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The Vegetative Cover on the Barrier Islands of North Carolina

by

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1. Introduction

Mainland North Carolina is separated from the Atlantic Ocean by a chain of narrow barrier islands. Pea-Hatteras Island alone is nearly 90 km long and averages less than 2 km wide. These barrier islands were formed by accretion of relict sands washed onto the beach from offshore deposits. The present barrier island system is a dynamic one characterized by exchanges of offshore and onshore sand with the direction of transport at any given time or place being a function of wind direction, current pattern, and storm frequency (RIGGS 1976). Gentle onshore waves transport sand toward the beach where it is eventually deposited in the swash zone. During the subsequent falling tide, the freshly deposited sand will dry and can become airborne if wind velocity is sufficient. Windblown sand accumulates as sand dunes. Dunes absorb wave energy and the dune sands may be swept back to sea during severe storms. Alternatively sand may be washed or blown landward and help build the island vertically.

Vegetative communities inhabiting the barrier must face a variety of environmental stresses including: exposure to salt mist, limited fresh-water supply, well drained nutrient poor soils, unstable substrate, burial, and sandblasting. A surprising variety of trees, shrubs, and herbs are able to survive and even flourish in the harsh barrier island environment. Except for the active beach strand, well developed plant communities exist in consecutive zones parallel to the beach. Four vegetation zones can be distinguished in almost any sea to estuary transect of the barrier island. The (1) front beach or strand is exposed to tides and storm waves and supports little vegetative cover. The visual aspect is that of a light colored sand apron gently sloping into blue surf. The upper strand usually ends abruptly at a low scarp formed by the (2) primary dune system. Various grasses clothe these dunes. Landward, the dunes grade into a broad (3) sand flat dominated by other grasses and low shrubs. Finally the back side of the barrier island is separated from the estuary by a band of (4) salt marsh. The front beach, primary dune system, sand flat, and salt marsh are ubiquitous along barrier islands exposed to ocean overwash. However, some segments of the barrier islands are relatively wide (3-5 km) and include relict sand dunes and ridges stabilized by (5) maritime forests of life oak and other trees. Maritime forests usually occur at too great an elevation to be inundated by typical storm tides. However, even these forests are eventually destabilized by the vegetation-killing effects of salt mist and transformed into a plane of migrating dunes. This paper will summarize the floristics and ecological functioning of each of the five floristic zones listed above.

2. Historical changes in vegetative cover of the Barrier Islands

Detailed floristic and ecological studies of North Carolina barrier island vegetation date from the beginning of this century (JOHNSON 1900, KEARNEY 1900, LEWIS 1917, BOYCE 1954, BURK 1961). Therefore, our knowledge of floristic patterns prior to the present century must depend upon oral tradition or casual observations recorded by historians (PRICE 1926) and foresters (PINCHOT and ASHE 1897). DOLAN et al. (1973) have summarized these descriptions and support a majority opinion that these islands have always been sparsely vegetated. BROWN (1948, as cited by DOLAN et al. 1973) suggested that the barrier islands originally supported denser vegetation, but this cover was reduced by grazing cattle and wood cutting following occupation by men of European origin.

The process of landward migration of the barrier islands in response to slowly rising sea level (about 30 cm per century) has only recently been widely recognized (GODFREY 1976, RIGGS 1976). I believe that some of the older accounts of the barrier islands being covered by extensive forest may have been based on the observation of tree stumps and roots exposed along the beach or uncovered by retreating dunes. Such evidence suggested to earlier observers that forests once reached nearly the sea. We now believe that stumps and roots represent maritime forests that were buried under landward migrating dunes only to be subsequently uncovered by the encroaching sea. RIGGS and O'CONNOR (personal communication) have used the carbon-14 dating technique to show that these relict forests were alive some 200 to 900 years ago. They also noted that the pine trees and large red cedars which appear so frequently among the roots and stumps of the relict forest are not particularly salt tolerant. Relict forests exposed on the beach thus document barrier island migration and their ephemeral nature rather than the present of denser forest cover in former times.

While the questions concerning the precolonial vegetation of the barrier islands cannot be answered with certainty because documentation is absent, we do have direct evidence of the changes brought about by construction of an artificial barrier dune ridge. Begun in the 1930's as means of protecting beach development from ocean storms, the dune system, complete with snow fences and planted beach grasses (*Ammophila breviligulata*)(SAVAGE and WOODHOUSE 1969) stretched the entire length of Bodie, Pea-Hatteras, and Ocracoke Islands by the 1950's. SCHROEDER et al. (1976) have documented vegetation changes associated with construction of the artificial dune ridge. Prior to the dune ridge, salt mist drifted across the island and storms periodically swept beach sand across it forming overwash fans which buried existing vegetation. The artificial dune ridge prevented sediment overwash and absorbed much of the salt mist thus encouraging growth of less salt tolerant and slower growing woody plants. Rhizomatous perennial grasses such as *Uniola paniculata*, *Spartina patens*, *Andropogon* spp. and *Muhlenbergia capillaris* became crowded out by perennial evergreen or semi-evergreen shrubs such as *Myrica cerifera*, *Ilex vomitoria*, *Baccharis halimifolia*, and *Juniperus virginiana*. Extensive shrub thickets have developed in interdune swales behind the manmade dune ridge.

