

Interisland Variability of Dune Plant Community Structure

on Virginia's Barrier Islands

by

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ABSTRACT

INTERISLAND VARIABILITY OF DUNE PLANT COMMUNITY STRUCTURE ON VIRGINIA'S BARRIER ISLANDS

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The barrier islands of the Virginia Coast Reserve LTER site provide an opportunity to study interisland variability of dune plant communities. My research focused on the variation in biomass and diversity of communities among islands and dune positions. Grassy dunes of young, intermediate and old age were sampled on Smith, Hog, and Parramore Islands. Aboveground biomass was obtained from harvest plots, and roots were extracted from cores. Data were collected on depth to groundwater and total soil nitrogen. Variation in mean aboveground biomass was evident among the islands with the highest values on Hog Island, followed by Smith, then Parramore Island. Results for belowground biomass were similar, except the highest values were on Smith Island and then Parramore Island. Aboveground biomass was greatest on intermediate dunes, followed by the older dunes. The young dunes, frequently disturbed by overwash, had the least. Patterns in belowground biomass were variable among the different age dunes, with significant differences on Smith Island. In general, the oldest dunes had the highest biomass and the youngest the least. Species richness ranged from 40 species on Smith Island to 33 species on Parramore. Among dunes, results varied from an average of 17 species on the older dunes to 10 species on the youngest. The oldest dunes had the

highest levels of total soil nitrogen, followed by the intermediate and young dunes. Smith Island in particular showed significantly greater values on the old and intermediate dunes. The taller intermediate dunes had the greatest mean depth to freshwater and the young foredunes the least. Aboveground biomass increased as depth to freshwater increased on both Hog and Smith Islands, perhaps due to increased partitioning of resources to shoots rather than roots. Greater soil nitrogen correlated with higher belowground biomass on Smith Island, while on Hog depth to freshwater seemed to be more important. On both islands, higher soil nitrogen correlated with increased species richness. In this study, both depth to freshwater and the availability of soil nitrogen had variable effects on above- and belowground biomass, as well as species richness, depending on the island and position on the island.

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INTRODUCTION

OVERVIEW. Nearly thirteen percent of the Earth's coastlines have barrier islands offshore (King 1972). Originating after the last major glacial period, which peaked approximately 1800 years ago (Clark et al. 2009), these sandy islands buffer coastal regions from large ocean storms by diverting flood waters, breaking up long-fetch storm waves and weakening the systems themselves. Equally important, barrier islands are breeding and migratory grounds for many organisms (Haslet 2000). Human development on barrier islands has obvious effects on these ecosystems, in many cases lessening the historic ability of the islands to protect mainland coasts from tropical systems and strong winter storms (Ray and Gregg 1991). With an increase in severe storms in recent years, there has been great interest in determining the extent to which islands can be developed, if at all, before their natural benefits are lost.

The barrier islands of the Eastern Shore of Virginia represent some of the least developed islands on the east coast of the United States. Managed for the most part by the Nature Conservancy, the only obvious signs of human impact on most islands are scattered, abandoned Coast Guard stations and the remnants of historical fishing towns, though sites on some islands were used extensively through the 1930s (Dueser et al. 1976). These barrier islands provide an excellent location for the study of coastal ecosystems as well as the effects of global events such as climate change and human development. Towards this goal, a National Science Foundation (NSF) Long Term

