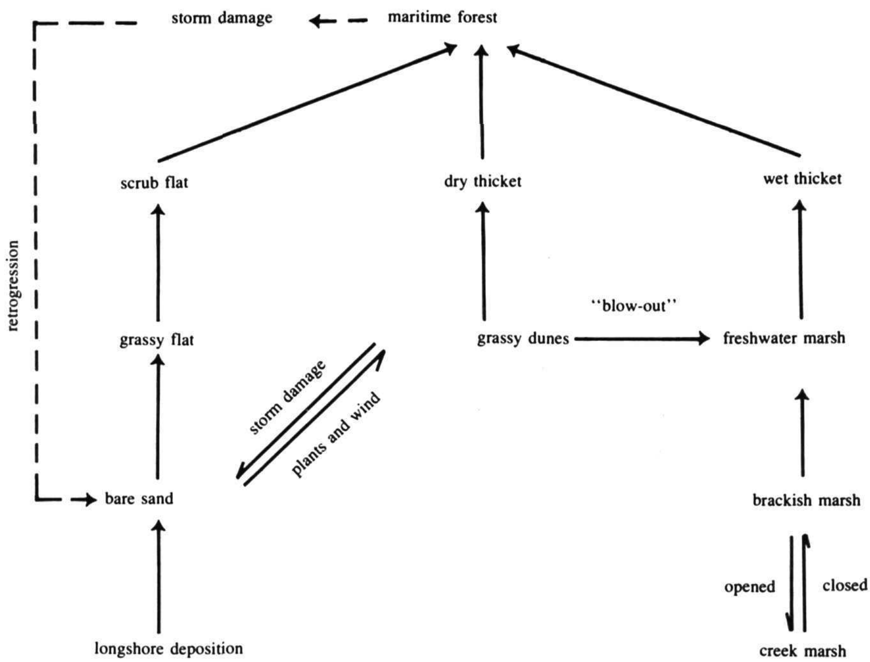

Fig. 4. Schematic relationship in successional stages of coastal vegetation.

onshore wind and the vegetative propagation of sea oats creates numerous incipient dunelets. As these dunelets grow bigger and connect to each other, a series of grassy dunes is produced. Because of the lack of available water, grassy dunes develop very slowly through a dry thicket stage and finally into a maritime forest. The last pathway may begin with an enclosed creek marsh, which, after continuous leaching by rainwater, is converted into a fresh-water or slightly brackish marsh. The marsh then develops through a wet thicket to a maritime forest.

Environmental factors such as shifting sand, salt spray, and topography may hold one type of vegetation in a comparatively stable condition for a long while. Succession does not follow a definite pathway, for many environmental factors may change or even reverse its direction completely. In short, the topography and the vegetation are constantly modified by all environmental factors, and vice versa. Therefore, the ecosystems on the island are not static, but dynamic and subject to frequent changes. However, plant succession occurs in a more restricted way on the island in comparison with the old field succession of Piedmont, N.C.

Table 1 shows the land surface occupied by major vegetation types in terms of percentage, acres, and hectares. The area of each vegetation type was determined with a planimeter from the vegetation map. Grassy sand flat, grassy dunes, and bare sand account for 82% of the total area while less than 4% of the island is currently covered by forest. However, as indicated in the foregoing descriptions of plant communities, the vegetation on the island is rather diversified and certainly represents one of the few rich remnants of maritime vegetation on the North Carolina coast. The diversified habitats and complex vegetational patterns resulting from the varied physiographic features support a surprisingly rich flora on such a small island. The second portion of this study will investigate some aspects of these complex environmental and topographic patterns.

Table 1. Areas occupied by major vegetation types.

Vegetation	%	Acres	Hectares
Beach and bare sand	22.4	511.5	207.0
Grassy dunes	34.7	791.9	320.4
Grassy sand flat	25.0	570.3	230.8
Fresh to brackish marsh	6.9	156.4	63.3
Salt marsh	3.0	68.9	27.9
Scrub flat	1.8	41.8	16.9
Thicket	2.4	54.2	21.9
Forest	3.8	85.6	34.6
Total	100.0	2280.6	922.8

5
Physical Environment

Climate

Methods

A microclimatic station was established on the top of the rear dunes. The station was at approximately the same level as the canopy of the maritime forest which is on the leeward side of the dunes. The station was thus without surrounding obstacles. The instruments used were a three-cup anemometer and a hygrothermograph which was placed inside a well-ventilated, white shelter on the ground. The anemometer was mounted at a height of 1 m above the ground; the accumulated air movement was recorded weekly from 10 July 1967 to 8 July 1968. Data concerning temperature and humidity were classified arbitrarily in terms of day (8 a.m. to 8 p.m.) and night (8 p.m. to 8 a.m.) periods. For each week, mean day and night temperatures (average of 6 readings at 2-hour intervals), weekly mean maximum and minimum temperatures, the highest and the lowest temperatures in a week, and vapor-pressure deficit (VPD) were calculated. The VPD was determined from Murphy's (1961) conversion table based on the relative humidity and temperature.

Nineteen years of climatic data were also obtained from the U.S. Weather Bureau station in Morehead City, about 3 miles northwest of Shackleford Bank. From these data, monthly mean maximum and minimum temperatures, the highest and the lowest temperatures in a month, monthly precipitation, and the number of rainy days each month were calculated.

Results

Temperature: The climate of Shackleford Bank is moderate due to the amelioration by the ocean and the nearby Gulf Stream. The monthly mean minimum temperature never drops below the freezing point (Fig. 5a). In fact, only in 3 months—January, February, and December—does the monthly mean minimum temperature reach 4°C. However, from November until March, the highest monthly temperatures occasionally drop below 0°C. Consequently, the first frost-free month may be as late as April. The slowness of the arrival of spring and the breaking of plant dormancy is possibly due to the maritime influence. The monthly mean maximum temperatures from April to October are higher than 20°C, possibly due to the high reflective sand with low specific heat. In short, the island has a milder climate in winter than that of inland areas. During the 19-year period at Morehead City, the highest temperature in a standard shelter was 107°F (41.7°C) and the lowest, 12°F

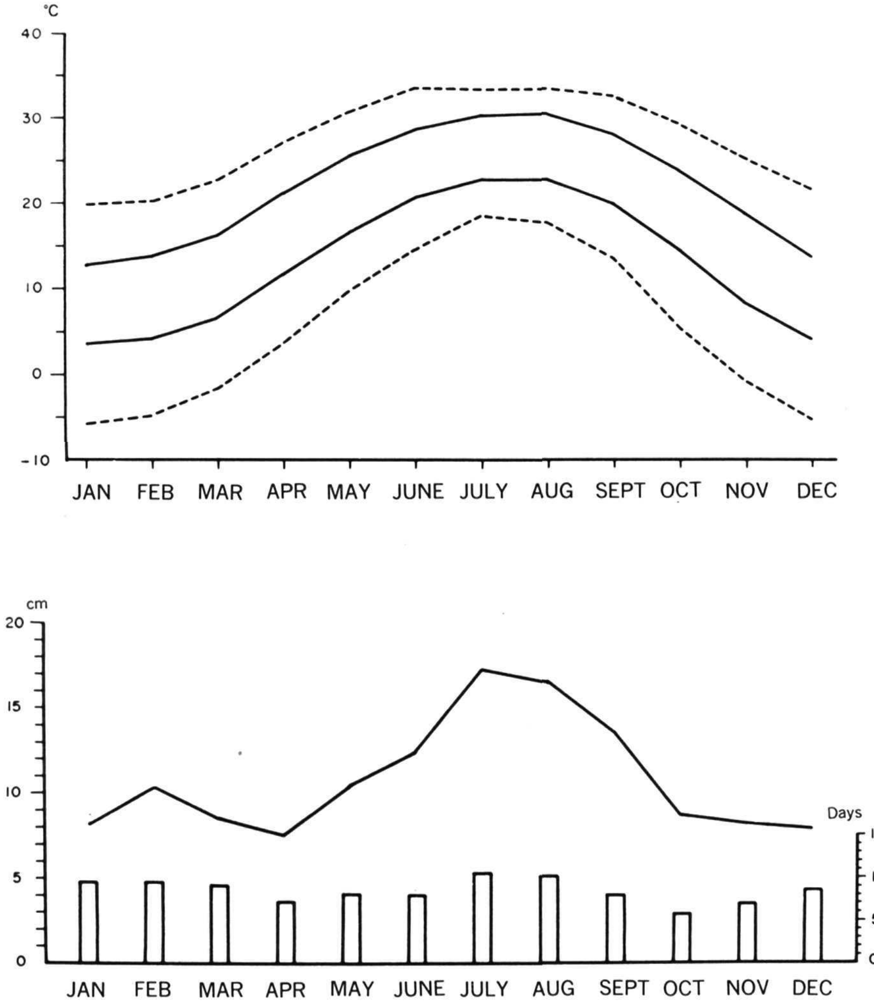

Fig. 5. (*top*) Average of 19-year temperature records at Morehead City, North Carolina. Upper and lower solid lines show monthly mean maximum and minimum temperatures respectively; upper and lower broken lines show monthly highest and lowest temperatures respectively; (*bottom*) average of 19-year precipitation records at Morehead City. Solid line shows average monthly precipitation in centimeters; unshaded bars show the number of rainy days for each month.

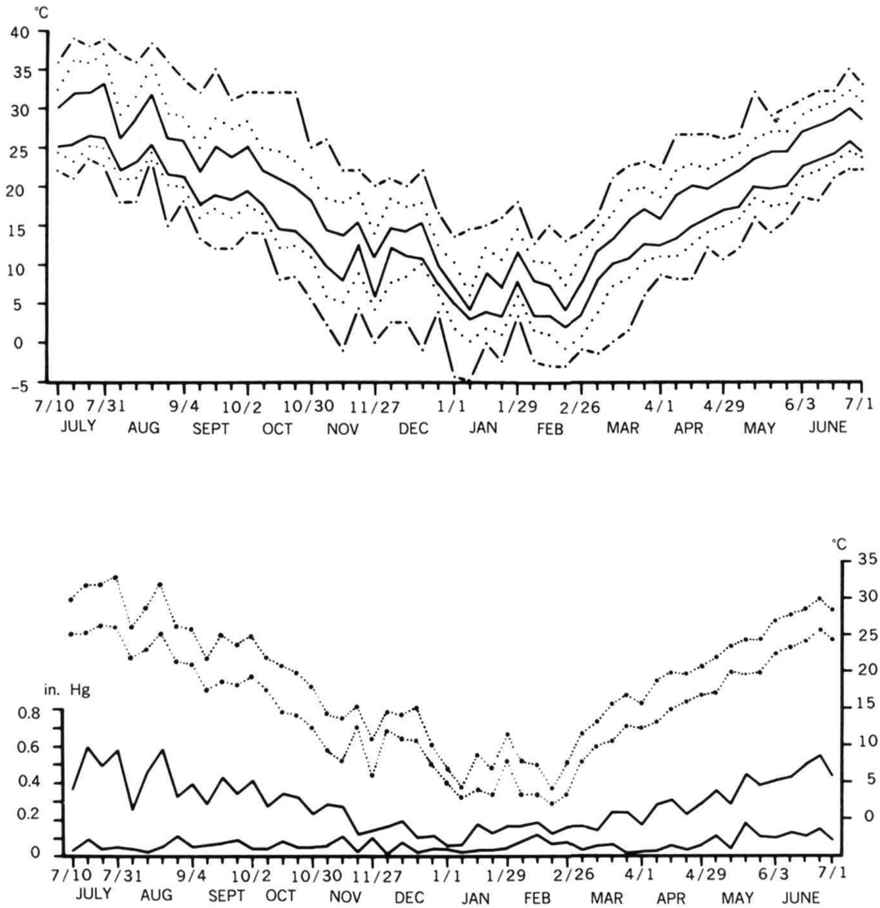

Fig. 6. (*top*) Weekly temperatures recorded from July 10, 1967, to July 8, 1968, at the microclimatic station on Shackleford Bank. Upper and lower solid lines refer to weekly mean day and night temperatures respectively; upper and lower dotted lines refer to weekly mean maximum and minimum temperatures, respectively; and upper and lower broken lines refer to the highest and lowest temperatures in each week, respectively, (*bottom*) weekly vapor pressure deficit and temperatures recorded at the microclimatic station on Shackleford Bank. Upper and lower dotted lines refer to weekly mean day and night temperatures, respectively; and upper and lower solid lines refer to weekly mean day and night vapor pressure deficit of the atmosphere, respectively.

(-11.1°C). These are probably more extreme than the temperatures on the water-surrounded Shackleford Bank.

The extremes of dune environment are evidenced in Fig. 6a. Within a well-ventilated, white-painted shelter, the highest temperature near the ground was 35°C or more for a period of 8 weeks. For 13 more weeks, the highest temperature was in excess of 30°C. The fluctuation between the highest and the lowest temperature in every week is very wide, usually in a range of 20°C. Again, the frost season extends from mid-November to mid-March.

Vapor pressure deficit: VPD of the air is primarily determined by air temperatures as well as humidity. The weekly mean VPD in "daytime" follows air temperatures closely (Fig. 6b). The highest values of weekly mean VPD are recorded between June and August, and the lowest values occur from October through February. On the other hand, VPD varies little at night during the year. Consequently, no definite seasonal pattern can be defined. The weekly mean VPD of 0.5-0.6 inches (12.7-15.2 mm) of Hg in the summer is high compared with those obtained by Mowbray and Oosting (1968) in a southern Blue Ridge gorge (about 7.6 mm Hg). In an environment of high VPD, active air turbulence caused by constant sea breezes in summer, high temperatures, and intense sunlight at the soil surface, a high rate of evaporation is inevitable. However, evapotranspiration occurs mostly in the daytime, with little or none at night under nearly zero VPD values.

Precipitation: Snowfall is a rare event for the island, occurring once every 2 or 3 years. According to Engels (1952), there are only 3.2 cm (1.3 inches) of snow per year on the average. Precipitation is almost entirely in the form of rain and averages about 129 cm per year, of which most falls during the summer (Fig. 5b). There is an average of about 103 rainy days per year, with the distribution of rainy days evenly spaced throughout the year. Therefore, the higher summer precipitation is due to heavier rainfall, especially from thunderstorms. Rains of lighter intensity and longer duration prevail in the winter and spring. Although the autumn and winter months are slightly drier, abundant precipitation along with uniform seasonal distribution of rainy days indicates that there is no threat to the vegetation from periods of prolonged climatic drought.