What does the future hold? The artificial dune ridge prevented ocean washovers and stopped the flow of blowing sand, both of which are needed for island migration and for the island to remain in equilibrium with rising sealevel. The steepened beach resulting from the dune ridge eroded more rapidly than the former broad natural beach. During the past thirty years the ocean front has moved beyond the original barrier dune throughout most of its length, the dune ridges having to be continuously rebuilt. Much of the 150 km or more of the present dune ridge is in imminent danger of being lost. The National Park Service has finally recognized the futility of trying to permanently hold back the rising sea with a wall of sand and will now financially support massive berm construction or replacement only in a few critical developed areas along the National Seashore.

A sequence of events is presently occurring which will lead to the following scenario: (1) artificial dune ridge will be breached with increasing frequency, (2) shrub thicket vegetation killed as the interdune flats are once again subjected to salt mist and overwash, (3) soil destabilized on sand dunes and in swales once shrubs are dead, (4) massive migration of sand toward the estuary by wind transport of vegetated dunes and renewed ocean washover. This washover may be more severe than it might have been under natural conditions since the island has been deprived of fresh increments of sediment for two to five decades. Barring massive human intervention the barrier islands should rapidly become more dynamic and return to vegetation dominated by rhizomatous grasses rather than perennial evergreen shrubs.

3. Floristic zones

3.1. *Front Beach*

The beach zone is exposed to storm waves and tidal wash and is essentially devoid of rooted plants (Fig. 1). Only one vascular plant is found in significant abundance in this zone. Sea rocket (*Cakile* spp.) is an annual herbaceous member of the cabbage family. Its triangular fleshy (edible) leaves contain abundant water storage mesophyll and its salt resistant seeds become distributed along the high tide drift line. *Cakile* occurs as scattered individual plants or small clones along the upper storm beach and at the toe of the dune line where it functions as a trap for windblown sand. Small dunelets of fine grained sand usually accumulate around these plants.

3.2. *Primary Dune System*

Prior to human intervention the barrier islands presented a low profile and were often exposed to storm overwash and salt mist. These processes continue today on Core Banks and on the numerous small barrier islands south of Bogue Banks; however, the northern barrier islands (mainly within Cape Hatteras National Seashore) have been altered by construction of a barrier dune ridge which prevents ocean washover and retards salt mist transport (Fig. 1). This artificial dune is vegetated primarily by various rhizomatous grasses and is described in the 'Historical Changes' section of this paper.

The unaltered frontal dune system typically consists of scattered low dunes and dunelets from one to three meters in height or, occasionally, a continuous frontal dune up to three meters in elevation. The dune system is typically broken by overwash passes which carry storm tides and sediment onto the sand flats beyond.

HOSIER and CLEARY (1977) have shown that dune fields flattened by major storms undergo a recovery sequence with new dunes beginning to form in response to the growth of *Iva imbricata*, *Uniola paniculata*, and other dune plants. Flat washover terraces are invaded by *Spartina patens*, *Solidago sempervirens*, and several less abundant species. The grasses *Spartina* and *Uniola* extend vegetatively and stabilize freshly deposited sand by means of extensive rhizomes. *Solidago* and *Iva*, both shrubby members of the *Asteraceae*, produce abundant airborne seeds. All of these pioneers, except *Solidago*, are well adapted to burial under blowing sand.

Older dunes are more stable, exhibit greater floristic diversity and have more pronounced zonation. Characteristic plants of the more stable dune, in addition to those mentioned above, often exhibit various xeromorphic adapta-

Figure 1. Beach strand and artificial barrier island dune ridge within Cape Hatteras National Seashore, Ocracoke, North Carolina - June 1979.

This dune was built during the 1950's in order to facilitate construction of the highway and telephone line seen on the right. Shoreline erosion has already removed much of its front side, and continued loss of the dune is inevitable because the National Park Service has adopted a policy opposed to expensive and futile dune maintenance. Soon ocean overwash will destroy the highway and once again provide sediment needed for island migration landward and vertically.

Leaves of eel-grass (*Zostera marina*) form wind rows of drift on the beach. Rhizomatous culms of sea oats (*Uniola paniculata*) stabilize the dune crest and lee slope. Various herbs and shrubs cover broad sand flats currently protected from salt mist by the dune.

tions: succulent stems or leaves (*Opuntia drummondii, Cakile edentula*), extensive taproot or woody rhizome (*Oenothera humifusa, Smilax bona-nox*), pubescent stems or leaves (*Euphorbia polygonifolia, Croton punctatus*), or leathery leaves (*Hydrocotyle bonariensis*). *Fimbristylis spadicea, Rubus trivialis,* and *Parthenocissus quinquefolia* also occur among the more stable dunes.

The functional advantage of these adaptive characteristics is evident when one considers that these plants are exposed to salt mist, sandblasting, shifting substrate, intense insolation and reflection from the light colored sands, and an uncertain freshwater supply. Vegetative cover is often sparse with much bare sand evident. The general aspect is usually one of sandy hummocks covered by grass culms and less conspicuous herbaceous annuals, vines, and compact shrubs.