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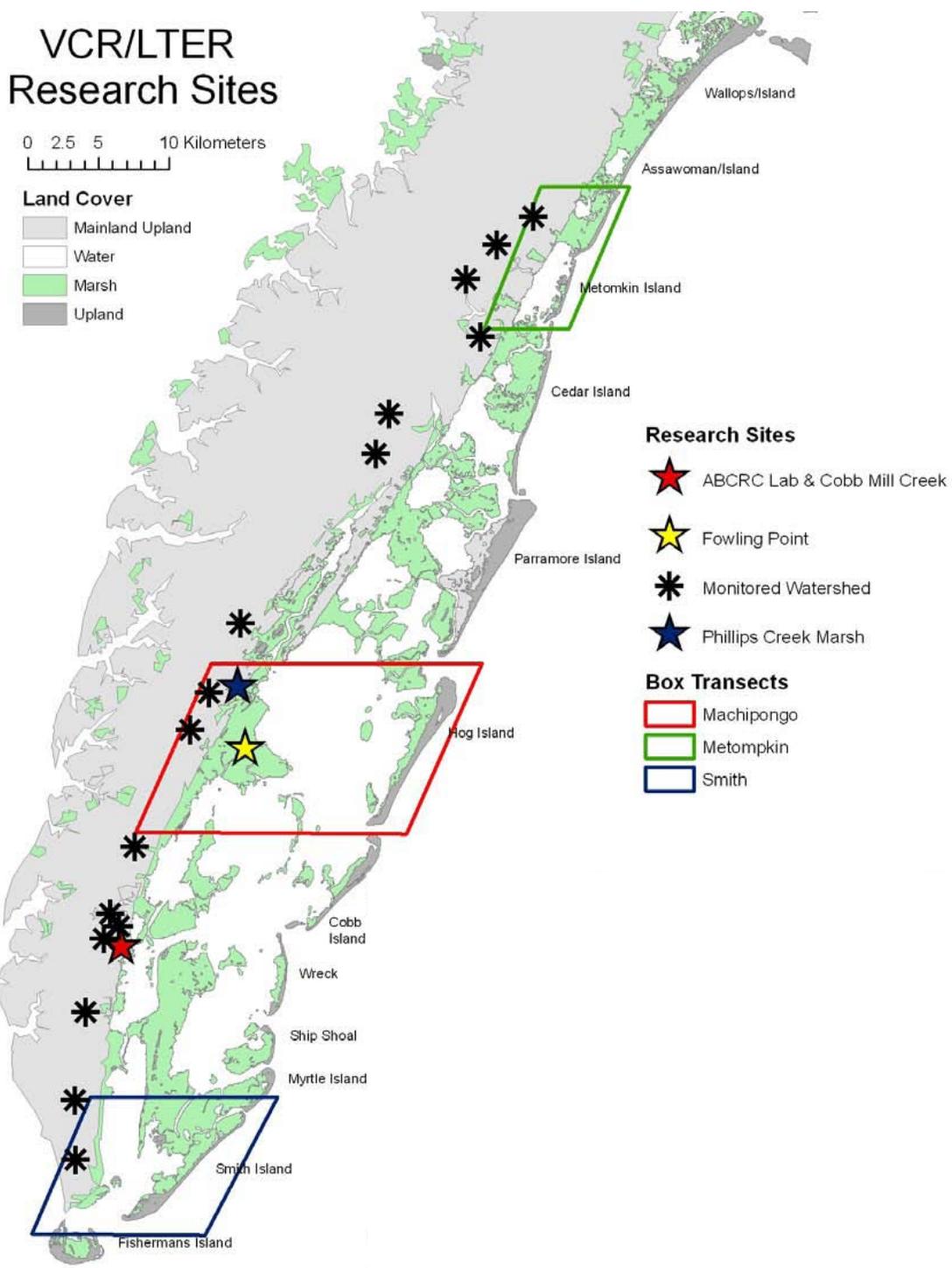


Fig. 1- Virginia Coast Reserve Long-Term Ecological Research Site. Box transects indicate primary VCR LTER study sites, encompassing barrier islands, lagoons and mainland habitats.

Ecological Research (LTER) site (Fig. 1) was established on the Eastern Shore of Virginia. The primary goal of the Virginia Coast Reserve (VCR) LTER is to study the effects of and relationships between biological, physical and anthropogenic factors on the barrier islands, the mainland coast, and the lagoons separating the two. Hog and Parramore Islands have been studied for more than twenty years. In order to further analyze spatial variability across the study area, studies needed to be expanded to include more of the barrier islands in the chain. Specifically, Smith Island near the southern end of the chain and Metompkin Island further to the north have been identified for this expansion. The goal of the current study was to conduct parallel research on three islands within the VCR: Smith, Hog, and Parramore. I hypothesized that there is significant variation in plant biomass, both above and belowground, and community diversity among the three islands. Further, I expected differences in these parameters among different aged dunes on each island along a chronosequence of young foredunes, tall intermediate dunes, and the oldest grassy dune. Lastly, it is believed that factors such as depth to water and total soil nitrogen, in addition to dune age, may be important controls on dune plant biomass and diversity on the VCR barrier islands.