Wind

Methods

Two-year records (March 1966 to February 1968) of wind direction and maximum wind speed were obtained from the laboratory of the University of North Carolina at Morehead City, about 4 miles west of Shackleford Bank and one mile inland from Bogue Banks. Since the anemometer was mounted at rooftop, about 20 m above the ground, the protective interference of Bogue Banks is minimized. Thus, these data can be accepted as a reasonable approximation of the wind regime on Shackleford Bank, although tending to overestimate the wind speed somewhat due to the high altitude of the instrument. Weekly accumulated wind movement was obtained from the anemometer set up at the microclimatic station on the island as mentioned earlier.

There are generally two windy and two calm periods in a day. Wind speed begins gradually building up at 10 a.m., reaches its peak at about 1 or 2 p.m., then drops to a calm period from 5 to 7 p.m. The wind regains its vigor at about 8 p.m., while around 4 p.m. there is another calm period. In the present study, both wind directions and maximum wind speed were recorded in terms of day and night periods as used earlier. The percentage of each wind direction in each month is graphically expressed as the length of a corresponding column in a radial diagram. According to Mitsudera et al. (1965), 22.5 km/hr (6.25 m/sec) is the critical velocity for moving of sand with an average diameter of 0.25 mm. Thus, winds above this velocity are likely to have important effects on sand movement and on the vegetation. Accordingly, only the maximum wind velocity, which more likely exceeds the critical point for sand movement, is taken for each day.

Results

Wind direction: The monthly distribution of winds is shown in Fig. 7. The prevailing wind is predominantly from the southwest in summer, being 72% in July and 56% in August (average of day and night). The prevailing wind gradually shifts to northwest in the fall and north in winter, being 36% from the northeast and 29% from the north in October, and 39% from the north in February. The diurnal changing of wind direction indicating land and sea breezes associated with thermal gradients is recognized in all months. The prevailing wind is from the southwest both day and night during summer and loaded with salt spray and thus is an important factor in limiting the distribution of strand species.

Wind velocity: Although the strongest winds occur in the summer (April to July), as shown in Fig. 8b, the average monthly maximum wind velocity in winter and spring (October to February) is only about 5 mph less than that of the summer. Moreover, if we look at the highest wind velocity encountered in each month (Table 2), there are actually stronger winds in winter than in summer. The wind velocity at night generally subsides as shown in both Fig. 8b and Table 2.

One may conclude that the average monthly maximum velocity of the wind is considerable (15-20 mph), and the variation in the mean from month to month is small. Since most plants die back during the winter leaving the substratum almost completely exposed, extensive sand movements can easily take place in the winter.

Figure 8a illustrates that more air movement is recorded at the microclimatic station in summer than in winter. Since the variation of maximum wind velocity in a year is small, more air movement in summer must be attributable to the prolonged sea breezes from the southwest while short duration gales prevail in winter.

Sand Movement

Methods

A transect was set up extending from the ocean beach to the edge of the forest. Wooden stakes 1.5 m in length were driven vertically into the sand to a depth of about 1 m at appropriate distances. A string marked at 1 m intervals was connected at the tops of successive stakes. The distances between stakes and the angle of inclination were measured.

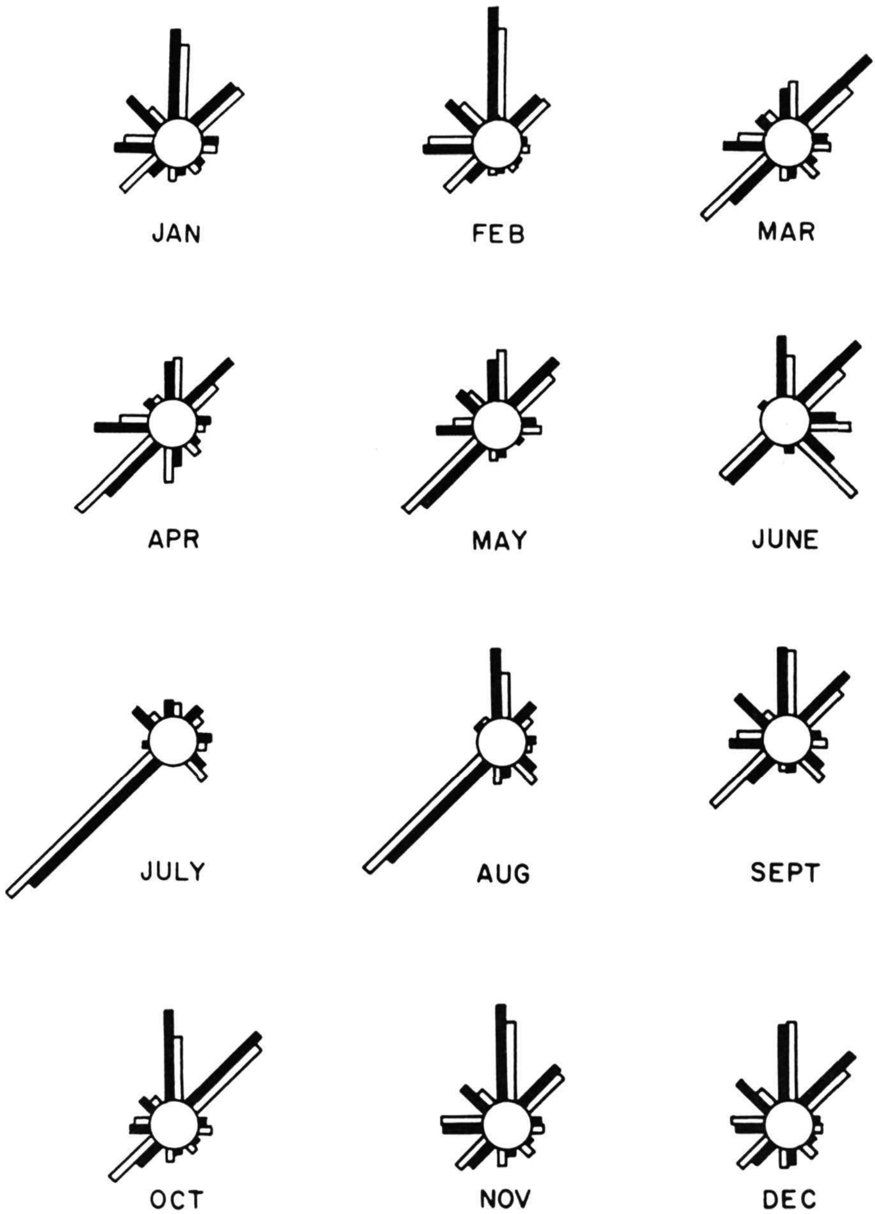

Fig. 7. Monthly distribution of wind directions as recorded from March 1966 to February 1968 at Morehead City, North Carolina. White bars represent % of wind direction in day time while black bars represent % of wind direction at night.

After a year, the same string was mounted and the distances from the marked points of the string to the ground surface were measured again. The differences between the first and second measurements of two adjacent stakes, regardless of whether positive (deposition) or negative (deflation or erosion), were averaged and expressed in centimeters.

To record the rate of sand dunes advancing to the forest, 20 wooden stakes 1.5 m long were driven to a depth of 1 m into the sand at the bottom edge of the sand wall at about 100 m intervals. The relative locations of the wooden stakes to the edge of the sand wall were reexamined a year later.

Table 2. The maximum wind velocity for each month recorded from March 1966 to February 1968 at Morehead City, N.C.

	Miles/Hour	
	Day	Night
January	48	46
February	38	40
March	54	54
April	39	37
May	50	36
June	58	52
July	41	24
August	40	35
September	30	38
October	55	38
November	48	52
December	64	44

Results

The transect across the dune community is drawn in Fig. 9, with numbers in centimeters indicating the average change of the dune profile between successive stakes. Data show a quite unstable dune system under the impact of winds. The absolute average change ranges from 1.5 to 21.0 cm/yr. The amount of change does not correlate with the distance to the ocean, but depends primarily upon the vegetational cover and then on the topographic shelter. The change is highest at places without vegetational cover, mainly the steep dune slopes and the bare dune troughs. From a close scrutiny of the recorded data, it is evident that generally the wind erodes the ocean side (prevailing windward side) of the dune and deposits sand on the leeward side of the dune. Although both inshore and offshore winds can cause the sand movement, the direction tends to be landward due to the more exposed condition on the ocean side. In contrast, the forest protects the low dunes from the offshore winds.

From observations throughout a year, the period of maximum sand movement seems to occur in winter (November to March). At this season, without the stabilization of growing plants, the dry surface is easily blown away by winds. Since the general sand movement determined by the prevailing wind is landward, as evidenced in the erosion on the windward slopes and the deposition on the leeward slopes of the dunes, the dunes apparently progress landward. However, the average change of the dune profile in a normal year is likely to be less than 10 cm.

All 20 wooden stakes set up behind the sand wall were intact after a year; none were buried by sand. Apparently, the encroachment of the dunes upon the forest has not advanced to a sufficient extent to be measurable. Nevertheless, locally, wherever a main animal trail is present, a sand tongue is formed extending to the forest. It seems that only an inexorable hurricane could move the sand wall sufficiently to inflict catastrophic damage on the forest. Otherwise, it appears that sand encroachment has subsided and will not be a serious threat to the present forest in a normal year unless the vegetation is destroyed or badly damaged by animals or man.

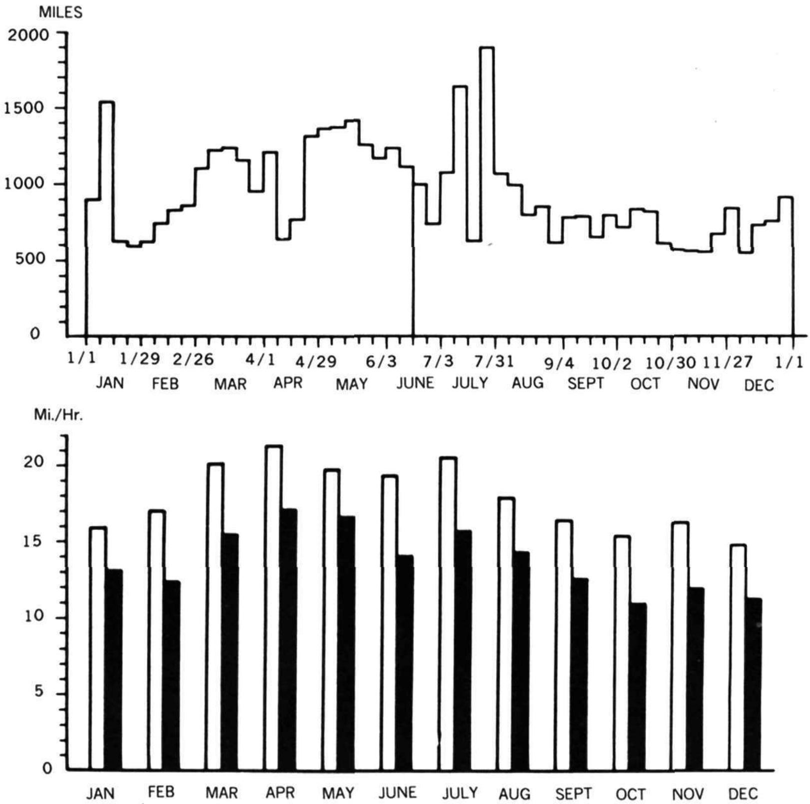

Fig. 8. (*top*) Weekly accumulated run of the wind as recorded at the microclimatic station on Shackleford Bank from 10 July 1967 to 8 July 1968; (*bottom*) monthly means of daily maximum wind velocity as recorded from March 1966 to February 1968 at Morehead City. White bars refer to wind velocity during daytime; black bars refer to wind velocity at night.

Edaphic Factors

General description

Soils developed on Shackleford Bank consist of siliceous sands with various proportions of shell fragments, depending upon the closeness to the ocean and the wind velocity. There is a striking contrast in nutrient content between forest soil and dune soil. As a result of the absence of vegetational cover and the mobility of the sand, dune soil shows little, if any, profile development and contains meager amounts of organic material. On the contrary, well-developed forest soil usually has a large amount of humus in the top 10 cm of soil. This is visible as a dark-stained layer accumulated under long-term conditions of stability. However, humus accumulation has very little effect on structural development of these sandy soils, and usually the transition from one horizon to another is rather vague.

The soil developed under yaupon differs appreciably from the soil formed under live oak in having relatively little humus; in some cases, development is scarcely better than in a well-developed dune soil. The humus content of the soil developed under red cedar is intermediate to the forest soil and dune soil. Regardless of whether it is forest soil or dune soil, due to their deep sand nature all profiles have low water-retaining capacity and thus are well drained.

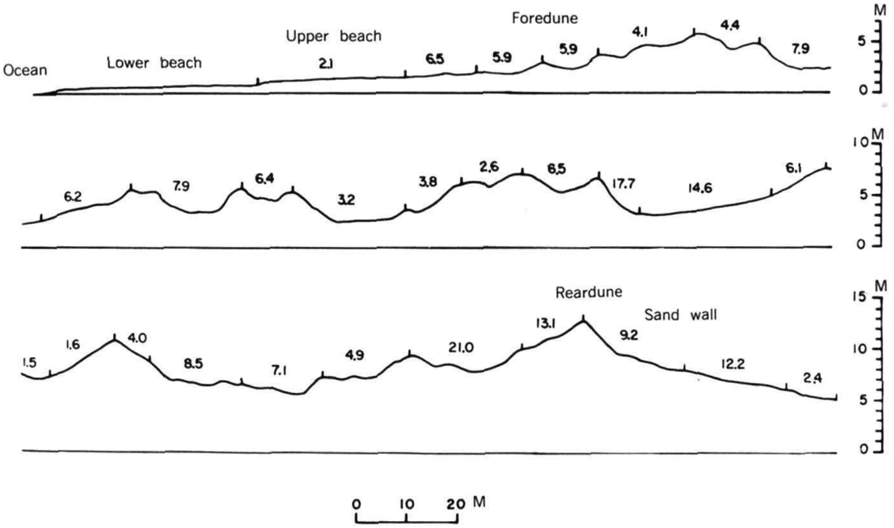

Fig. 9. Dune transect showing amount of sand movement. The numerical values between two stakes represent the absolute values of depth change in centimeters.