The beach grasses *Uniola* and/or *Ammophila* are conspicuous elements of the dune cover (WAGNER 1964). Since dune sediments are well leached and nutrient poor, these grasses must obtain most of their mineral nutrients from ocean derived seawater mist. WOODHOUSE and HANES (1966) demonstrated that growth of dune grasses could be stimulated by application of commercial fertilizer. However, this technique is of limited utility in promoting dune stabilization because plants supplied with optimum nutrients become fleshy and more susceptible to salt injury and sandblasting. Earlier BOYCE (1954) had pointed out that dune grasses require suboptimal nutrient concentrations for survival in their natural habitat. A recent suggestion by SENECA (1972) that dune grasses might response to foliar uptake of nutrients (especially nitrogen) was tested by VAN DER VALK (1974) who determined from greenhouse foliar application experiments using artificial sea water, microelements and 1 mg/l nitrate that neither species showed statistically significant increases in height or weight as a result of any of the salt spray treatments. VAN DER VALK concluded that foliar uptake of nutrients would be of little adaptive advantage to dune grasses. Considering the earlier observations by BOYCE (1954), foliar uptake could actually have a negative impact on their survival.

3.3. *Sand flats*

Sand flats typically resemble grassy meadows and, in fact, were used until very recently for grazing cattle, goats, pigs, and horses (Fig. 2). A small herd of 'outer banks ponies' is still maintained by the National Park Service on Ocracoke Island; otherwise roads, power lines, and tourists have replaced

Figure 2. Dune and swale topography of the sand flats on Ocracoke Island, Cape Hatteras National Seashore, North Carolina - June 1979.

Evergreen shrubs (wax myrtle - *Myrica cerifera*) and trees (eastern red cedar - *Juniperus virginiana*) crowd together in a swale between two sand dunes. Swales provide protection from salt mist and a surer supply of fresh water. A single *Juniperus* on the far dune exhibits the pruning effect of salt mist. Vegetative cover of the dunes is sparse and dominated by rhizomatous grasses (sea oats - *Uniola paniculata*, salt meadow cord grass - *Spartina patens*) and low herbs (seaside pennywort - *Hydrocotyle bonariensis*, ground cherry - *Physalis viscosa*).
Since completion of the artificial barrier island dune within Cape Hatteras National Seashore shrubby vegetation has expanded into areas formerly occupied by dune grasses.

grazing herds on the sand flats throughout most of the barrier islands. Along most barrier islands the sand flats are the broadest and highest part of the island and constitute the only land stable enough for locating man's structures.

Sand flats are formed by sediments swept over or through the frontal dune system during ocean storms. From the air, sand flats often appear as a series of fanshaped lobes. Vegetative cover in the sand flats is largely a function of the recovery since the last ocean washover. HOSIER and CLEARY (1977) proposed a model to describe the washover and recovery sequence observed on a barrier island still largely unmodified by human activity (Masonboro Island). Vegetation on well established sand flats is extensive, diverse, and well zoned.

The vegetative cover on well established sand flats at Masonboro Island is dominated by grasses. *Uniola paniculata* is most conspicuous on higher seaward sand flats and intergrades to a dominance by *Spartina patens* nearer the salt marsh. Both of these grasses spread by extensive underground rhizomes and both respond favorably to burial. Their tall clums function as windbreaks and assist in vertical growth of the island by trapping fine sand blown over the dunes from the beach.

Many vines which normally grow as lianas hanging from the canopy in mainland forests also grow well among the shrubs and low dunes where they receive full exposure to the sun. *Rhus radicans*, *Parthenocissus quinquefolia* and *Ampelopsis arborea* form spreading mats. These vines readily survive burial and their creeping stem tips, rooting at the nodes, exploit the limited freshwater supply while simultaneously stabilizing the sand. Similarly herbs within the sand flat also show adaptation to xeric conditions. *Heterotheca subaxillaris* has a perennial taproot and *Erigeron canadensis* spreads rapidly from seed. *Galium hispidulum* is a low spreading perennial as is *Lippia nodifera*. *Lippia* also roots readily at its nodes. *Physalis viscosa* is a rhizomatous perennial.

Low places within the mature sand flats often develop into shrub thickets dominated by the evergreen *Ilex vomitoria*, semi-evergreen *Myrica cerifera*, or deciduous *Iva imbricata* (fig. 2). *Myrica* is of special significance because its roots contain a symbiotic nitrogen fixing actinomycete. Shrubs may grow better at the base of the dunes and along the backside of the sand flat because topographic lows are better protected from salt mist and are more likely to contain freshwater.

In contrast, flats recovering from recent overwash exhibit lower diversity, poor zonation, and sparse vegetative cover. Dominant plants are fast spreading grasses *Triplasis purpurea, Panicum amarum, Uniola paniculata, Spartina patens,* and seed dispersed herbs (HOSIER and CLEARY 1977).
Vegetation of the sand flats on Core Banks has been described by DOLAN et al.

Figure 3. Howard Street in Ocracoke Village, Ocracoke Island, North Carolina - June 1979.