BARRIER ISLAND ECOLOGY. The study of barrier islands must necessarily start with an understanding of the formation of the islands themselves. Found globally, on nearly every shoreline, barrier islands exist in numerous forms. Three theories are most commonly used to explain barrier island formation. De Beaumont (1845) proposed that barrier islands were built through the deposition of sand on offshore bars, eventually overtopping the water level and forming an island. Though more recent research has

shown this theory to be unlikely (McKee and Steward 1961), theories by Oertel suggest that submerged barrier platforms (flooded barrier islands, mud flats or mainland dunes) may be wide enough to become barrier islands through de Beaumont's upbuilding process under certain scenarios. Another historical explanation for barrier island formation suggested that they were formed when barrier spits were breached by wave action, creating inlets and islands (Gilbert 1885). Fisher (1968), then Oertel and Kraft (1992), further developed this theory to break the coastal system into components, including headlands, left- and right-side spits, tide-dominated barrier islands and wave-dominated barrier islands. It has also been theorized that mainland areas are inundated by sea level rise and higher elevation locations, such as tall dune ridges, are left above water level as barrier islands (McGee 1890).

These theories and current research generally agree that modern barrier islands formed after the last glacial maxima (Haslet 2000). At that time, eustatic sea-level was approximately 45 meters below the current level and large river systems had deposited large sediment loads along the coast, creating coastal headlands along which large dunelines formed. Rising temperatures in the Holocene melted glaciers and sea level rose, flooding lower areas behind dune ridges and breaching mainland spits, both leading to the creation of barrier islands. As sea levels continued to rise toward modern levels, storm events constantly battered the islands, moving sand across them into interior swales and the backbarrier lagoon. Through this process of overwash, islands were able to migrate landward as sea level rose. Continued erosion and accretion of sand across and along islands, as well as gradual changes in sea level from modern glacial melt, thermal

expansion, geological uplift and subsidence, all lend to the continued formation, destruction and expansion of barrier islands (Easterbrook 1999).

The landscape of a typical barrier island consists of a sequence of dunes with lower elevation swales between them. The creation of dunes allows barrier islands to survive, migrate and possibly expand, be it landward, seaward or alongshore (Godfrey 1976). Material deposited along the seaward high tide line, known as a wrack line, allows for the initial development of dunes. A combination of plant material, large shells, and assorted debris, the wrack line traps blowing sand and slowly builds small dune ridges, known as embryo dunes. As these grow and are colonized by hardy plant species, they are able to trap more sand, expanding and connecting to one another. Wind and water roll the sand from the ridge away from the shoreline, slowly moving the growing ridge, which eventually forms a new primary foredune. Interior secondary dunes may build for a time due to prevailing onshore winds, but eventually are cut off from this source of sand and may even begin to erode into nearby swales over time. This process may lead to wide areas of eroded dunes and partially filled swales where large areas of shrubs or even forests may develop. Fresh to brackish marshes and ponds commonly fill the inner swales and the backbarrier of the island is usually bordered by a wide salt marsh (Haslett 2000). Variability in this geomorphology may be affected by a number of factors, all generally controlled by the geographic location of the island or changes in sea level. These factors may include prevailing wind speed and direction, tidal range, wave action, orientation, direction and speed of currents, type and supply of parent material, precipitation, frequency of major storm events, and the development of vegetation (Dolan et al. 1979, Godfrey 1977, Haslett 2000).

The numerous geomorphological states found on barrier islands lead to a wide range of plant communities. The swales and back-barrier marshes display vegetation typical to these habitats, while the dunes frequently undergo extensive succession over time, becoming more stable. Hardy rack line species allow the development of primary dune ridges and the associated early successional species of graminoids and forbs, all tolerant of exposure to salt water and spray (Ranwell 1972). Inland, secondary dunes are vegetated by similar species, with shrubs growing in increasing density along dune/swale margins. Eventually, maritime forests can develop on the most stable islands (Haslett 2000).

Variation in these plant communities can occur as a result of many factors. Regularly battered by heavy ocean winds and waves, layered in salt spray, flooded by surges developed along seasonal storm fronts and tropical cyclones, and dry the remainder of the year, barrier islands represent relatively harsh environments for plants. Initial colonization and survival of dune plants is directly related to the frequency of flooding, the effect of wind and salt spray due to island orientation, stability of the dune, and the rate of sea level changes (Fahrig et al. 1993).