To acquire a better understanding of edaphic effects on the vegetation, both physical properties and chemical properties of the soil were evaluated. Physical properties studied include the composition of particle size, the amount of available water, and vertical distribution of soil water over time; while chemical properties include salinity, pH, organic content, nitrogen, phosphorus, calcium, magnesium, potassium, and sodium in the soil. Most earlier analyses of dune soils of the eastern United States have been done on the top 2-3 inches (5-8 cm) of soil and are probably not very representative of the entire root zone. Therefore, the present study sampled 1 ft (30 cm) of surface soil which is a more significant stratum for seedling development and plant growth. Finally, the ionic constituents of plant tissue were analyzed for comparison with results of the soil analyses.

Methods

To investigate soil moisture and salinity of soil profile, three transects parallel to the ocean (the fore dunes, the rear dunes, and the forest, respectively) were selected. On each transect, soil samples were collected on five sites about 100 m apart at depths of 0-2, 5-7, 11-13, 17-19, and 23-25 inches (0-5, 13-18, 28-33, 43-48, and 58-63 cm). Fresh weight of about 50 g of soil from each sample was determined immediately upon return to the laboratory. The samples were oven-dried at 110°C for 24 hours and reweighed. The loss of water was expressed as percentage of oven-dry weight of the soil. After adding 100 ml of water to each dry soil sample and shaking for 30 minutes, electrical conductance of the supernatant soil solution was measured with a conductivity bridge. Salinity was estimated from a standard curve prepared with known concentration of sodium chloride. In order to investigate the change of water content in soil profile over time, soil collections were repeated on each sample site 1 day after a rain, 3 days after a rain, and 2 weeks after a rain.

For the determination of soil pH, 10 samples of the top 2 inches (5 cm) of soil were taken about 100 m apart at each of the following locations: on the crest of the fore dunes, on the crest of the middle dunes, on the crest of the rear dunes, under red cedar, and under live oak. Soil pH measurements were taken with a Beckman pH meter on a 1:5 soil/water mixture after soaking for 1 hour while stirring frequently.

Particle size analysis and the determination of soil water content at 1/3 and 15 atmospheres (atm) pressure were made on the soil collections taken for chemical analyses which are described below. In the separation of sand, percentages of various sand particle sizes were determined from 50 g samples after shaking in a column of sieves with a reciprocating shaker for 15 minutes. The sand held in each sieve was weighed and expressed as percentage of total soil dry weight. Soil moisture content at 1/3 and 15 atm, for estimating the field capacity and wilting percentage, respectively, were determined by pressure plate apparatus. The difference between these two measurements is considered an index of available water in the soil.

Soils developed under live oak trees, on the crest of the rear dunes, and on the crest of the fore dunes were compared for organic content and nitrogen, phosphorus, calcium, magnesium, potassium, and sodium contents. Ten sites at about 100-m intervals along each of two parallel transects, on the rear dunes and fore dunes, respectively, were selected. Soil samples were collected at each site at depths of 0-3 and 3-12 inches (0-8 and 8-30 cm). Equal amounts of samples taken from corresponding horizons of two adjacent points on each transect were thoroughly mixed and dried at 110°C. Thus, there were five composite samples of each horizon from each transect. Soil samples were also collected at 10 sites under live oak trees (the most mature soil) at depths of 0-3 and 3-12 inches (0-8 and 8-30 cm). Samples of corresponding horizons from pairs of adjacent points were also combined for analysis. The procedures for chemical analyses were adopted from those of Jackson (1958).

Organic matter content of soils developed under live oak trees was estimated by the loss-on-ignition method. Four replicates of about 20 g were taken from each sample previously dried to 110°C and weighed, then ignited to 650°C for an hour and reweighed. The organic content was expressed as the percentage of soil dry weight at 110°C. Organic carbon of the soil samples taken from the rear dunes and fore dunes was determined by wet combustion method, and the amount of organic matter was estimated as twice the organic carbon value. The nitrogen content was determined by semimicro Kjeldahl procedure, and the available phosphorus in the soil was determined by the molybdenum blue procedure.

Soil extracts for ionic analyses were obtained by adding 1 N HNO_3 to 5 g soil and boiling for 10 minutes. Magnesium and calcium were determined with a Model 290 Perkin-Elmer Atomic Absorption Spectrophotometer. Sodium and potassium were determined with a Model 21 Coleman Flame Photometer.

Species selected for leaf analyses were live oak, red cedar, and sea oats. Live oak and red cedar are the major constituents of the maritime forest, whereas sea oats is the predominant species on the grassy dunes. Both old and young leaves of each species were collected on the windward and leeward sides of the plant and wiped with moist cheesecloth. Five samples were collected for each species and mixed together thoroughly after grinding. Samples were dissolved in 70% perchloric acid after predigestion with concentrated nitric acid. Potassium, sodium, calcium, and magnesium contents were measured by the procedures mentioned above for the soil extracts.

Results

Physical properties: Data in Table 3 indicate that soil textures in the soils investigated range from medium to coarse sand. The most obvious difference noted was at the fore dunes which contain higher percentages of coarse sand than the rear dunes. For example, on the top 8 cm of soil, the fore dunes have 34% coarse sand (larger than 0.5 mm), while the rear dunes have only 5.8%. Conversely, there is 65% fine sand (0.10-0.25 mm) on the rear dunes but only 30% on the fore dunes. Apparently, lighter sands are carried farther inland, leaving a larger proportion of coarse sand on the fore dunes (Pl. I-5). Data also show that in every location there is a slightly higher percentage of coarse sand in the top 8 cm of soil than in the layer below. The cause of this is not clear; perhaps it reflects leaching effects or possibly an anomalous sampling error.

Kearney (1900) stated that there is no lack of moisture in beach sand because water usually stands at a depth of only 15-30 cm from the surface. From the field experience in digging up soil samples, it was found that subsurface layers were moist, though not as near the surface as 15 cm; more commonly, at a depth of 30-60 cm. Frequently, the water table, as indicated by saturated soil, stands at a depth of only a meter or so from the surface.

Table 3. Percentage of sand particles in each size class.

Depth (cm)	Size class (mm)	Forest	% Rear dunes	Fore dunes
	>1.00	1.20[a]	0.11	4.73
	>0.50	7.90	5.78	34.00
0 - 8	>0.26	25.61	27.73	29.58
	>0.105	64.31	64.95	29.82
	<0.105	0.98	1.42	1.87
	>1.00	0.12	0.17	2.51
	>0.50	5.22	4.86	23.39
8 - 30	>0.26	25.33	27.39	32.44
	>0.105	68.77	66.48	41.24
	<0.105	0.57	1.11	0.41

[a]Due to plant debris

Figure 10 illustrates the distribution of water in soil profiles of the fore dunes, the rear dunes, and the forest. The upper graph shows the comparison between the fore dunes and the rear dunes. Comparison of curves for 1 day and 3 days after rain, in both upper and lower graphs, demonstrates the rapidity of downward water movement. Only 1 day after rain, gravitational water had moved to a depth of 15-30 cm below the surface soil. After 3 days of drainage, the moisture profile is not much different from that of 2 weeks after rain, as shown in the upper graph. One may conclude that soils of all areas studied are well drained. Partly due to rapid drainage and partly due to speedy evaporation, the top 15 cm of soil dries quickly after rain. Then, the dry surface layer probably acts as a mulch and contributes materially to the preservation of soil moisture in the lower zones.

A trend of increasing soil moisture from the fore dunes to the forest also is evident. This increase may be caused by the accumulation, over a period of time, of organic matter in the soil of the forest sites. However, soil-moisture content of individual sites in the forest also varies considerably, mainly due to the variations in the depth of the water table. The water table is only 60 cm deep at one site, thus the soil is completely saturated at that depth in some places.

Table 4 shows the approximate wilting percentage (15 atm), approximate field capacity (1/3 atm), and available water of sandy soils on the island. Due to their sandy nature, i.e., large pore space and little surface tension, dune soils retain very little water at 15 atm, ranging from 0.2 to 0.4% by oven-dry weight. On the other hand, top layers of forest soils with higher organic content retain larger amounts of water, ranging from 1.7 to 2.5% by oven-dry weight. However, lower layers of the forest soils retain only slightly higher amounts of water than the dune soils. Similar differences between forest soils and dune soils occur in moisture retention at equilibrium with a pressure differential of 1/3 atm. Again, less water is retained in the dune soils (0.8-1.7% by weight) than in the forest soils (4.9-9.0% by weight). After gravitational water is lost, about 0.8-1.2% water on an oven-dry weight basis in the dune soils is available for plant growth. In the forest soils, about 4% water by dry weight in the top soil and 1% water by dry weight in the lower layer of soil is available for plant growth. Apparently, the greater amount of available water in the forest soil is due to the accumulation of humus, since the mechanical analysis showed little difference in texture between the forest soils and rear dune soils.

Chemical properties: Soil reaction changes from alkaline to acid from the fore dunes to maritime forest as the distance from the ocean increases (Table 5). The increase of acidity in the forest soils probably is due to the presence of organic acids, as indicated by a larger amount of organic matter. Conversely, the alkaline reaction of the fore dunes is probably due to the presence of free carbonate derived from shell fragments and possibly a gradual leaching out of the carbonate over a period of time. The amount of salt in all soil samples is miniscule (in a range of 10^{-4}N) as compared with sea water which is about 0.6 N (35 ppt). The salinity of the top 5 cm of soil is not considered here because the water content is so low that the salinity of the soil solution would be greatly increased. Nevertheless, there is a trend for increased salinity as proximity to the ocean increases. The increase is probably due to the greater salt spray deposited on the surface of the fore dunes and subsequent leaching by rainwater.

Chemical analyses of soils taken from the fore dunes, the rear dunes, and the live oak forest are summarized in Table 6, including analytic data of inland Sandhills soils from Ralston (1962 pers. comm.). The percentage of organic matter is extremely low in the dune soils. As one would expect, soil organic matter content is least on the fore dunes (less than 0.1%), a little higher at the rear dunes (0.1-0.2%), and greatly increased in the forest soils (as high as 5% in the top layer). In all areas studied, the top 8 cm of soils always contain more organic material than the layer below. The forest soil has much more organic material than the dune soils due to the accumulation of abundant humus and plant debris. Analytic results also indicate extremely low nitrogen contents in the dune soils, even though the rear dunes contain a little more nitrogen. The same trend occurs in regard to phosphorus supply,

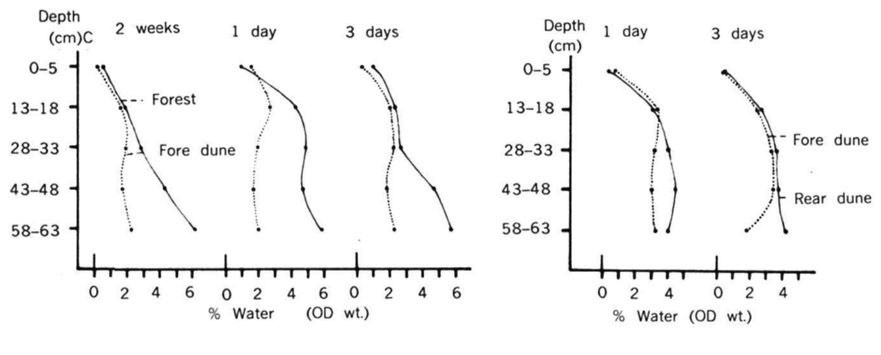

Fig. 10. Changes of water content in soil profiles measured 1 day, 3 days, and 2 weeks after a rain.

Table 4. Soil water content at 1/3 and 15 atm, and available water of different vegetation zones.

		g H_2O/100 g soil			
		0 - 8 cm		8 - 30 cm	
		Mean	Range	Mean	Range
1/3 atm	Fore dunes	1.01	0.88 - 1.12	1.04	0.90 - 1.12
	Rear dunes	1.53	1.19 - 1.72	1.10	0.81 - 1.21
	Forest	6.39	4.89 - 9.03	1.87	1.43 - 2.24
15 atm	Fore dunes	0.20	0.19 - 0.22	0.20	0.17 - 0.23
	Rear dunes	0.31	0.25 - 0.41	0.23	0.20 - 0.26
	Forest	2.16	1.72 - 2.46	0.61	0.46 - 0.72
Available water	Fore dunes	0.81		0.84	
	Rear dunes	1.22		0.87	
	Forest	4.23		1.26	

Table 5. Soil pH and salinity under different vegetation zones.

Location	pH Range	Salinity $\times 10^{-4}$N
Under live-oak	3.70 - 6.30	7.4 (forest)
Under red cedar	5.70 - 6.85	
On rear dunes	7.44 - 8.50	3.3
On middle dunes	7.70 - 8.50	
On fore dunes	8.55 - 8.90	6.1

Table 6. Chemical analyses of soils under different vegetation zones.

Locality	Horizon (cm)	O.M (%)	N (ppm)	P (ppm)	Ca (ppm)	Mg (ppm)	K (ppm)	Na (ppm)
Fore dunes	0 - 8	0.01	30	0	38100	281	44.0	1165
	8 - 30	0.01	20	0	27700	251	36.0	990
Rear dunes	0 - 8	0.22	100	5.90	4640	163	36.8	337
	8 - 30	0.14	70	4.15	7020	152	35.2	470
Forest	0 - 8	5.18	1450	17.40	920	109	63.4	353
	8 - 30	0.95	330	9.10	240	31	28.2	252
Kershaw series[a]	A_1		470	164[b]	25	10	57	
(Sandhills)	A_2		290	112[b]	19	8	55	

[a]Ralston 1962
[b]Total P (approximately equal to 10 × P)

which is too low at the fore dunes to be detectable. Therefore, the rear dunes seem to be relatively mature as compared with the fore dunes. On the fore dunes, nitrogen and phosphorus components are so low that only a few low-nutrient-requiring species, such as sea oats, seaside spurge, and sea rocket, can survive in such environments.

Generally speaking, dune soils are conspicuously low in nitrogen and phosphorus, and thus the supply of these elements may be a limiting factor for many species. By contrast, in well-developed forest soil, organic matter content, nitrogen, and available phosphorus are very high, even compared with the forest soil from other types of vegetations.