Until quite recently permanent occupation of the barrier islands was restrict- to wider portions of the 'outer banks' where relict sand dunes have become stabilized by maritime forest. The evergreen forest canopy of live oak (*Quercus virginiana*) and yaupon (*Ilex vomitoria*) provides residences with shade and protection from strong winds and the sand ridges usually represent the highest and safest point on the island.
Other canopy trees in this photo include eastern red cedar (*Juniperus virginiana*) and loblolly pine (*Pinus taeda*).

(1973) as sparse along the higher front of overwash terraces. Cover dominance was described as *Spartina patens* and *Solidago* spp. Further back on the terrace, grasses and sedges (*Fimbristylis, Muhlenbergia, Eragrostis,* and *Scirpus*) produced a denser cover. Less frequent overwash produced thickets of *Baccharis halimifolia, Myrica cerifera,* and *Iva frutescens.* Well protected sites produced a compact shrub thicket with a canopy of *Ilex vomitoria, Juniperus virginiana,* and *Quercus virginiana.*

Artificial front barrier dune ridges have never been constructed on Core Banks or on Masonboro Island, thus sand flat vegetation on these two barrier islands probably approaches that typical under natural conditions. The general aspect of mature sand flats is that of grass covered low dunes or overwash terrace grading into shrub thicket in topographic lows and toward the estuary side of the barrier island. Perennial woody and shrubby components indicate relative stability and maturity while rhizomatous grasses, herbs, and vines indicate overwash terraces of more recent origin.

As noted in the section on historical changes the barrier islands encompassed by Cape Hatteras National Seashore (Ocracoke, Hatteras, Pea, and Bodie) are partially developed with roads, transmission lines, and small resort villages. Limited development has been made possible by construction of the barrier dune ridge which has effectively prevented overwash and reduced salt mist transport. Consequently the protected sand flats behind the berm developed toward vegetative maturity in the twenty to fifty years existence of the berm. Shrub thickets and incipient maritime forest now occupy extensive areas of the sand flats formerly dominated by grasses and herbs. This vegetation change is considered undesirable by managers of the Pea Island National Waterfowl Refuge because soft weeds and grasses which form the winter diet of Canada geese, snow geese, ducks, and whistling swans are being replaced by perennial woody shrubs. The refuge staff periodically carry out controlled burns of the shrub thicket in order to maintain adequate waterfowl habitat.

3.4. *Salt Marsh*

Two floristically similar, but geographically separate types of salt marsh occur along North Carolina's estuaries. Marshes occupying the estuary side of barrier islands are typically narrow bands of shallow peat, while marshes bordering the mainland tend to be broader and have a thicker peat accumulation. Because barrier island marshes differ from mainland marshes in origin, structure, and function these two types will be described separately.

Barrier Island Salt Marsh

Sand flats generally taper to a lower and more level profile as they approach the estuary. Shrubs decrease in abundance and the vegetation becomes dominated by a dense cover of grasses, sedges, and rushes. Two general zones are recognized within the marsh (GODFREY 1976). High marsh is irregularly flooded and is characterized by the presence of *Spartina patens, Juncus roemerianus,* and *Distichlis spicata.* Low marsh is regularly flooded at high tide and is characterized by the dominance of *Spartina alterniflora* (Fig. 4).

All of these salt march plants proliferate by means of rhizomes which root at their nodes. Often a single species will account for almost all the vascular plant biomass over extensive areas of marsh. These grasses and grass relatives are very effective in trapping decaying vegetative matter (from the marsh itself and from leaves of *Zostera marina,* a submergent aquatic washed from the estuary bottom) and silt (derived from turbid floodwaters during storms of high tides). These nutrient inputs contribute to the high biological productivity of the salt marsh. Conspicuous marine animals dependent upon the salt marsh include nereid worms, small crabs: fiddler crab (*Uca*), hermit crab (*Pagurus*), wharf crab (*Sesarma*), mollusks: periwinkle snail (*Littorina*), oyster (*Crassostrea*), ribbed mussel (*Modiolus*), and other invertebrates. Food produced by plants and animals within the salt marsh is exported to the estuary via fish and elsewhere via marsh birds (herons, osprey, fish crows, ducks, geese, etc.)

Less conspicuous primary production is accomplished by epiphytic (*Cocconeis, Synedra*) and epipelic (*Achnanthes, Navicula, Nitzschia, Amphora, Pleurosigma, Diploneis,* and others) diatoms. The seaweeds *Codium, Enteromorpha, Ulva, Polysiphonia,* and *Agardhiella* commonly occur among the salt marsh culms at appropriate times of the year.

Barrier island salt marsh usually develops on freshly overwashed sediments by rhizome invasion or fragmentation from adjacent marsh. There is little evidence that North Carolina barrier island salt marshes can spread horizontally simply by culm trapping of estuarine sedimemts or rhizome extension. Almost without exception these marshes exhibit an erosional scarp along their low side bordering the estuary. GODFREY (1976) noted that "although salt marshes can form behind barrier beaches in four ways: invasion of uplands as the sea level rises, sediment buildup from river outflow, ocean overwash, and inlet

Figure 4. Salt marsh along the Pamlico Sound estuary, Ocracoke Island, Cape Hatteras National Seashore, North Carolina - June 1979.