Community development and success is influenced by the availability of soil nutrients, temperature fluctuations, humidity, precipitation and the depth of the fresh water (Gregory 1987). In particular, dunes with more soil nutrients and closer access to fresh water due to a shallower fresh water lens may exhibit increased above- and belowground biomass, providing more structural stability. However, these resources can be quickly depleted through use, lack of input and natural losses. Fresh groundwater, for

instance, can fluctuate dramatically depending on precipitation and evapotranspiration (Tolliver et al. 1997).

The diversity of the plant community may also play a role in dune development and stability. Moreno-Casasola (1988) found that variability in dominant species may lead to different dune morphology. Dunes dominated by *Spartina patens* may be low and flat, *Ammophila breviligulata* may create taller ridges, and *Uniola paniculata* may allow for development of hummocks on open sand or atop ridges. In many of these situations the roots effectively change the morphology of the dune. It has been found that belowground biomass, relative to aboveground, is of equal or greater importance to the function of many systems (Nadelhoffer and Raich 1992). Each of these morphological characteristics provides varying degrees of support for the developing community and protection against state change events. It is clear that the dynamic nature of barrier islands, as well as the nutrient stressed, salt-sprayed environment, makes understanding the relationship of community composition and biomass to these environmental factors important (Gleeson and Tilman 1990).

Soils beneath dunes on sandy Atlantic barrier islands are generally classified as either Typic or Spodic Udipsamments. Secondary dunes on many Atlantic coast barrier islands undergo podzolization as they grow older. Rainfall percolates down through the dune, leaching materials deposited by salt aerosols and leaving behind a soil of grey to white quartz sand. Moving downward, the leached materials interact with iron oxides, aluminum and magnesium (Salisbury 1952). The leached materials accumulate at lower levels in the subsoil, creating an orange-to-brownish-colored spodic horizon. Research has shown that the upper horizons of young foredunes and many primary dunes maintain

a slightly yellow color as they are not fully leached (Salisbury 1952). As plant communities move through succession, soil building processes may produce vastly different surface horizons from those found closer to the oceanfront, though the underlying characteristics can still be found at depth.

Salt water surrounds barrier islands on all sides, commonly rising high enough to wash over all but the tallest dunes during regular storm events. Despite this obvious influence, a fresh water lens is formed under most islands. As overwash moves sand into the backbarrier lagoon in a transgressive setting, a permeable sediment layer develops over top of the impermeable lagoonal muds (Heron et al. 1984). As the island continues to migrate these sediments become a sink for fresh water, creating a lens across the island. Convex in shape, the lens rises upward at the center of the island, sloping down steeply as it nears the ocean and lagoon margins (Willis et al. 1959). The depth of the fresh water lens depends on variations in geographic and seasonal weather patterns. At times the lens may rise higher than the level of the swale soils, leading to interior ponds.

Studies have shown soil moisture to remain relatively constant to depths of 30 – 50 cm above the fresh water lens. The porous nature of the sandy soil limits capillary rise above this point (Willis et al. 1959). In the area above this depth, moisture content is generally between 0 - 4 % of the soil. This dry surface layer acts much like a cover of mulch on a flowerbed by decreasing evaporation in the soil below it, thus conserving soil water from rapid loss in dry atmospheric conditions (Au 1974). The depth to which roots must extend commonly prevents dune plants from utilizing capillary water, much less the fresh water lens itself. Unable to utilize these normal sources of water, plants have adapted in ways similar to those seen in desert communities. Studies have shown less

water beneath heavily vegetated dunes than those that are more sparsely vegetated. Plants inhabiting barrier island dunes are well adapted to quickly absorb all available surface water when it rains, leaving little to percolate downward into the local fresh water lens (Willis et al. 1959). Fresh water is clearly an essential resource on barrier island dunes, but many studies have also found nutrients to be important limiters (van der Valk 1974).

Relative to other soils, barrier island sands are low in macronutrients due to leaching of phosphorous, nitrogen and cations (Willis 1963). Overwash and a lack of plants leave foredunes the most depleted of many necessary nutrients. Decomposition of strandline materials releases just enough nitrogen for the survival of hardy, salt tolerant plants (Ranwell 1972). As these areas develop into primary dunes, they are generally increasingly nitrogen deficient as new foredunes block the input of strand material. Inland, nitrogen and phosphorous become more prevalent in older secondary dunes (Lakshmi and Day 1993). This change is likely due to the expansion of shrubs, such as *Myrica cerifera* and *Ilex opaca*. As evergreens, they drop leaves throughout the year, thereby adding nitrogen and phosphorous to the soil. On older dunes, soil moisture appears to become more of a limiting factor as plant biomass is reduced despite increased soil nitrogen (Day 1996). A reverse sequence of deficiency has been seen for potassium and magnesium, both becoming sparser as dunes grow older. Neither, however, is initially as depleted as either nitrogen or phosphorous (Willis et al. 1959).