The amount of potassium in dune soils is generally fairly low (about 40 ppm), but this element is very abundant in the leaves of sea oats (about 1.1%), as illustrated in Table 7. In contrast, sodium content of dune soils is high, especially on the fore dunes, but not saline. The fore dunes have two to three times more sodium than the rear dunes, which generally receive much less salt spray. Both potassium and sodium contents of the forest soils do not differ much from those of the rear dunes. Slightly lower sodium content of the forest soils indicates that higher values estimated by conductance methods are due probably to the organic acids rather than to sodium chloride. Higher potassium levels in the upper layers of the forest soil probably reflect larger amounts of this ion accumulated in plant tissues and subsequent deposition on that layer.

A marked depletion of calcium in surface sands of the rear dunes, accompanied by a rise in humus content, seems characteristic of the coastal sandy soils. Since the fore dunes have almost 4% calcium by weight, the chief source of calcium must be calcium carbonate of the shell fragments which are washed up by waves and carried inland by winds. Magnesium content of the maritime sandy soils falls in the same range as that of the Sandhills soils. A little higher magnesium content in the fore dunes probably is due to the salt spray.

The elements in the leaves of different species do not seem to vary according to soil nutrient supply status (Table 7). For instance, sea oats contain much less calcium (5-35 times less) than the other two species, even though it grows on the fore dunes which have the highest calcium values among the three sampling zones. Red cedar has a much higher calcium content (0.35%) than live oak (0.05%).

Table 7. Chemical analyses of leaves of sea oats, red cedar, and live oak.

	% of OD wt. (110°C)		
Element	Sea oats	Red cedar	Live oak
K	1.09	0.31	0.79
Na	0.51	0.22	0.15
Ca	0.01	0.35	0.05
Mg	0.12	0.17	0.15

6
Biotic Factors

As mentioned earlier, during the recent history of the island the elimination and desecration of habitats through man's misuse of land initiated or at the least vastly accelerated the devastation of the original vegetation. This kind of destruction could be started again by developing the island into a public amusement playground. At the time of this writing, only one family lives on the island and does so only during the summer. The vegetation is damaged mainly by livestock. However, weekend intruders make campfires, carry away driftwood, and carelessly leave behind a large number of tin cans and other garbage.

There is no good method for counting the exact number of grazing animals on the island, but the highest number I encountered in the field at one time is as follows: 52 sheep, 15-20 goats, 20 cows, and 26 horses. Cows (Pl. III-24) and horses (Pl. IV-29) are owned by persons living on Harkers Island, while the goats (Pl. II-13) and sheep (Pl. II-14) are wild. The damage done by these animals is considerable, not only because they graze on the grasses but also by their roaming and trampling. Animal trails are numerous. Besides feeding on young leaves and twigs of woody species, the goats and sheep do much physical destruction on the dunes and accelerate the encroachment of sand on the forest. Therefore, if natural conditions on the island are to be restored and maintained, the livestock must be removed.

Physiological Responses of Plants

Methods

Since no study of water relations of coastal plant species has been reported in North Carolina, the water potentials of plants developing under moist root environments and extreme dry conditions above ground (i.e., under full sunlight, high temperature, and constant wind in the summer on highly reflective sands) were measured. The effects of salt water, salt spray, drought, shade, and nutrients on the growth of selected dune species were also investigated.

The water potential of 16 species was measured with the Shardakov dye method (Knipling 1967). Leaf samples were taken between 1:30 p.m. and 2:30 p.m. on a sunny day at least 3 days after rain in both summer and winter. Twenty measurements were taken for each species and the daily patterns of several species were observed also.

Four species growing on the dune proper, horseweed, sandgrass, seabeach evening primrose, and ground cherry, were selected and young plants with soils were collected from the field in 10-cm diameter plastic pots. The size of plants was kept as uniform as possible and special care was taken to minimize the damage during the transplantation. All plants were used for each of the following treatments every 3 days: sea water, 1:3 diluted sea water, salt spray, shaded with canvas, solution containing N, K, and P (Hoagland and Arnon 1938), solution containing K only, drought, and a control plant watered with tap water. Dates of death were recorded for each plant that received treatments of sea water, 1:3 diluted sea water, salt spray, and drought. For the nutrition treatments as well as the control, the height and dry weight of above-ground portions of the plants were measured after 2 months.

Results

Water potential: There is a wide range of variation in water potential among species, ranging from −5 bars to −18 bars (Fig. 11a). A variation of 4 bars is quite common within a species, possibly due to the difference of individuals, of various habitats, and in different months. However, a 2-bar difference in one species measured on the same day from different individuals is not uncommon. The water potential is lower in woody species, namely, red cedar, yaupon, live oak, and wax myrtle, than in herbaceous species: seashore elder (semiherbaceous), sea oats, seaside spurge, saltmeadow cordgrass, silver-leaf croton, horseweed, camphor weed *(Heterotheca subaxillaris),* seabeach evening primrose, wild bean, seaside pennywort, sandgrass, and sandspur. Also, the variation of water potential is larger in woody species than in herbaceous ones. Among herbaceous species, those which occur frequently on fore dunes or on dry sites have a little lower water potential, such as seashore elder, sea oats, beach spurge *(Euphoria polygonifolia),* saltmeadow cordgrass, and silver-leaf croton. Therefore, there seems to be a correlation between the water potential of plants and the nature of habitats.

The water potentials of all species in the early morning are quite close (Fig. 11b). Approaching midday, water potentials decrease; again, much lower water potentials are detected among the woody plants. Since the water potentials of woody species drop to −14 to −15 bars while the lowest water potentials of the herbaceous plants are only −5 to −10 bars, the difference is quite clear. Because there is always abundant water about 30 cm below the soil surface, the decrease in water potential in the afternoon apparently is due to the lack of absorption under the stress of excessive transpiration on leaves rather than to the lack of water supply in the soil. In other words, under high light intensity, excessive heat, and constant wind, the rate of transpiration from leaves exceeds the water absorption by roots. Nevertheless, the water potentials of all species studied usually recover overnight.

Effect of salt spray, salt water, and drought: In regard to the accumulated number of dying individuals vis-a-vis the number of days after detrimental treatments (Fig. 12), horseweed appears to be the species most susceptible to salt spray, followed by seabeach evening primrose, ground cherry, and sandgrass. Evening primrose *(Oenothera)* and ground cherry have dense epidermal hairs, while sandgrass has a wax layer on the leaf surface. Since salt water kills plants of all these species in 10-13 days (Fig. 12), none of them should be considered as true halophytes. Plants of all species studied, except ground cherry, died on

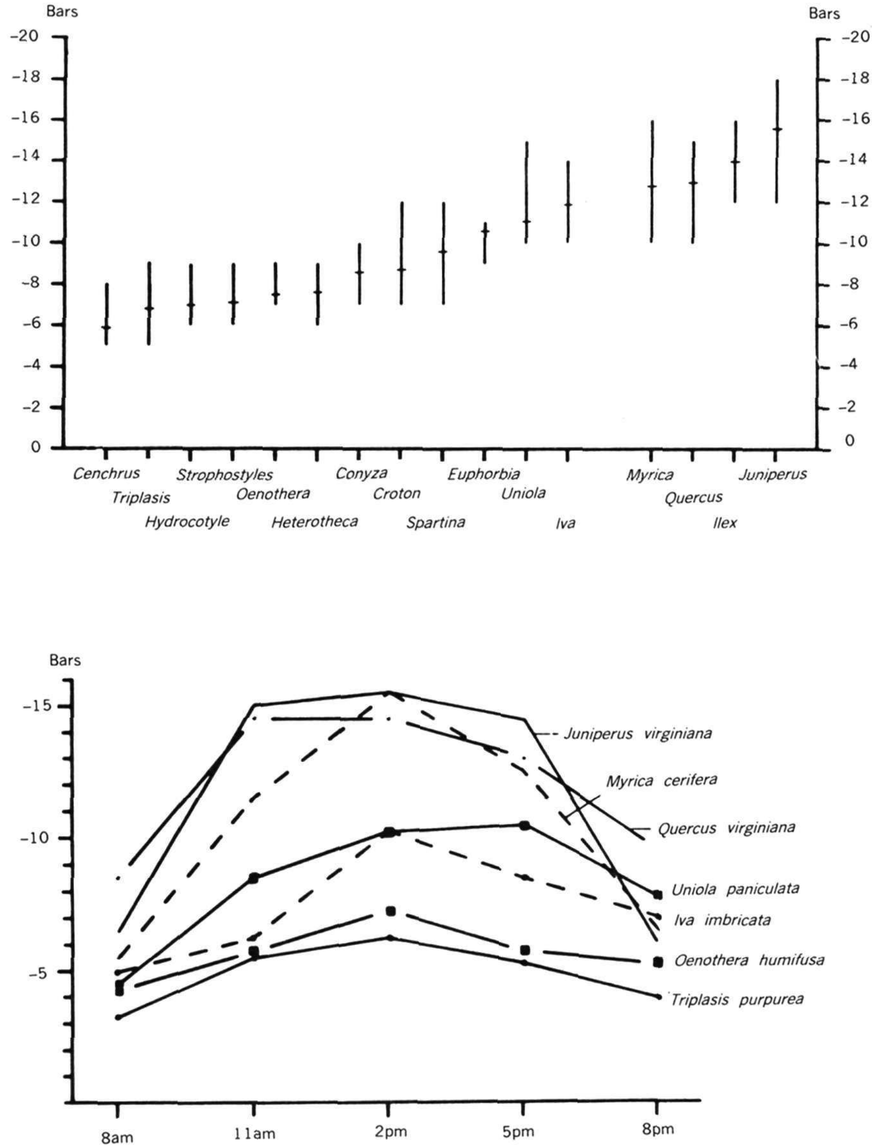

Fig. 11. (*top*) Water potentials of various species. Vertical lines refer to the range of water potentials of corresponding species recorded in the early afternoon while the cross bars refer to the average values of 20 measurements for each species; (*bottom*) changes of water potentials of different species from 8 a.m. to 8 p.m.

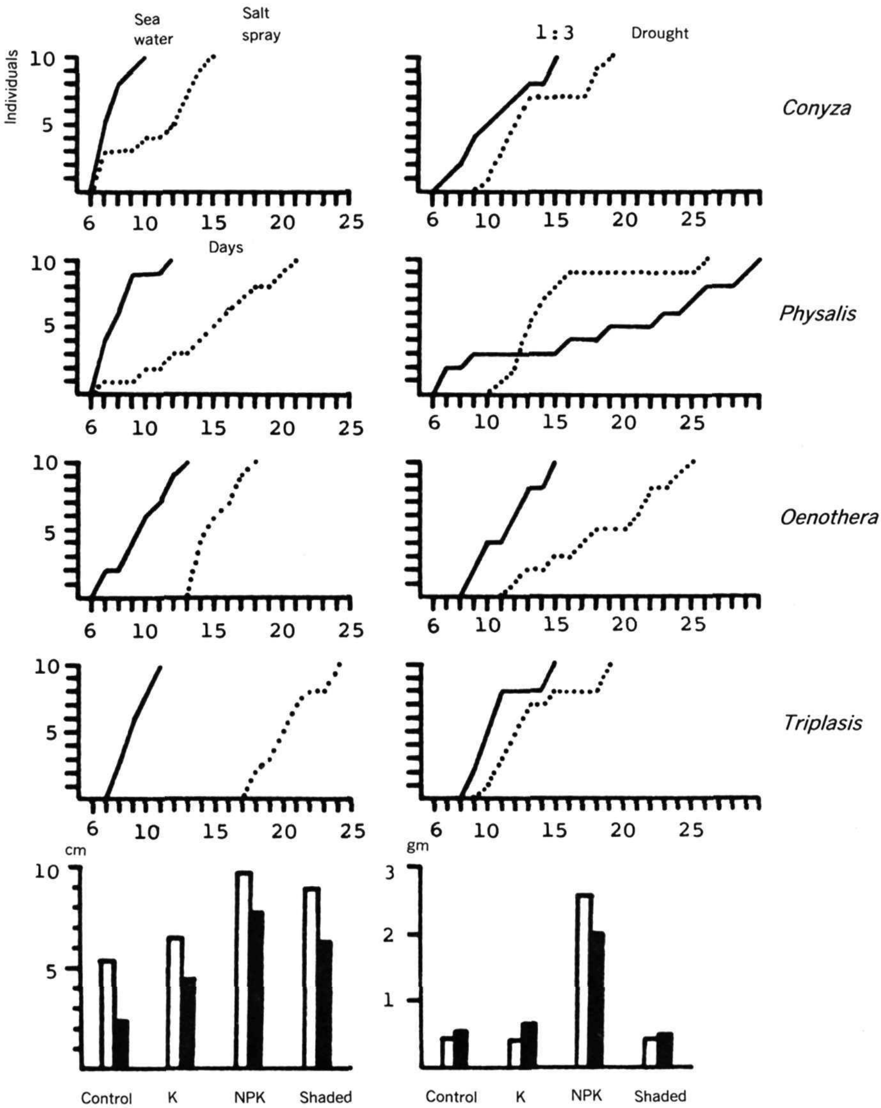

Fig. 12. Top eight graphs show the results of an experiment in which horseweed, ground cherry, seabeach evening primrose, and purple sandgrass were subjected to seawater, diluted sea water (1:3), salt spray, and drought stress. Accumulated number of dead individuals is plotted against the date of death. The bottom two graphs show the effects of nutrients and shade on plant growth. White bars represent horseweed; black bars represent sandgrass. Left graph shows the effect on plant height; right graph shows the effect on standing crop in even-dry weight.

the 15th day after treatment with 1:3 diluted sea water. Apparently their resistance to diluted sea water is only slightly better than to the full-strength sea water. The longest survivor, ground cherry, probably depends on the merit of its thick fleshy rhizome.

Generally speaking, all species have slight resistance to drought, the death date for the last individual of each species ranges from 19 to 26 days after the initial watering (Fig. 12). One may note that the planting pot is only 10 cm in diameter and contains no more than 500 g of sand.