Salt marsh develops on marine sediments swept across the barrier island during major storms. Subsequent growth of cord grass (*Spartina alterniflora*) and other marsh plants may result in accumulations of peat or organic rich mud. Erosion of the accumulated organic matter is an important source of food for estuarine animals, and many of them also depend upon the marsh for habitat and nursery grounds.
The regularly flooded low marsh shown here at high tide presents an irregular shoreline to Pamlico Sound. Marsh islands indicate a general pattern of salt marsh erosion rather than expansion.

dynamics ... the most common (and usually most significant) processes along the East Coast are the latter two."

Marshland is being lost to the estuary through wave erosion even as new marsh is being formed. Continued marsh development requires periodic overwash or inlet migration. Although these marshes lack the ability to spread horizontally, they do grow vertically and in some areas one meter or more of marsh peat may overlie the original estuarine substrate.

The uppermost layer of salt marsh consists of a dense network of living roots and rhizomes. Annual production of grass leaves and stems together with washed-in organic debris, sand and silt, add incrementally to the vertical structure of the marsh. Anaerobic conditions often exist in the saturated zone just beneath the living roots and rhizomes. Annual burial of these rhizomes causes them to sprout at the nodes and grow vertically in phase with mean tide level. This growth pattern allows marsh grasses to maintain a constant relationship to mean sea level and adapt to a rising sea. The previous years' rhizome mat becomes buried and slowly decays until only a few wood fiber strands and the waxy cuticle remain distinguishable. When this condition is reached, after many years of compaction and decay, the upper living layer of marsh is supported by a fibrous cushion of soft peat. Erosion of the marsh occurs at an accelerated rate once the waves begin to cut into this soft underlayer and undermine the living mat. Peat of sufficient depth to exhibit this type of erosion occurs rarely along the barrier island and is usually restricted to well protected sites where the island is wide (i.e. marshes of the Nags Head Woods along Roanoke Sound). Thick marsh peats of the type just described likewise dominate the estuary-salt marsh interface on the mainland. Narrow barrier islands are too mobile and subject to overwash for deep marshes to develop behind them.

Generally the salt marsh peat immediately behind narrow segments of the barrier island is 0.5 m deep or less and contains a much higher sand content than the thicker peat occurring within the estuary. Living roots and rhizomes often comprise more than half of the peat cross section. Erosion in this relatively tough and resistant peat is facilitated by fiddler crabs. These small invertebrates infiltrate the peat with a network of burrows. Burrows exposed along the edge of the estuary widen as water is pumped through them by wave action. Eventually the entire peat face becomes so corroded that irregular pieces break off and wash out into the estuary where they continue to disintegrate and finally become part of the rich organic sediments so productive of polychaete worms, mollusks, infaunal crustaceans and other invertebrates which form the base of the estuarine food web.

Mainland Salt Marsh

Although rare along the barrier islands, thick salt marsh peat occurs generally along some 1500 km of marsh shoreline bordering the mainland side of the estuarine system. In the northern portions of North Carolina estuaries most of this marshland is irregularly flooded high marsh dominated by *Juncus roemerianus*. Biological productivity in *Juncus* marsh has generally been assumed to be lower than that of *Spartina* marsh (WILLIAMS and MURDOCK 1972). It is reasoned that regular flooding of the low *Spartina* marsh is more effective in transferring excess organic matter from the marsh to the estuary than could possibly be the case for high *Juncus* marsh which may be flooded only during major storms. This reasoning is probably correct for the regularly flooded salt marshes of Georgia where most of the work on marsh productivity has been carried out; however, important differences exist between Georgia salt marshes and those of northeastern North Carolina. In Georgia the daily tidal amplitude is greater (> 2 meters) than for North Carolina (< 1 meter). In northern North Carolina the barrier islands are often quite long and are interrupted by only three major inlets. Thus the ocean tides are damped to such an extent that wind tides are of greater significance in the estuaries than astronomical tides. North of Cape Hatteras vast areas of mainland are less than 2 meters above sea level: thus very small rises in water level result in broad lateral inundation. All of these conditions lead to extensive development of *Juncus* marsh rather than *Spartina* marsh as in Georgia where astronomical tidal flooding dominates. The contribution of organic matter from *Juncus* marsh to the estuary will be greatly underestimated if one only measures the amount of organic transport occurring during storms. In fact, under storm conditions, the net transport may be into the marsh. Thick salt marsh peat may approach 3-4 meters in depth and frequently exceeds one meter. The salt marsh-estuary interface is typically a steep scarp or even a concave face in which soft peat is eroded from beneath the rhizomatous living layer at the surface. Given the broad wind fetch of the wide North Carolina estuaries it should be of little surprise to learn that linear loss through shoreline erosion of deep marshland averages 1-1.5 meters annually and may reach 6 meters locally (BELLIS et al. 1975). If we assume a conservative average erosion rate of one meter per year to a depth of one meter multiplied by 1,500,000 meters of salt marsh shoreline gives one and one-half million cubic meters of organic matter contributed annually from the marsh to the estuary. Whereas excess *Spartina* marsh production is exported continuously from the horizontal surfaces of the marsh, *Juncus* production accumulates as thick peat and is contributed as vertical slices of modern and fossil peat (S.B. BENTON, personal communication).