A nutrient generally found in large amounts on barrier islands is calcium. The deposition and breakdown of shells over time leads to deposits large enough to supply dunes for long periods (van der Valk 1979). Research indicates, however, that over

hundreds of years, even these thick deposits of shell material will be leached away, leading to a potential deficiency of calcium in the upper soil horizons (Boaden and Seed 1985). Most dune soils appear to have adequate micronutrients for plant growth, possibly resulting from occasional flooding during major storm events. In areas of less frequent overwash, salt spray has been shown to provide these nutrients (Art et al. 1974).

Research indicates that organic matter content may be as low as 0.01 % in foredunes. It is clear this property is not a key soil factor in the initial formation of dunes (Johnson 1981). As dunes develop further, however, increased vegetation leads to more organic matter incorporation. As in most soils, this is a major factor in moisture retention, clearly important in a barrier island setting. In turn, this increase in moisture in old dunes can lead to the development of maritime forests, themselves adding even more organic matter in the form of increased input of decaying leaves and roots (Ranwell 1959). Perhaps more importantly, these trees and shrubs work to bolster the physical stability of the island as a whole.

Data show that salt input from overwash and salt aerosols may exceed 1,300 kg/ha, more salt than many plant species can tolerate (van der Valk 1993). An unrelated adaptation seems to have benefitted many fore- and primary dune plants. Their adaptations to reduced levels of nitrogen have left them less prone to the influences of the spray-deposited salt aerosols that regularly leach into soils in oceanfront areas of barrier islands (Erikson and Young 1995). Most islands receive enough precipitation to reduce chloride concentrations below toxic levels, further aiding plant survival. The effects of this chemical poisoning can be seen, however, as many trees bend at odd angles due to death of branches from chloride poisoning. The effects of salt fall off sharply towards the

center and backbarrier dunes as winds are blocked and overwash is less common (Boyce 1954).

STUDY OBJECTIVES. Previous studies of the dunes on Hog Island have examined aboveground biomass (Dilustro and Day 1995, Day et al. 2001), belowground biomass (Conn and Day 1993, Stevenson and Day 1996), plant species diversity (Dueser et al. 1976), the effects of soil nitrogen (Day 1996, Day et al. 2004, Heyel and Day 2006), and the influence of depth to fresh groundwater (Day et al. 2001). No previous studies at the VCR LTER have collected and analyzed community data of this sort for other islands in the complex. Additionally, no studies have attempted to evaluate variability of these ecological and environmental factors among islands and dune positions. This study aimed to examine variability in above- and belowground biomass, and in diversity, among dune sites on Hog, Smith and Parramore islands respectively, as well as several environmental factors that may influence community structure. An additional goal of analyzing variability in community structure and its influencers among these islands, and among dune positions, was also undertaken. Separated by other islands along the chain and exhibiting a variety of physical characteristics in their formation (Leatherman et al. 1982), these islands provided a good sample of variability within the VCR system.

On each island, three grassy dunelines were identified, based on their relative position, and sampled: the fore-dune, the next oldest dune inland, and the oldest grassy dune that could be located along the leeward side of the islands. The dunelines represent historical shorelines (Oertel 1974) and analysis on each dune allowed assessment of the variability of above- and belowground biomass and of community composition and

diversity on grassy dune ridges among the three islands. I hypothesized that there were significant differences among dunes on each island. Additionally, I proposed there were significant differences among the three dune positions studied and among islands, and that these differences among islands or dunes are a result of a number of factors, including distance from the ocean, depth to the fresh water lens and the abundance of total soil nitrogen.

STUDY SITES

The dune sites selected for this study are on three barrier islands (Table 1) located off the coast of Virginia's Eastern Shore, part of the Delmarva Peninsula: Parramore Island (Fig. 2), Hog Island (Fig. 3), and Smith Island (Fig. 4). These islands are part of a long chain of barrier islands stretching from Assateague Island at the southern tip of the Ocean City, MD spit in the north, southward to the chain's terminus at Fisherman's Island at the tip of the Delmarva Peninsula and the mouth of the Chesapeake Bay. More than twenty islands, either bordering the ocean or scattered throughout the back-barrier lagoons, comprise the chain. Numerous other island-sized mud flats, deltas and sand islands, all of which become exposed at low tidal levels, can be found along the coast.