Effects of nutrient solutions and shade on plant growth: Only two species, horseweed and sandgrass, were studied (bottom two graphs of Fig. 12). Plants of both species show a greater increase in height under all treatments than that of the control. The increase is greatest in the complete nutrient solution treatment, the shaded treatment is next, and the one treated only with K solution shows the least increase. However, concerning the net gain in dry weight, the adding of NPK solution shows prominantly the highest increase, while the net gains of the shaded plant and the plant treated with K only are substantially reduced and not significantly different from that of the control. There seems to be no improvement in plant growth by just adding K to the water. Therefore, potassium alone is not a limiting factor to the growth of these dune species. However, nitrogen and phosphorus are shown to be extremely important in enhancing plant growth. Finally, the height increase under shaded condition does not indicate a higher productivity, but mainly etiolation.

7
Discussion

Geological and Historical Factors

Geological history indicates that Shackleford Bank is of recent origin and is probably less than 2000 years old. Through years of colonization and succession by plants, the once barren island became covered with a diversified maritime vegetation. If the U.S. Coast and Geodetic Survey map of 1853 is dependable, the island was almost completely covered with maritime forest prior to human occupation. However, the force of wave erosion, the deposition of sand by longshore current, the opening and closing of inlets (Dunbar 1956), and occasional hurricanes all contribute to the physical and biological oscillations of the island. Consequently, a high degree of instability is an inherent characteristic of Shackleford Bank.

The western end of the island provides a vivid example of such instability. According to Engels' study (1952), the configuration of that part of the island in 1851 was similar to the present one except that it was covered with maritime forest. In contrast, the 1949 map shows that a large area at the western end of the island has been eroded away. Now, in a 10-year period, approximately 1956-66, about 150 acres (60 ha) of land have been deposited back on more or less the same locality. Radical changes seem possible in less than 100 years. Oosting (1954) stressed the point that "such a bank, once formed, is still constantly subject to the same forces which created it and, as a consequence, it is essentially a transient physiographic feature, or at least an unstable one." Therefore, it is impossible to acquire a full understanding of the ecological processes on the island without paying due consideration to geological factors.

The intervention of European man on Shackleford Bank about 200 years ago initiated a gradual attrition and degradation of the primeval vegetation. Such disturbance of vegetation by man and domestic animals is also reported by De Bolòs and Molinier (1958) on the Spanish island of Majorca, by Whitehead (1964) on sand dunes of New Zealand, and by Esler (1967) on Kapiti Island of New Zealand. The modification on vegetation by human activities such as tree cutting, forest burning, and livestock grazing accelerated wind erosion and sand movement of the area. Finally, the catastrophic hurricane of 1899 almost denuded the whole island. The present geomorphological status of the island is thus the end product of a combination of both natural and man-caused havoc. Ominously, human activities on Shackleford Bank are more likely to increase than subside in the future.

Climate

Under the amelioration of the ocean and the nearby Gulf Stream, the general climate of Shackleford Bank is warmer than inland areas. Snow is a rare event on the island, occurring on an average only once in 2-3 years; a monthly mean minimum temperature never drops below 4°C. Only in 5 months, from November to March, does the lowest temperature occasionally drop below the freezing point. Engels (1952) found that the frost-free season is more than 8 weeks longer at Beaufort than at Rockingham, which is located about 120 miles inland at about the same latitude and has an elevation of only 210 ft. There is no lack of water supply as indicated by the annual precipitation of 129 cm and no prolonged drought period as shown by the even distribution of 103 rainy days per year. Therefore, the general climate of the island is quite favorable for plant growth. Consequently, such a mild oceanic climate ought to be considered as a factor in determining the species composition on the island.

In regard to the microclimate of the dune environment, the temperature and humidity conditions are quite extreme for plant growth. In summer, the temperature on the surface of bare sand usually reaches 51-52°C. Even inside a white shelter, the temperature still reaches 35°C for 8 weeks and 30°C for 13 more weeks during the summer period. In addition, the plants growing in such an environment must be prepared to endure a temperature fluctuation with an amplitude of 20°C in a week or even in a day. At the same time, the vapor pressure deficit can be as high as 15 mm Hg in the atmosphere. Under high air temperature, constant air turbulance due to sea breezes, and a high vapor pressure deficit in the air, dune plants growing on the island are subject to high evaporative stress on a summer day.

Wind and Salt Spray

The wind regime of Shackleford Bank is characterized by a predominant southwest wind in summer. Such oceanic wind is heavily loaded with salt spray (Pl. I-3), and after blowing over beach and fore dunes is loaded with fine sand particles. The salt- and sand-laden wind thus becomes a particularly important environmental factor for maritime vegetation. As early as the turn of the century, Shreve (1910) suggested that salt wind rather than salt soil is the factor most detrimental to the maritime vegetation. Wells and Shunk (1937, 1938) emphasized the toxic effect of salt spray on the buds and young leaves of the woody species. Oosting and Billings (1942), Oosting (1945), Boyce (1954), and Numata et al. (1948) demonstrated, with both field measurements and control experiments, the harmful effects of salt spray on plant growth. Since a salt-laden southwest wind prevails on the island at the time of fast plant growth, salt spray rather than desiccation probably is the chief fatal factor in the death of young tissues (Pl. III-19) of susceptible species. However, Davis (1942) suggested that the dehydration effect of wind due to excessive transpiration may be more important in the south (Florida) to the formation of flag-form trees.

Oosting and Billings (1942) observed a correlation between intensity of salt spray and zonation of dune grasses. Martin (1959) suspected that it is difficult to distinguish between the effects on plants of flying sand particles and salt spray because both are carried by the wind and the zonation pattern of dune grasses may also be due to the amount of sand deposition. The evidence of dune bluestem at the mid-section of Bogue Banks, immediately on the back of the high fore dunes facing the open ocean, may clarify such doubt. Since the deposition of sand is largely at the back of the fore dunes while the intensity of salt spray is drastically reduced on the leeward side of the fore dunes (Oosting and Billings 1942), sand deposition should be disregarded as the chief limiting factor. The zonation of dune grasses is thus determined mainly by the intensity of salt spray. However, the extent of salt spray affecting the characteristics of maritime forest is still open to discussion.

Strong wind may cause mechanical injury such as the frequently observed broken branches and defoliation of woody species. Sand blasting also injures plant leaves (Cowles 1899; Purer 1936), which in turn become vulnerable to salt spray (Boyce 1954). The silvery colored "ghost trees" on the island often reach a height of 15 ft (5 m). This distinctive color is the polishing work of sand blasting, intensive sunlight, heat, and possibly salt spray. The height of "ghost trees" thus may serve as an indication of the height that sand blasting can reach. Doutt (1941) stated that salt, ice, and sand carried by wind, together with the drying effect of wind, produce the sheared effect on trees.

The maximum wind velocity of at least 40 mph has been recorded in every month, and the monthly average is also rather high during a whole year. Violent wind is able to produce "blow-outs" or at least cause sand movement on the dunes. Salisbury (1952) stated that a wind velocity of only about 1 mile an hour is necessary to make grains of 0.25-mm diameter begin to move along the surface. As the present measurements along the dune transect demonstrated, a detectable amount of change in the dune profile has taken place in a year in the form of sand deflation on the windward slope and deposition on the leeward slope of the dunes. Also, the amount of change is very much a function of the vegetational cover. Nevertheless, the change is relatively small, no more than an average of 20 cm/yr. Ranwell (1958) reported sand accretion up to 2-3 ft/year on lee slopes and sand erosion up to 3-4 ft/year on windward slopes in the most mobile dune regions of Newborough Warren, England. However, extensive sand movement may be caused by erratic hurricanes or wind storms and it is therefore possible that the original vegetation will be buried or destroyed by encroaching sand, as evidenced by the present "ghost trees" standing on the island (Pl. I-6). Moreover, wind causes an unstable substratum which is unsuitable for the growth of some species. Hence, Willis et al. (1959a, b) regarded wind and sand movement as the most important factors of the dune environment in England.

In contrast to Lewis' (1917) estimation of 4-12 ft/year sand movement on the island, the present study at the back of the sand wall shows no measurable sand encroachment upon the forest in a normal year. Cowles' (1899) similar measurements on Lake Michigan dunes showed that a rapidly advancing lee slope of the rear dune covered up a 1-m stake in a year; Ranwell (1958) detected the sand encroachment at a rate of 5-22 ft/year in England. Apparently, in the absence of a catastrophic hurricane, the overall sand encroachment upon the forest on the island has largely subsided and dunes are not an imminent threat to the remnant forest.

The wind velocity on the island by no means subsides in winter, though its duration and frequency are reduced. Consequently, winter gales may cause sea-water erosion on the beach, flooding to the strand, and acceleration of sand movement which in time will cause weakening of the vegetational cover on the dunes. Northerly winds have been undercutting maritime forest on the sound side of the island in winter (Pl. III-22). Nobuhara et al. (1962) stated that wind-borne salt spray, mechanical action of the wind, the invasion of sea water, and sand movement caused by winds inflict damage to coastal vegetation in Japan. They (Nobuhara and Toyohara 1964) considered sand movement and wave erosion to be the most important factors of the strand vegetation. As shown in the present study, their statements also hold true for Shackleford Bank.

It seems that apart from the manifold effects of wind on the coastal vegetation, wind-borne salt spray is the most important factor in summer, while sand movement replaces salt spray as the most active factor in winter. During the winter, herbaceous plants are either dormant or dead and thus nothing can prevent the movement of sand.

Of all physical environmental factors influencing coastal vegetation, wind seems to be the most important. Its profound impact on vegetation can be summarized as follows: (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.

Edaphic Factors

The soils of Shackleford Bank have been developed from medium to coarse siliceous sands containing various amounts of shell fragments. The size of sand particles and the quantity of shell fragments depend on the closeness to the Atlantic Ocean, as a result of the sorting effect of the onshore wind (Pl. I-5). Hence, the soil on the fore dunes has the highest proportion of coarse sand and highest percentage of shell fragments. Due to their sandy nature, water contents of all soils at 1/3 and 15 atm are generally low, averaging 1-6% of oven-dry weight at 1/3 atm and 0.2-2.2% of oven-dry weight at 15 atm. Although measurements of available water in soils are low in percentage (0.8-4.2%) of oven-dry weight due to high permeability and low water-holding capacity of sandy soil, there is no real lack of moisture in the subsurface layers of the dunes. In places, the water table approaches the ground surface at a depth of only 60 cm. This phenomenon was first recognized by Cowles (1899) and Kearney (1900) and later by Olsson-Seffer (1909b) and Conard (1935). Also, the available water in sandy soil is higher than shown by the data because of the higher bulk density of sand. The percentage of water content will be higher if it is expressed on a volumetric basis. Moreover, sand particles do not hold soil water as firmly as fine clay particles, i.e., the matrix potential of sand is higher than that of clay.

Measurements of water content in soil profiles show a rapid downward movement of rainwater in such well-drained sandy soils over a period of time. Only 3 days after rain, the distribution of soil moisture in the soil profile becomes almost the same as the soil profile after a long period (2 weeks) of drought. The surface layer of dune soil drys quickly after rain and is unsuitable for plant growth. However, the dry surface layer acts as a mulch and substantially reduces evaporation of soil water of subsurface layers.

There is a general increase in soil moisture as the soil progresses to maturity, probably due to the accumulation of humus. Kearney (1904) recognized that the strand plants are not true halophytes on the low salinity beach soil. The same conclusion can be drawn from the present study which shows the salinity of soil solution in a range of merely 10^{-4} N. Similar results have been obtained by Olsson-Seffer (1909a), Kelly (1925), Davis (1942), and Oosting and Billings (1942) in the United States; Robertson and Gimingham (1951) and

Gorham (1958) in England; and Tsuda (1961) in Japan. The salt in soil apparently comes from the wind-borne salt spray which is carried downward through the soil by rainwater. The continuous leaching by rainwater results in little salt accumulation in soil. Though tidal fluctuation of the water table occurs in foreshore regions, Ranwell (1958) found no penetration of sea water beneath the coastal dunes in England.

Soil chemical analysis shows that soil reaction changes from alkaline to acid and the organic matter increases in relation to distance from the ocean shore. Salisbury (1922, 1925) explained the cause of this trend as progressive leaching of the carbonates and progressive increase in the organic matter with increasing age of the vegetation. Much the same pattern is shown in data obtained by Kelly (1925) and Davis (1942) in the United States; Gooding (1947) in British West Indies; and Wilson (1960), Ranwell (1959), and Etherington (1967) in England. Olson (1958) and Scott (1965) concluded that plant succession is dependent basically on the accumulation of humus in the soil from dead plant remains. Webley et al. (1952) found a close association between the development of the soil microflora and the progress of vegetational succession. However, the development of the sandy soil progresses very slowly. Even under mature live oak forest, the distinction of horizons is vague in a poorly differentiated soil profile (Bourdeau and Oosting 1959). Wright (1955, 1956) also observed, in England, no measurable effect of trees on the mechanical composition of the sand, apart from the deposition of litter and humus.

The organic materials in soils range from an extreme low of 0.01% at fore dunes to as high as 5% in the top soil under mature live oak forest. The same trend occurs as regard to nitrogen and phosphorus. Apparently, soil fertility may be an important factor in determining the species composition on the dunes. On the other hand, soil fertility will not be a limiting factor in maritime forest. A comparison of maritime dune soil and Carolinian Sandhills soil reveals that they are similar in many aspects except for a higher calcium and magnesium constituent in the maritime dune soil. Maritime dune soil has a little higher sodium content than inland soil due to the continuous supply from wind-borne salt spray. However, the amount of potassium in maritime dune soil is not much different from inland soil. Some Sandhills soil could have been of submarine origin, but after thousands of years of leaching, both calcium and magnesium have been reduced to the point of nearly complete depletion.

Two pieces of evidence may help to explain the importance of such a difference between maritime sandy soil and inland Sandhills soil. A small area behind Front Street in Beaufort not far from the ocean is possibly a relict of Sandhills soil on which turkey oak *(Quercus laevis),* black jack oak *(Q. marilandica),* and wire grass *(Aristida stricta)* grow. The surrounding areas are occupied by maritime forest. Such an island of Sandhills vegetation can only be explained on the basis of edaphic conditions. Another example is red cedar which grows in the mountains and piedmont areas, but not in the Sandhills and coastal plain (except a few planted for decoration). It reappears along the coast as a major component of maritime forest. Sometimes it even grows on a little brackish substratum or at the fringe of beach with sea water only a meter away at high tide. From leaf analyses, red cedar shows a higher calcium content (0.35% by oven-dry weight) than either live oak (0.05%) or sea oats (0.01%). Coile (1937) found a higher calcium content (2.2% by oven-dry weight) in undecomposed litter of red cedar than those of pines and oaks in Piedmont, N.C. Under the influence of calcium, the litter of red cedar has reaction of about pH 6.0, whereas the litter of pines and oaks has a very acid reaction (pH 4.1). It is possible that a certain amount of calcium is essential for the growth of red cedar; if less than the required minimum quantity is available, the growth of the species may be retarded. Edaphic factors, possibly the richness in calcium and magnesium, may act as compensatory factors to red cedar on the coast, which would explain the disjunct distribution of the species.