The aspect of the salt marsh is that of a grass prairie. The substrate gradient can be measured in centimeters over many hectares. Uniform stands of even topped grasses extend to the horizon. The vegetation is often so uniform that one tends to overestimate distances. The casual observer sees only monotony and desolation. More careful observation reveals variations. A few shrubs (*Iva frutescens*, *Baccharis halimifolia*, *Myrica cerifera*) or large flowered annuals (*Borrichia frutescens*, *Sabatia stellaris*, *Kosteletskya virginica*, *Hibiscus moscheutos*, *Ipomoea sagittata*) may occur scattered among the grasses.

Patches of waist high *Juncus* may give way suddenly to rounded low growing *Distichlis spicata*. Irregularly lobed or rounded areas of *Distichlis* represent areas where wind rows of loose vegetation drifted during a previous storm. The consequent mulching effect of this mat killed the *Juncus* beneath and the *Distichlis* found a favorable open habitat following decay of the mat. Sometimes decay of the mat results also in decay of the rhizome layer of marsh exposing the soft decayed peat beneath. This peat is below the mean water table and usually anaerobic. Ponds formed in this manner are only slowly revegetated and may become hypersaline by evaporation during the summer.

Head high culms of tall cord grass (*Spartina cynosuroides*) often occur in a narrow band between the eroding marsh face and *Juncus* marsh along marsh coves exposed to heavy storm waves. *Spartina cynosuroides* seems to prefer a slightly higher and better drained site than *Juncus*. Floating vegetation tends to accumulate in marsh coves and is washed over into the marsh during storms forming a natural levee around the marsh. The accumulated drift forms a higher substrate needed by *Spartina*. Once established the robust *Spartina* produces dense tough culms which are effective in catching still more debris. Thus a low self perpetuating organic berm is formed along the top of the eroding marsh face.

A transition zone exists whereever salt marsh backs onto sandy forested soils. Trees cannot remain anchored in the soft substrate of the marsh and the 'canopy' consists of low grasses and shrubs. The substrate in the transition zone consists of water-saturated sandy soil. Brackish water may cover this soil during extreme flood tides. Large trees such as *Pinus taeda* cannot survive the flooding and many dying pine trees and decaying trunks characterize the transition zone. Loss of the pine canopy promotes the growth of evergreen shrubs and understory trees producing a thick wall of *Persea borbonia*, *Ilex vomitoria*, *Juniperus virginiana*, and *Myrica cerifera*. Vines such as *Rhus radicans* and *Smilax* spp. often overgrow the dwarfed trees and shrubs and contribute to the impenetrable thicket appearance of the transition zone. Landward the transition zone grades into pine forest on mineral soils elevated above the water table.

Salt marshes are important components of the barrier island system because they constitute the platform which supports the sandy barrier island for a time during its migration toward the estuary. Salt march productivity and nursery habitat is essential to the estuary.

3.5. *Maritime Forest*

Maritime forests do not occur ubiquitously along the barrier islands as do all of the other vegetation zones described here. Instead they occur infrequently as a stabilizing protective cover on elevated sand dunes or ridges. Some of these geological structures represent recently accreted sands while others are segments of relict beach scarps left by ocean regression during the last glacial advance. Whatever their origin, maritime forest covered dune systems prevent ocean overwash and give unusual breadth to portions of barrier islands. The relative stability of maritime forest, in contrast to the inherent instability of barrier islands generally, was appreciated by earlier inhabitants of the barrier island. Villages such as Corolla, Duck, Nags Head, Buxton, Ocracoke, Portsmouth, and Salter Path were established within the protective canopy of live oaks (*Quercus virginiana*) on the island (Fig. 3). Abundant American Indian shell middens within these forests attest to their earlier use by the former inhabitants of the island. Only during the present century has development beyond the maritime forest been encouraged by the temporary protection offered by artificial dune ridges and a two decade respite from major hurricane activity. Prospective purchasers of beach property might do well to read accounts of the impact of former hurricanes on North Carolina beaches (SNOW 1955).

Several of the earliest studies of North Carolina maritime forests (WELLS and SHUNK 1937, WELLS 1939,and OOSTING 1954) dealt with the controversy as to whether the sheared and dwarfed aspect of maritime forest canopy resulted from substrate characteristics, wind force, evapo-transpiration, or salt mist. Even though all of these reports implicated salt mist as the major factor, the issue was not finally resolved until the detailed field studies and laboratory experiments of BOYCE (1954). Currently it is generally accepted that the sculptured appearance of the maritime forest results from impact of ocean derived salt aerosols onto growing branch tips. Death of the terminal buds releases axillary buds which grow to produce a dense canopy in which all species have a uniform height regardless of their genetic potential.