Topography

The importance of topography lies in its indirect effects on the gradient of other environmental factors: mainly, soil water content; distance to the water table; exposure to wind; intensity of salt spray; and amount of sand movement. On grassy dunes the water table usually approaches the ground surface at dune trough, where consequently many mesophytic to hydrophytic species grow. In maritime forest, a depressed area frequently becomes an intraforest fresh-water marsh, or at least a wet thicket. In contrast, dry thicket develops from places higher than surrounding areas. The effects of topography on the intensity of salt spray and sand movement have previously been discussed in detail. Temperature and light may also be modified directly or indirectly to some extent. In short, the topography modifies the microenvironments of the organisms. A moist, well-protected area is always a better place for plant succession. Willis et al. (1959a) suggested that the zonation of coastal vegetation in England closely reflects differences in shelter and accessibility of available water.

Plant Adaptation

Most of the anatomical work on strand plants was done early in the century by Kearney (1900), Chrysler (1904), Harshberger (1908, 1909), Starr (1912), and later by Purer (1936). Their general findings can be summarized as follows. Morphological adaptations of dune plants include reduction in plant size; dwarf, prostrate, or creeping growth form; massive root system or rhizome; and smaller leaves. Xerophytic adaptations in leaf structure include dense hair, heavy wax, or cutinization on the epidermal surface; thick and multiple epidermal layers; stomata in depressions; the presence of palisade tissue both under upper and lower epidermis; increasing number of palisade layers; and succulent or latex-bearing structure. They regarded such xeromorphic structure as a means of adaptation to reduce transpiration. The same idea was expressed by Bowman (1918), Martin and Clements (1939), and Davis (1942).

Maximov (1931) defined xerophytes as dry-habitat plants, with transpiration reduced to a minimum in time of drought and an ability to endure desiccation. From the foregoing soil analyses, soil salinity and soil water content should be discounted as causes of a xerophytic environment on Shackleford Bank. Since there is always a supra-optimal water supply in the subsurface layers of the soil, the structural adaptations appear to be mainly connected with atmospheric stress upon the leaves. The high vapor pressure deficit in the atmosphere coupled with constant wind in summer provides an extremely arid condition in the air for plants. The author is inclined to agree with Kearney (1900) and Olsson-Seffer (1908) that strong wind, intensive light, and great heat are the three physical environmental factors which tend to accelerate transpiration and thus cause xeromorphic characteristics in strand plants. Water deficiency occurs in plants when the rate of transpiration (loss through leaves) far exceeds the rate of absorption (uptake through roots). Consequently, the plant develops xeromorphic characteristics on its above-ground portion not because of soil-dryness, but rather, air dryness.

Root systems of strand plants do not have to extend as deep as those of desert plants because there is always adequate water in the soil not far below the surface. Though dune species showed a mild drought resistance in the control experiment, the measurements of water potential indicate that herbaceous dune species do not develop as high water stress in leaves as those of xerophytes in deserts (down to −80 atm, Scholander et al. 1965) or halophytes (−25 to −75 atm, Yabe et al. 1965; −35 to −60 atm, Scholander et al. 1965). On the contrary, the lowest water potential accounted in the afternoon falls in a range from −5 to −15 bars in dune species studied.

The value of leaf water potential measured in the afternoon within a species varies from 3 to 6 bars. Such variation is relatively small as compared with Klepper's (1968) findings that a 7- to 8-bar difference was detected on the same pear trees at one time. Daily measurements of water potential of selected species indicate that the replenishment of water is generally completed overnight. The lower water potential detected among the woody species may be explained in terms of the lag in transporting water from the root through a longer distance to the leaf. Matubara (1965) found that the higher the tree, the lower the water content of the leaf.

Coupin (1900) stated that 1.5% of common salt in soil will kill the nonhalophytic dune plants in France. Kearney (1904) also recognized that dune plants are not true halophytes. Under my treatments of full strength sea water as well as 1:3 diluted sea water, the dune species under study died quickly. Similar results were obtained by Oosting (1945). It seems that species usually found on dunes are not edaphic halophytes after all.

Although dune plants are not true halophytes, their above-ground portion must structurally adapt to wind-borne salt spray and sand blasting due to their proximity to the ocean. Investigations of Oosting and Billings (1942), Oosting (1945), Boyce (1954), Martin (1959), and the present study show that dune species are generally tolerant to salt spray. Sauer (1965) suggested that seashore plants are adapted to tolerate salt spray, sand blast, and other special habitat conditions. In the case of prostrate species such as seaside spurge and seaside pennywort, the plants also are possibly adapted to tolerate high temperature (frequently recorded at 51-52°C on the ground surface in the afternoon), and great fluctuation of diurnal temperatures. The slightly succulent stem with milky latex of spurge and the more or less vertically orientated leaves of water pennywort may serve as a structural and morphological adaptation to such extremes.

Organic matter content of forest soil is rich, whereas that of dune soil is extremely low, especially the nitrogen and phosphorus components. The treatment of complete nutrient solution increases plant growth drastically. However, adding potassium alone does not improve the growth of dune plants. It is clear that low fertility of dune soil may reduce or even limit the growth of dune plants. Boyce (1954) and Willis (1965) both found vigorous growth of dune plants after adding complete nutrients to the sand, though at the expense of becoming more susceptible to salt spray (Boyce 1954). Willis and Yemm (1961) noticed that the deficiency of nitrates and phosphates in dune soil limits the growth of tomato plants. Therefore, competition for meager nutrition in the soil may explain to some degree the open vegetation in the dune environments.

Dune plants must have the ability to survive under sand (the result of sand deposition) or partial root exposure (the result of sand erosion) because of the inevitable sand movement in a dune environment. Wagner (1964) demonstrated that moderate sand deposition stimulates the growth of sea oats and that its massive branching roots (Pl. I-4) firmly hold considerable amounts of sand. It is no wonder that sea oats make up 90% of the vegetational cover on the unstable dunes on Shackleford Bank. The stimulative effect of sand deposition on dune grasses also is reported by Farrow (1919), Greig-Smith et al. (1947), and Gemmell et al. (1953) in England, and by Laing (1958) on inland dunes in the United States. Finally, seeds of dune plants also have to germinate and send down a root quickly and deep enough to reach the moist subsurface soil. Under the condition of deep burying, young seedlings must also be able to grow out into the light.

Wells and Shunk (1938) explained the almost complete absence from the spray zone of inland species such as turkey oak, wire grass, longleaf pine *(Pinus palustris),* and persimmon *(Diospyros virginiana)* by their susceptibility to salt spray. Wells (1939) named the live oak-dominated forest as the "salt spray climax" and attributed this to the greater salt tolerance of the species. In my opinion, salt spray may kill intolerant trees which openly face the ocean. However, it is difficult to conceive that salt spray can penetrate very deeply into the maritime forest. Persimmon and another inland species—flowering dogwood—are quite common and thoroughly mixed with live oak inside the maritime forest on Shackleford Bank.

As mentioned earlier, an island of Sandhills vegetation surrounded by maritime forest makes it impossible to explain the absence of these Sandhills species on the Banks solely on the basis of salt spray, without a consideration of edaphic factors. Furthermore, turkey oak and longleaf pine can be found within 0.25-0.50 mile (400-800 m) of the ocean at Southport, N.C. At that location, no Outer Banks exist and the strand vegetation develops directly on the fringe of the mainland. A comparison among the maps of live oak distribution, late Pleistocene deposition, and 20°F isothermal line of average annual minimum temperature (Fig. 13) shows remarkable resemblance. In addition to the possible geologic or edaphic effects on the distribution of the species, the lower limit of temperature may possibly be another effective factor. The extension of live oak up to the southern Virginia coast may be attributed to the amelioration of the Gulf Stream on the coastal climate. Therefore, salt spray, edaphic conditions, and temperature may be important in determining the distribution of live oak.

Conclusions

Cain (1944) stated that it is erroneous to single out one factor as limiting and forget the others. The present study shows that no single factor can explain satisfactorily the occurrence of the coastal vegetation. Actually, it is difficult to evaluate accurately the relative importance of different factors to the vegetation or to give preference to one factor. Numerous distinctive factors are operating on the Outer Banks. For example, a milder climate prevailing on the Banks may affect the species composition of the maritime forest, especially when closely allied with edaphic factors. On the other hand, the extreme dune environments require specially adapted species.

Although a great deal of similarity exists between coastal dunes and inland dunes, such as high light intensity, high evaporative stress in the air, excellent drainage, and shifting sand,

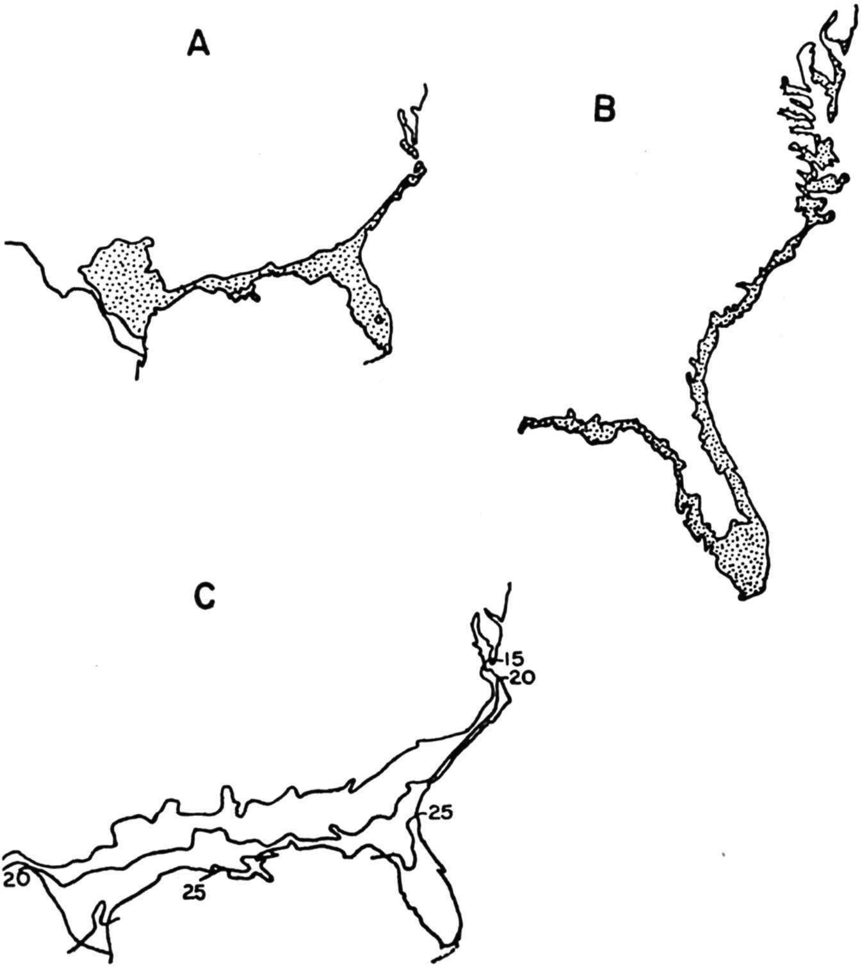

Fig. 13. (A) Distribution of live oak (adapted from USDA Agriculture Handbook No. 271, 1965); (B) Pamlico shore line (adapted from Richards, 1950); (C) Average annual minimum temperature (°F) (adapted from USDA Yearbook, 1941).

the prevailing southeastern sea breeze loaded with salt spray becomes an extremely important factor for the sand strand plants. Moreover, coastal dune soils contain a higher amount of calcium and magnesium than do the inland sands. The instability of coastal habitats is augmented by the occasional, unpredictable, and catastrophic hurricane. Sea water erosion and invasion created by winter storms are also special factors pertaining to the strand vegetation. Consequently, the species composition of the coastal dunes is almost completely different from that of inland dunes.

A diversified maritime vegetation with a rich flora on Shackleford Bank is due to the existence of diversified habitats. Each vegetation type is determined by a combination of a few critical environmental factors which produce a specific habitat. A single factor may be predominant at a certain time and space. For examples, salt spray exerts a limiting effect on the strand plants within a short distance from the ocean; and the leaching of calcium and magnesium through time also modifies the chemical properties of coastal soils, which in turn affects the vegetation. Time and space are considered by Billings (1952) as four dimensions of the holocoenotic environment.

As a result of this study, I consider wind, soil, and topography to be the most important factors in the maritime environment. Wind influences the vegetation, salt spray, sand blast, sand movement, and wave erosion directly; but it also indirectly affects temperature and humidity in the atmosphere. The effects of topography on other environmental factors are always indirect (Billings 1952). Edaphic factors, mainly the chemical properties of the soil, are emphasized here for determining the characteristics of maritime forest.

As a whole, maritime vegetation on the island is determined by the interactions of edaphic, biotic, topographic, and environmental factors, as well as the interactions among the organisms themselves. There are interrelated, simultaneous, and compensative effects which cannot be dealt with separately. The maritime vegetation, without exception, is also a biotic expression of the holocoenotic environment.

Conservation

Due to its relative isolation and lack of permanent residents, though after intensive devastation caused by both men and hurricanes, Shackleford Bank still possesses a relatively rich flora and sufficient diversified habitats to make the island scientifically most interesting. It is an irreplaceable remnant of the maritime vegetation of the Atlantic Outer Banks. The isolation which has spared the island for the past 6 decades now is challenged again by man.

The National Park Service is planning to acquire the island as a part of the Cape Lookout National Seashore. Fortunately, an earlier proposal to build a causeway connecting the island to the mainland at Beaufort has been dropped. Nonetheless, such a threat may be revived in the future. Iltis (1967) warns us that we "need to keep watch of a major trend in national and state parks in this country which can have disastrous consequences; namely, the efforts, under tremendous pressure from the public and from vested interests, to turn these into giant amusement parks and picnic grounds."

For years, concerned ecologists have attempted to preserve representative ecosystems for experimental research at a time when human population and activity expands in an unrestrained way. Oosting (1954), in his gloomy prediction of such expansion, said, "Dunes have been leveled, vegetation has been destroyed, and roads have been built, and this goes on at an accelerated rate from year to year. Each time a new causeway makes accessible another island, it dooms another segment of the natural vegetation." The active dunes, the rich maritime forest, and the productive salt marsh on Shackleford Bank are extremely valuable for ecological and physiographic studies. Adding to its isolation and small size, the island is a unique ecosystem for scientific investigations and should be set aside as an example of the natural ecosystem of the Outer Banks for the benefit of generations to come—generations who have no voice in present decisions. Shackleford Bank unquestionably is one of those precious natural features. One thing is certain: a few days of bulldozing is enough to destroy the vegetation produced in centuries, and we may lose such prime vegetation forever.

Appendix I

CHECKLIST OF PLANTS ON SHACKLEFORD BANK

Macrolichens

Cladonia bacillaris (Ach.) Nyl.[1]
Cladonia coniocraea (Flörke) Spreng.
Cladonia cristatella Tuck.
Cladonia evansii Abb.
Cladonia leporine Fr. ex Tuck.
Cladonia parasitica (Hoffm.) Hoffm.
Cladonia subcariosa Nyl.
Cladonia subtenius (Abb.) Evans
Collema subfurvum (Müll. Arg.) Degel.[1]
Dirinaria aegialita (Ach.) Moore
Leptogium cyanescens (Pers.) Körb.[1]
Leptogium phyllocarpum (Pers.) Mont.
Parmelia dominicana Vain.
Parmelia perforata (Jacq.) Ach.
Parmelia reticulata Tayl. in Mack.
Parmelia rudecta Ach.
Parmelia tinctorum Nyl.
Physcia albicans (Pers.) Thoms.
Physcia tribacoides Nyl.
Ramalina willeyi Howe.
Teloschistes flavicans (Sw.) Norm.
Usnea strigosa (Ach.) A. Eat.

BRYOPHYTA

HEPATICAE

Frullania eboracensis Goffsche
Leujeunea flava (Sw.) Nees.

Musci

Amblystegium serpens (Hedw.) B.S.G.
Campylium chrysophyllum (Brid.) J. Lange
Ceratodon purpureus (Hedw.) Brid.
Clasmatodon parvulus (Hampe) Hook. & Wils. ex Sull.
Cicranum scoparium Hedw.

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[1]collected by Martyn Dibben

Dicranum sabuletorum Ren. & Card.
Entodon cladorrhizans (Hedw.) C. Müll
Entodon seductrix (Hedw.) C. Müll.
Isopterygium micans (Sw.) Broth.
Leucodon julaceus (Hedw.) Sull.
Rhynchostegium serrulatum (Hedw.) Jaeg. & Sauerb.
Sematophyllum adnatum (Michx.) Britt.
Thelia lescurii Sull.
Tortella humilis (Hedw.) Jonn.

PTERIDOPHYTA

OSMUNDACEAE
Osmunda regalis var. *spectabilis* (Willd.) Gray (Royal fern)
PTERIDACEAE
Pteridium aquilinum (L.) Kuhn (Bracken fern)
ASPIDIACEAE
Thelypteris palustris Schott (Marsh fern)
BLECHNACEAE
Anchistea virginica (L.) Presl (Virginia chain fern)
ASPLENIACEAE
Asplenium platyneuron (L.) Oakes (Ebony spleenwort)
POLYPODIACEAE
Polypodium polypodioides (L.) Watt (Resurrection fern)

GYMNOSPERMAE

PINACEAE
Pinus taeda L. (Loblolly pine)
CUPRESSACEAE
Juniperus virginiana L. (Red cedar)

ANGIOSPERMAE

Monocotyledons

TYPHACEAE
Typha latifolia L. (Common cattail)
ZOSTERACEAE
Zostera marina L (Eel-grass)
JUNCAGINACEAE
A. *Triglochin striata* R. & P. (Arrow grass)
ALISMATACEAE
Sagittaria falcata Pursh (Arrow-head)
Sagittaria latifolia Willd. (Duck potato)

POACEAE (GRAMINEAE)
B. *Andropogon littoralis* Nash (Dune bluestem)
Andropogon virginicus L. (Broom sedge)
Cenchrus tribuloides L. (Sandspur, sandbur)
Chloris petraea Swartz (Finger grass)
Cynodon dactylon (L.) Pers. (Bermuda grass)
Digitaria filiformis (L.) Koel. (Crab grass)
Digitaria anguinalis (L.) Scop. (Crab grass)
Distichlis spicata (L.) Greene (Salt grass)
Echinochloa crusgalli (L.) Beauv. (Barnyard grass)
Echinochloa walteri (Pursh) Heller. (Walter's barnyard grass)
Elymus virginicus L. (Wild rye grass)
Eragrostis elliottii S. Wats. (Love grass)
Festuca myuros L. (Fescue)
W. *Festuca octoflora* Walt. (Fescue)
Festuca rubra L. (Fescue)
Melica mutica Walt. (Melic grass)
Muhlenbergia capillaris (Lam.) Trin. (Purple muhly)
Oplismenus setarius (Lam.) Room. & Schult.
Panicum anceps Michx. (Beaked panic grass)
Panicum anceps var. *rhizomatum* (Hitchc. & Chase) Fern
Panicum commutatum Schult. (Panic grass)
Panicum lancearium Trin. (Panic grass)
Panicum sphaerocarpon Ell. (Panic grass)
Panicum spretum Schult. (Panic grass)
Panicum virgatum L. (Switch grass)
F. *Panicum virgatum* var. *cubense* Griseb. (Panic grass)
Paspalum distichum L. (Paspalum)
Paspalum floridanum Michx. (Paspalum)
W. *Paspalum laeve* Michx. (Paspalum)
Paspalum setaceum Michx. (Paspalum)
Paspalum vaginatum Swartz (Smooth-knotgrass)
Phalaris caroliniana Walt. (Canary grass)
Poa annua L. (Blue grass)
Poa pratensis L. (Blue grass)
Polypogon monospeliensis (L.) Desf. (Rabbitfoot grass)
Sacciolepis striata (L.) Nash
Setaria geniculata (Lam.) Beauv. (Foxtail grass)
Setaria glauca (L.) Beauv. (Foxtail grass)
A. *Setaria magna* Griseb. (Foxtail grass)
Sorghastrum olliottii (Mohr) Nash (Indian grass)
Spartina alterniflora Loisel. (Salt marsh cordgrass)
Spartina patens (Ait.) Muhl. (Salt meadow cordgrass)
Sphenopholis obtusata (Michx.) Scribn. (Wedge grass)
Sporobolus poiretii (R. & S.) Hitchc. (Smut grass)
Stipa avenacea L. (Needle grass)
Tridens flavus (L.) Hitchc. (Red-top)
Triplasis purpurea (Walt.) Chapm. (Purple sand grass)
W. *Trisetum pennsylvanicum* (L.) Beauv.
Uniola laxa (L.) B.S.P. (Spike grass)
Uniola paniculata L. (Sea oats)

CYPERACEAE

A. *Bulbostylis stenophylla* (Ell.) Clarke
Carex alate Torr. (Sedge)
F. *Carex nigromarginata* var *floridana* (Schwein.) Kukenth.
Cladium jamaicense Crantz (Saw grass)
Cyperus filicinus Vahl. (Cyperus)
Cyperus flavescens L. (Cyperus)
Cyperus globulosus Aubl. (Cyperus)
A. *Cyperus haspan* L. (Cyperus)
Cyperus odoratus L. (Cyperus)
Cyperus polystachyos var. *texensis* (Torr.) Fern. (Cyperus)
Cyperus retrorsus Chapm. (Cyperus)
Cyperus strigosus L. (Cyperus)
Dichromena colorata (L.) Hitchc. (Whitetop-sedge)
Eleocharis albida Torr. (Spike rush)
A. *Eleocharis fallax* Weath. (Spike rush)
Eleocharis flavescens (Poir.) Urban. (Spike rush)
F. *Fimbristylis caroliniana* (Lam.) Fern.
Fimbristylis castanea (Michx.) Vahl
F. *Fuirena breviseta* Coville (Umbrella grass)
Fuirena squarrosa Michx. (Umbrella grass)
Rhynchospora odorata Griseb. (Beak-rush)

ARECACEAE (PALMAE)

Sabal minor (Jacq.) Pers. (Palmetto)

ARACEAE

Acorus calamus L. (Calamus)

BROMELIACEAE

Tillandsia usneoides L. (Spanish moss)

COMMELINACEAE

Commelina erecta L. (Day flower)

JUNCACEAE

Juncus biflorus Ell. (Rush)
Juncus coriaceus Mackenz. (Rush)
W. *Juncus dichotomus* Ell. (Rush)
Juncus megacephalus M. A. Curtis (Rush)
Juncus roemerianus Scheele (Rush)
Juncus tenuis Willd. (Rush)

LILIACEAE

F. *Nothoscordum bivalve* (L.) Britt. (False-garlic)
Smilax auriculata Walt. (Catbrier)
Smilax bona-nox L. (China brier)
Smilax glauca Walt. (Glaucous-brier)
Smilax laurifolia L. (Bamboo)
Yucca gloriosa L. (Spanish dagger)

IRIDACEAE

Sisyrinchium mucronatum var. *atlanticum* (Bickn.) Ahles (Blue-eyed-grass)

ORCHIDACEAE
Corallorhiza wisteriana Conrad (Coral root)
Spiranthes vernalis Engel & Gray (Nodding ladies'-tresses)

Dicotyledons

SALICACEAE
Populus alba L. (White poplar)
Salix caroliniana Michx. (Swamp willow)
MYRICACEAE
Myrica cerifera L. (Wax myrtle)
BETULACEAE
Carpinus caroliniana Walt. (Ironwood)
FAGACEAE
Quercus phellos L. (Willow oak)
Quercus virginiana Mill. (Live oak)
MORACEAE
Maclura pomifera (Raf.) Schnoid. (Osage-orange)
Morus rubra L. (Red mulberry)
URTICACEAE
Boehmeria cylindrica (L.) Sw. (False-nettle)
A. *Parietaria floridana* Nutt.
Pilea pumila (L.) Gray (Clearweed)
LORANTHACEAE
Phoradendron serotinum (Raf.) M.C. Johnston (Mistletoe)
POLYGONACEAE
Polygonum glaucum Nutt. (Smartweed)
Polygonum lapithifolium L. (Smartweed)
Polygonum punctatum Ell. (Smartweed)
CHENOPODIACEAE
Atriplex arenaria Nutt. (Sea beach orach)
W. *Atriplex patula* L.
Chenopodium ambrosioides L. (Mexican tea)
Salicornia bigelovii Torr. (Dwarf glasswort)
Salicornia virginica L. (Perennial glasswort)
Salsola kali L. (Goosefoot saltwort)
AMARANTHACEAE
Amaranthus pumilus Raf.
A. *Iresine rhizomatosa* Standl.
PHYTOLACACEAE
A. *Phytolacca americana* L. (Pokeweed)
AIZOACEAE
Mollugo verticillata L. (Carpet weed, Indian-chickweed)
CARYOPHYLLACEAE
Arenaria lanuginosa (Michx.) Rohrb. (Sandwort)
Arenaria serpyllifolia L. (Sandwort)
Cerastium glomeratum Thuillier (Mouse-ear chickweed)
Paronychia riparia Chapm.

Silene antirrhina L. (Sleepy-catchfly)
Stellaria media (L.) Cyrill. (Chickweed)
CERATOPHYLLACEAE
Ceratophyllum demorsum L. (Hornwort)
RANUNCULACEAE
A. *Clematis ligustioifolia* Nutt. ex T. & G.
Ranunculus scleratus L. (Buttercup)
MAGNOLIACEAE
Magnolia virginiana L. (Sweet bay)
LAURACEAE
Persea borbonia (L.) Spreng. (Red bay)
BRASSICACEAE (CRUCIFERAE)
Cakile edentula (Bigel.) Hook. (Sea rocket)
Cardamine hirsuta L. (Bitter cress)
Lepidium virginicum L. (Peppergrass)
ROSACEAE
Prunus caroliniana (Mill.) Ait. (Laurel cherry)
Rubus trivialis Michx. (Dew berry)
FABACEAE (LEGUMINOSAE)
Desmodium paniculatum (L.) DC. (Beggar lice)
Desmodium perplexum Schub. (Beggar lice)
Calactia macreei M. A. Curtis
Strophostyles helvola (L.) Ell. (Wild bean)
A. *Strophostyles umbellata* (Muhl. ex Willd.) Britt.
Trifolium dubium Sibth. (Clover)
LINACEAE
Linum virginianum var. *medium* Planch. (Flax)
OXALIDACEAE
F. *Oxalis europaea* Jord.
GERANIACEAE
Geranium carolinianum L. (Cranes bill)
RUTACEAE
Zanthoxylum clava-herculis L. (Hercules'-club)
EUPHORBIACEAE
A. *Acalypha gracilens* Gray (Three-seeded mercury)
Cnidoscolus stimulosus (Michx.) Engelm & Gray
Croton glandulosus L. (Croton)
Croton punctatus Jacq. (Silver-leaf croton, beach tea)
Euphorbia maculata L. (Spurge)
Euphorbia polygonifolia L. (Beach spurge)
ANACARDIACEAE
Rhus copallina L. (Dwarf or winged sumac)
Rhus radicans L. (Poison ivy)
AQUIFOLIACEAE
Ilex glabra (L.) Gray (Gallberry)
Ilex opaca Ait. (American holly)
Ilex vomitoria Ait. (Yaupon)
RHAMNACEAE
Borchemia scandens (Hill) K. Koch (Rattan vine)