Although the maritime forest has been characterized floristically on several occasions (WELLS 1939, BROWN 1959, BURK 1962, and BOURDEAU 1959), it has proved difficult to define the maritime forest unambiguously. Most definitions recognize the importance of live oak (*Quercus virginiana*) and other salt tolerant species and suggest that maritime forest extends inland to a point where less salt tolerant species such as *Pinus taeda* become evident. In North Carolina the maritime forest appears to be a variant of the mixed hardwood coastal forest which once covered most of the coastal plain. Some broadleaved deciduous components of the coastal forest such as *Acer rubrum*, *Quercus falcata*, *Q. marylandica*, *Cornus florida*, and *Carya* spp. seem to be excluded by xeric habitat conditions, while evergreen trees and shrubs which normally occur rarely or scattered among the understory have become dominant. Well adapted plants typically exhibit some combination of the following characteristics: evergreen or semi-evergreen, simple coriaceous leaves, aromatic leaves and twigs, oval or elliptic leaves with bristles or entire margins. Floristically important components of the maritime forest which exhibit some or all of these features include: *Quercus virginiana*, *Q. laurifolia*, *Persea borbonia*, *Myrica cerifera*, *Ilex opaca*, *I. vomitoria*, *Osmanthus americana*, *Juniperus virginiana*, and *Smilax laurifolia*.

BOYCE (1954) noted that leaves with entire margins were less likely to concentrate evaporative salt among their edges because they have a lower surface area to circumference ratio than lobed or compound leaves. A coriaceous texture and thick cuticle resist creasing or cracking of the epidermis by high winds and the consequent entry of salt into the mesophyll. At least one maritime forest tree (*Persea borbonia*) apparently has the ability to transport excess salt to leaf tips where 'V-shaped' necrotic zones form and die thus preventing more general defoliation.

Other adaptations to limited freshwater supply, strong winds, salt mist, and low nutrient level are evident in the maritime forest. Mature maritime forest canopy is kept at uniform height by salt mist pruning regardless of the genetic potential of component species. Topmost branches of individual trees are crowded together with little or no branch overlap. From above, the canopy appears as a dense mosaic of irregular pieces displaying various hues of green. Often the leaf layer of the canopy is less than one meter thick. Tree trunks are regularly spaced, lower limbs become leafless, die, and fall off as a result of shading. Upper limbs are heavily branched and consist of clusters of radiating short repeatedly rebranched twigs. The overall aspect is almost that of a thick green net cast over a forest of woody columns.

Most of the sun's heat and light is intercepted or reflected from the canopy such that the open space beneath is usually dark, moist, and cool. The value of this dead air space in reducing evaporative water loss is obvious. Coastal North Carolina receives in excess of 140 cm precipitation annually, mostly in the form of rain. Up to 30 % of the rain falling on the maritime forest is intercepted by the canopy and most of this water is guided down to the base of the tree by the highly branched limbs and/or grooved bark as in *Quercus virginiana*. Soils of the maritime forest consist of well drained relatively dry sand. All freshwater must come from rainfall. Unlike the canopy in which each tree remains as an individual, the root zone of the maritime forest is shallow (typically less then 0.5 meters) and densely interwoven. Thus the leaf area of each tree functions rather like a funnel, directing a high proportion of the rain to its own root system via interception and stemflow. Larger trees within the maritime forest often exhibit dark stained channels on their 'low' side which serve as rain gutters during storm.

Canopy-intercepted water tends to be enriched with ions washed or leached from leaves, Salt derived from salt mist contain sodium, chloride, calcium, magnesium, and other ions. Sodium and chloride are often in sufficient concentration to produce osmotic effects in bud tissues not yet hardened or cutinized. Chloride can become toxic to plants at high concentrations. Calcium and magnesium are much less abundant in sea salt and both are required for plant growth. Measurements of salt movement through the maritime forest on Bogue Banks by PROFFITT (1977) demonstrated that despite annual inputs of 104 $g \cdot m^{-2}$ chloride, 3 $g \cdot m^{-2}$ calcium, and 7 $g \cdot m^{-2}$ magnesium, salt accumulation did not occur in forest soils. Annual rainfall during this study measured 120 cm/year. Apparently excess salts were diluted and rapidly carried below the root zone into sandy dune soils. Chloride and sodium are very soluble and pass readily through the humus layer. Chloride and magnesium are less soluble and may become absorbed on humus by ion exchange thus remaining in contact with feeder roots for a longer period (ART 1974).

The North Carolina barrier islands are influenced by proximity to the Gulf Stream. This ocean current brings warm water from the Caribbean to our near-shore waters and moderates winter temperatures. Evergreen trees and shrubs may gain some advantage over deciduous species unter these conditions.

Dune sands consist of inert silicon dioxide and do not release ions by weathering and oxidation. Soluble ions are rapidly removed by leaching. Thus most minerals at any given time must be part of the existing vegetative biomass. ART (1974) suggested that the maritime dune forest (Sunken Forest in Fire Island, New York) "ecosystem is nearing a steady state and that meteorological inputs (of nutrient elements) balance losses to ground water ... The growth response of the (maritime) forest trees simultaneously adapts the ecosystem to wind-salt conditions and limits further biomass accumulation resulting from upward growth. However, proliferation of branches at the airstream-canopy interface guarantees a large surface area that (absorbs aerosols from the air-stream). Thus there are continual adjustments between the restriction of the system by toxic effects of salt spray and dependence of the system on salt spray as a source of nutrients" (emphasis mine).