VITACEAE
Ampelopsis arborea (L.) Koehne (Pepper vine)
Parthenocissus quinquefolia (L.) Planch. (Virginia creeper)
Vitis aestivalis Michx. (Summer grape)
W. *Vitis labrusca* L. (Grape)
Vitis rotundifolia Michx. (Muscadine grape)
MALVACEAE
Kosteletzkya virginica (L.) Presl (Seashore mallow)
HYPERICACEAE
Hypericum gentianoides (L.) B.S.P. (Pineweed)
Hypericum hypericoides (L.) Grantz (St. Andrew's cross)
W. *Hypericum mutilum* L. (St. John's-wort)
CISTACEAE
Helianthemum corymbosum Michx. (Frostweed)
Helianthemum georgianum Chapm. (Frostweed)
Lechea villosa Ell. (Pin weed)
VIOLACEAE
Viola primulifolia L. (Violet)
PASSIFLORACEAE
Passiflora lutea L. (Yellow-passion-flower)
CACTACEAE
Opuntia drummondii Graham (Fragile prickly pear)
F. *Opuntia humifusa* Raf. (Prickly pear)
LYTHRACEAE
Ammannia teres Raf.
A. *Cuphea carthagensis* (Jacq.) Macbr.
Lythrum lineare L. (Linear-leaved loosestrife)
ONAGRACEAE
Gaura angustifolia Michx.
Ludwigia alata Ell.
Ludwigia martima Harper
Ludwigia microcarpa Michx.
Ludwigia palustris (L.) Ell.
Oenothera humifusa Nutt. (Seabeach evening primrose)
APIACEAE (UMBELLIFERAE)
Centella asiatica (L.) Urban. (Pennywort)
Cicuta maculata L. (Water hemlock)
Hydrocotyle bonariensis Lam. (Seaside pennywort)
Hydrocotyle umbellata L. (Marsh pennywort)
Ptilimnium capillaceum (Michx.) Raf. (Mock bishops weed)
Sanicula canadensis L. (Black snakeroot)
NYSSACEAE
W. *Nyssa sylvatica* Marsh. (Black gum)
CORNACEAE
Cornus florida L. (Flowering dogwood)
Cornus stricta Lam. (Dogwood)
ERICACEAE
Vaccinium atrococcum (Gray) Heller (Blueberry)
PRIMULACEAE
Samolus parviflorus Raf. (Water pimpernel)

PLUMBAGINACEAE
Limonium carolinianum (Walt.) Britt. (Sea lavender)
SAPOTACEAE
Bumelia lyciodes (L.) Pers. (Chittumwood)
EBENACEAE
Diospyros virginiana L. (Persimmon)
OLEACEAE
Osmanthus americanus (L.) Gray (Wild olive)
LOGANIACEAE
A. *Cynoctonum mitreola* (L.) Britt. (Mitterwort)
Gelsemium sempervirens (L.) Ait. f. (Yellow jessamine)
Polypremum procumbens L.
GENTIANACEAE
Sabatia stellaris Pursh (Sea pink, marsh pink)
ASCLEPIADACEAE
Asclepias lancoolata Walt. (Marsh milkweed)
Cynanchum palustre (Pursh) Heller
Matelea suberosa (L.) Shinners
CONVOLVULACEAE
W. *Calystegia sepium* (L.) R. Br.
W. *Cuscuta gronovii* Willd. (Dodder)
Ipomoea sagittata Cav. (Morning glory)
VERBENACEAE
Callicarpa americana L. (Beauty berry, French mulberry)
Lippia nodiflora (L.) Michx. (Capeweed, frogbit)
Verbena scabra Vahl.
LAMIACEAE (LABIATAE)
Lycopus virginicus L.
Monarda punctata L. (Horsemint)
Teucrium canadense L. (Wood sage)
Trichostema dichotomum L. (Blue curls)
SOLANACEAE
F. *Physalis maritima* M. A. Curtis (Ground cherry)
Solanum carolinense L. (Nightshade)
A. *Solanum gracile* Link. (Nightshade)
SCROPHULARIACEAE
Agalinis maritima (Raf.) Raf. (Gerardia)
Aureolaria laevigata (Raf.) Raf.
Bacopa monnieri (L.) Pennell (Water hyssop)
Linaria canadensis (L.) Dum. (Blue toad-flax)
Verbascum thapsus L. (Mullen)
Veronica arvensis L. (Corn speedwell)
PLANTAGINACEAE
Plantago virginica L. (Dwarf plantain)
RUBIACEAE
Diodia teres Walt. (Poorjoe)
Diodia virginiana L. (Buttonweed)
A. *Galium obtusum* Bigel. (Bedstraw)
Galium pilesum Ait. (Bedstraw)
Mitchella repens L. (Partridge berry)

CAPRIFOLIACEAE
Lonicera japonica Thunb. (Japanese-honeysuckle)
VALERIANACEAE
Valerianella radiata (L.) Dufr. (Corn salad)
CUCURBITACEAE
A. *Melothria pendula* L. (Creeping-cucumber)
CAMPANULACEAE
Specularia perfoliata (L.) A. DC. (Venus looking glass)
ASTERACEAE (COMPOSITAE)
A. *Achilloa millofolium* L. (Milfoil)
Aster subulatus Michx. (Aster)
Aster vimineus Lam. (Aster)
Ambrosia artemisiifolia L. (Lesser-ragweed)
Baccharis halimifolia L. (Silverling, sea myrtle)
Bidens bipinnata L. (Spanish needles)
Bidens laevis (L.) B.S.P. (Beggar ticks)
Borrichia frutescens (L.) DC. (Sea ox-eye)
F. *Chrysopsis graminifolia* (Michx.) Ell. (Golden aster)
F. *Cirsium horridulum* Michx. (Yellow thistle)
G. *Conyza canadensis* (L.) Cronq. (Horseweed)
W. *Coreopsis*
Elephantopus nudatus Gray (Elephant's foot)
Elephantopus tomentosus L. (Elephant's foot)
Erechtites hieracifolia (L.) Raf. (Fireweed)
Erigeron quercifolius Lam.
Eupatorium capillifolium (Lam.) Small (Yankee weed)
Eupatorium dubium Willd.
Gaillardia pulchella Foug. (Blanket flower)
Gnaphalium obtusifolium L. (Rabbit tobacco)
Gnaphalium purpureum L. (Cudweed, Indian tobacco)
Gnaphalium purpureum var. *spathulatum* (Lam.) Ahles
Heterotheca subaxillaris (Lam.) Britt. & Rusby (Camphor weed)
Hieracium gronovii L. (Hawkweed)
Iva frutescens L. (Shrubby marsh elder)
Iva imbricata Walt. (Seashore elder)
Krigia virginica (L.) Willd. (Dwarf dandelion)
Lactuca canadensis L. (Wild lettuce)
Lactuca graminifolia Michx. (Button snakeroot)
Mikania scandens (L.) Willd. (Climbing hempweed)
Pluchea footida (L.) B.S.P. (Viscid pluchea)
Pluchea purpurascens (Sw.) DC.
Pluchea rosea Godfrey
Solidago
Solidago sempervirens L. (Goldenrod)
S. *Sonchus asper* (L.) Hill.
Xanthium strumarium L. (Cocklebur)

A. Specimens collected by W. R. Anderson
B. Nomenclature follows H. L. Blomquist (1948)
F. Nomenclature follows M. L. Fernald (1950)
G. Nomenclature follows H. A. Gleason and A. Cronquist (1963)
W. Specimens collected by R. L. Wilbur

Appendix II

SCIENTIFIC AND COMMON NAMES OF PLANTS

Scientific Name	Common Name
Amaranthus pumilus	Seabeach amaranth
Ammophila breviligulata	Beach grass
Ampelopsis arborea	Pepper vine
Andropogon	Beardgrass
A. littoralis	Dune bluestem
A. virginicus	Broom sedge
Aristida stricta	Wire grass
Asplenium platyneuron	Ebony spleenwort
Atriplex arenaria	Sea beach orach
Baccharis	Groundsel tree
B. halimifolia	Silverling, sea myrtle
Bacopa monnieri	Water hyssop
Berchemia scandens	Rattan vine
Bidens bipinnata	Spanish needles
Boehmeria cylindrica	False nettle
Borrichia frutescens	Sea ox-eye
Cakile edentula	Sea rocket
Callicarpa americana	Beauty berry
Carpinus caroliniana	Ironwood
Cenchrus tribuloides	Sandspur, sandbur
Centella asiatica	Pennywort
Chloris petraea	Finger grass
Cicuta maculata	Water hemlock
Cirsium	Common thistle
C. horridulum	Yellow thistle
Cladium	Twig rush
C. jamaicense	Saw grass
Cladonia	Sod lichen
Cnidoscolus stimulosus	Bullnettle
Conyza canadensis	Horseweed
Cornus florida	Flowering dogwood
C. stricta	Dogwood
Croton glandulosus	Croton
C. punctatus	Silver-leaf croton, beach tea
Cyperus filicinus	Cyperus
C. flavescens	
C. globulosus	
C. haspan	
C. ororatus	
C. polystachyos var. *texensis*	
C. retrorsus	
C. strigosus	

Scientific Name	Common Name
Dichromena colorata	Whitetop sedge
Diospyros virginiana	Persimmon
Dictichlis spicata	Salt grass
Eleocharis albida	Spike rush
E. fallax	
E. flavescens	
Elephantopus nudatus	Elephant's foot
E. tomentosa	
Erogeron quercifolius	Fleabane
Euphorbia maculata	Spurge
E. polygonifolia	Seaside spurge, beach spurge
Fimbristylis castanea	
Gaillardia pulchella	Blanket flower
Gnaphalium purpureum	Cudweed
Helianthemum georgianum	Frostweed
H. corymbosum	
Heterotheca subaxillaris	Camphor weed
Hydrocotyle	Water pennywort
H. bonariensis	
Ilex	Holly
I. glabra	Gallberry
I. opaca	American holly
I. vomitoria	Yaupon
Ipomoea sagittata	Morning glory
Iva	Marsh elder
I. frutescens	Shrubby marsh elder
I. imbricata	Seashore elder
Juncus biflorus	Rush
J. coriaceus	
J. dichotomus	
J. megacephalus	
J. roemerianus	
J. tenuis	
Juniperus	Juniper
J. virginiana	Red cedar
Kosteletzkya	Mallow
K. virginica	Seashore mallow
Lepidium virginicum	Peppergrass
Limonium carolinianum	Sea lavender
Lippia	Fogfruit
L. nodiflora	Capeweed

Scientific Name	Common Name
Lopadium leucoxanthum	Wedding ring lichen
Ludwigia	False loosestrife
Magnolia virginiana	Sweet bay
Mikania scandens	Climbing hempweed
Mitchella repens	Partridge berry
Morus rubra	Red mulberry
Muhlenbergia	Muhly
M. capillaris	Hair grass, purple muhly
Myrica cerifera	Wax myrtle
Oenothera	Evening primrose
O. humifusa	Seabeach evening primrose
Opuntia humifusa	Prickly pear
Osmanthus americanus	Wild olive
Panicum commutatum	Panic grass
P. lancearium	
P. sphaerocarpon	
P. spretum	
P. virgatum var. *cubonse*	
Parmelia	Shield lichen
Parthenocissus quinquefolia	Virginia creeper
Paspalum distichum	Paspalum
P. floridanum	
P. laeve	
P. setaceum	
Persea borbonia	Red bay
Phoradendron serotinum	Mistletoe
Physalis maritima	Ground cherry
Physcia	Blister lichen
Pinus palustris	Longleaf pine
P. taeda	Loblolly pine
Pluchea	Marsh fleabane
Polygonum	Knotweed
P. glaucum	Smartweed
P. lapithifolium	
P. punctatum	
Polypodium polypodioides	Resurrection fern
Pteridium aquilinum	Bracken fern
Quercus	Oak
Q. laevis	Turkey oak
Q. marilandica	Black jack oak
Q. phellos	Willow oak
Q. virginiana	Live oak

Scientific Name	Common Name
Ramalina	Twig lichen
Rhus copallina	Dwarf or winged sumac
R. radicans	Poison ivy
Sabal minor	Palmetto
S. palmetto	Cabbage palmetto
Sabatia stellaris	Sea pink, marsh pink
Sagittaria latifolia	Duck potato
Salicornia	Glasswort
S. bigelovii	Dwarf glasswort, dwarf saltwort
S. virginica	Perennial glasswort, perennial saltwort
Salsola	Saltwort
S. kali	Common saltwort, goosefoot saltwort
Samolus parviflorus	Water pimpernel
Scirpus americanus	Chairmaker's rush
Setaria geniculata	Foxtail grass
S. glauca	
S. magna	
Smilax	Greenbrier
S. auriculata	Catbrier
S. bona-nox	China brier
S. laurifolia	Bamboo
Solidago sempervirens	Goldenrod
Spartina alterniflora	Cordgrass, saltwater cordgrass
S. distichlis	Cordgrass
S. patens	Saltmeadow cordgrass
S. spicata	Cordgrass
Spiranthes vernalis	Nodding ladies -tresses
Stipa avenacea	Needle grass
Strophoatyles helvola	Wild bean
Teloschistes	Shore lichen
Tillandsia usneoides	Spanish moss
Triplasis	Sandgrass
Typha	Cattail-flag
T. latifolia	Common cattail
Uniola laxa	Spike grass
U. paniculata	Sea oats
Usnea	Beard lichen
Vitis aestivalis	Summer grape
V. rotundifolia	Muscadine grape
Xanthium echinatum	Sea burdock
Zanthoxylum clava-herculis	Hercules' club

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BEACH OR BARE SAND
WATER
SAND FLAT OR SWALE
YOUNG DUNES
FRESH MARSH
MYRICA-JUNIPER FLAT
DUNES
SALT MARSH
WOODLAND
½ MILE
BACK SOUND
MIDDLE MARSHES
BACK SOUND
BIG SHOAL MARSH
SHACKLEFORD SLUE
SHACKLEFORD SLUE
BEAUFORT INLET
JETTY
BOTTLE RUN PT.
SAM WINTER LUMP
JACKS ISLAND
SHOOTING HAMMOCK
CABS CREEK
WHALE CREEK
BALD HILL BAY
BACK SOUND
COW I.
HORSE PT.
WHITE SHOAL MARSH
JOHNSONS BAY
BUNCH OF HAIR
CONCH SHOAL MARSH
BAREGRASS I.
CEDAR HAMMOCK
MORGAN ISLAND
LIGHTHOUSE CHANNEL
WHITEHURST ISLAND
SHEEP I.
SHEEP ISLAND SLUE
GREAT MARSH ISLAND
LIGHTHOUSE BAY
BLINDS HAMMOCK
BLINDS HAMMOCK BAY
THE DITCH
DAILY SUBMERGED
CORE BANKS
CORE BANKS
ONSLOW BAY
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