An evergreen canopy is important to the process of nutrient cycling because continuous leaf fall resupplies decomposer fungi within the humus. Warm moist winter weather also stimulates both photosynthesis and decomposition at a

Table 1. Alphabetical list of vascular plant taxa listed in this paper together with colloquial name as used in North Carolina. Nomenclature is that of RADFORD et al. (1968).

Acer rubrum	red maple
Ammophila breviligulata	beach grass
Ampelopsis arborea	pepper vine
Andropogon sp.	broom sedge
Baccharis halimifolia	salt myrtle
Borrichia frutescens	sea ox-eye
Cakile edentula	sea rocket
Carya spp.	hickory
Cornus florida	flowering dogwood
Croton punctatus	silver leaf croton
Distichlis spicata	salt grass
Eragrostis sp.	love grass
Erigeron canadensis	horseweed
Euphorbia polygonifolia	dune spurge
Fimbristylis spadicea	fimbristylis
Galium hispidulum	bedstraw
Heterotheca subaxillaris	heterotheca
Hibiscus moscheutos	rose mallow
Hydrocotyle bonariensis	seaside pennywort
Ilex opaca	american holly
I. vomitoria	yaupon
Ipomoea sagittata	ipomoea
Iva imbricata	marsh elder
I. frutescens	marsh elder
Juncus roemerianus	black needle rush
Juniperus virginiana	eastern red cedar
Kosteletskya virginica	saeshore mallow
Lippia nodifera	lippia
Myrica cerifera	wax myrtle
Muhlenbergia capillaris	hair muhly
Oenothera humifusa	evening primrose
Opuntia drummondii	fragile prickley pear cactus
Osmanthus americana	american olive
Panicum amarum	panicgrass
Parthenocissus quinquefolia	virginia creeper
Persea borbonia	red bay
Physalis viscosa	ground cherry
Pinus taeda	loblolly pine
Quercus falcata	southern red oak
Q. laurifolia	laurel oak
Q. marylandica	blackjack oak
Q. virginiana	southern live oak
Rhus radicans	poison ivy
Rubus trivialis	dewberry
Sabatia stellaris	sabatia
Scirpus spp.	bulrush
Smilax bona-nox	greenbrier
S. laurifolia	bamboo
Solidago sempervirens	seaside goldenrod
Spartina alterniflora	cord grass
S. cynosuroides	tall cord grass
S. patens	salt meadow cord grass
Triplasis purpurea	sand grass
Uniola paniculata	sea oats
Zostera marina	eel-grass

time when inland deciduous forests are at their minimum of metabolic activity. Annual net losses of nutrients would occur through mineral dumping if the maritime forests were deciduous.

Recent recognition of the inherent instability and erosion potential of low-land portions of barrier islands by homeowners and subdivision developers has refocused attention toward the maritime forest as a desirable place to build. Almost all of the maritime forest in North Carolina is privately owned and is currently under severe development pressure. Maritime forests stabilize potentially mobile relict sand dunes and the forested dunes are the major reservoir of freshwater for all life on the barrier islands. Removal of vegetative cover for homesites, roads, and parking lots exposes dunes to evaporative water loss and extends the zone of salt mist influence. The loss of the vegetative biomass disrupts the mineral 'steady state'. Extraction of water by shallow wells for human consumption may compete with the vegetation for available freshwater from the freshwater lens. On the other hand, human activity such as drilling of deep wells into aquifers well below the freshwater lens and extensive use of septic tanks for sewage disposal may partially offset mineral and water losses.

Presently our knowledge of the quantitative functional relationships within the maritime forest is inadequate to predict how much additional man-originated stress they can absorb before becoming unstable and losing their grip on the relict dunes. These dunes will surely become active and begin migrating again once they lose their vegetative cover.

Summary

Plant communities of the barrier islands of North Carolina, USA, are described in terms of visual aspect, conspicuous flora and ecological adaptations. Five communities described are front beach strand, primary dune system, sand flats, maritime forest, and salt marsh. All plants within these communities must be able to survive some combination of salt mist, limited availability of freshwater, low nutrient level and rapid nutrient turnover, unstable substrate, burial, and sandblasting. Historical changes in the vegetative cover of the barrier islands are discussed briefly together with some speculations about the near future.

Zusammenfassung

Pflanzengesellschaften der "Barrier Islands" ausserhalb der Küste von North Carolina werden nach ihrem Aussehen, ihrer auffallenden Flora und den ökologischen Anpassungen beschrieben. Die folgenden 5 Gesellschaften werden unterschieden: äusserer Küstenstrand, Primärdünensystem, Sandebenen, Küstenwälder und Salzsümpfe. Die Pflanzen innerhalb dieser Gesellschaften müssen eine Kombination der nachstehenden Faktoren ertragen können: Salznebel, beschränkte Wasserzufuhr, niederer Nährstoffgehalt, rascher Nährstoffumsatz, unstabile Bodenverhältnisse, Ueberdeckung mit Sand und Sandgebläse. Geschichtliche Veränderungen der Vegetationsdecke der "Barrier Islands" werden kurz diskutiert und die mögliche zukünftige Entwicklung betrachtet.

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