Smith Island is located near the southern end of the chain, with only Fisherman's Island farther south. Hog Island is directly south of Parramore Island, with both located in the center of the chain. The islands in the center of the chain, including Hog and Parramore Islands, exhibit rotational instability in response to sea-level changes. While they do gradually move landward or seaward, they are more commonly seen to change shape, sometimes dramatically. Typical drumstick-shaped and equally influenced by waves and tides, the widest end of the island may change from north to south and vice versa over time due to changes to the ebb-tide deltas of the bordering inlets. Due to these changes, these islands appear to rotate over time (Leatherman et al. 1982). Both Hog and Parramore Islands exhibit a clockwise rotation, though others in this portion of the chain shift counter-clockwise, depending on the end of the island most commonly the widest

Table 1. Study site characteristics

	Parramore Island- North End	Hog Island- Northern Interior	Smith Island- South End
Location	37 34' 25" N 75 36' 14" W	37 26' 55" N 75 39' 58" W	37 06' 45" N 75 55' 19" W
Annual Rainfall (mm)*	850 -1400		
Annual Mean Temperature Range (C)*	2.8 – 25.1		
Soil Type **	mixed, thermic Typic Udipsamments		

* Greenland and Hayden 1997

** Dueser et al. 1976

over time. Dynamics of wave focus and longshore transport of sand have led to significant changes in orientation for many of the island in the southern end of the chain, including Smith Island. As a result, these islands are said to be in the process of non-parallel retreat where the southern ends are more landward than the northern. These two groups also vary from the Virginia barrier islands north of Parramore Island and south of Assateague Island, which are narrow, less influenced by tides, prone to sand overwash, and tend to retreat parallel to shore (Leatherman et al. 1982). These dramatic differences along the chain may correlate with the location of the inner and outer rims of the Chesapeake Bay Impact Crater, which has been shown to have important effects on local compaction and tectonics (Poag 1997). Another theory suggests the differences may be



Fig. 2- Parramore Island aerial view, research sites indicated with stars

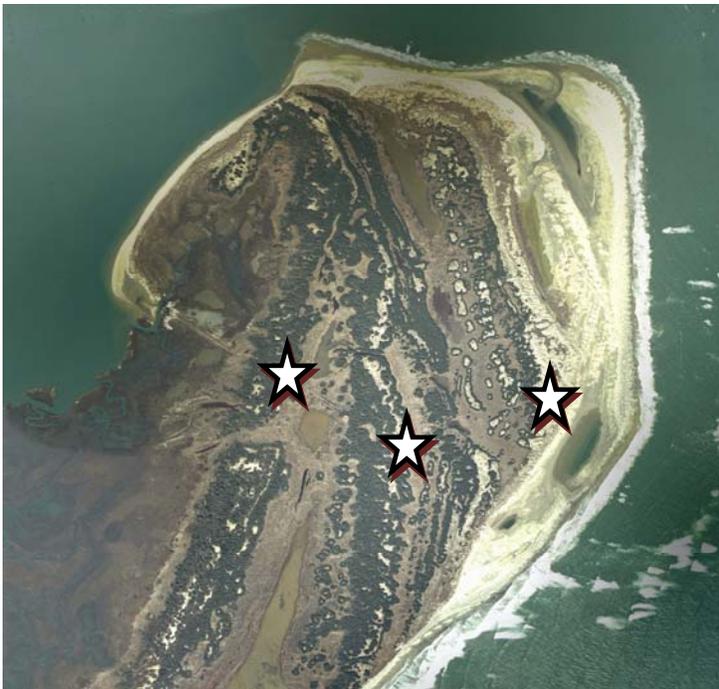


Fig. 3- Hog Island aerial view, research sites indicated with stars



Fig. 4- Smith Island aerial view, research sites indicated with stars

due to sediment deposition by ancient rivers, the streambeds of which lie near the boundaries of these different zones (Colman et al. 1990).

In order to meet the objectives of the study, the sites were selected for fairly open, grassy dune ridges, though shaded sections were not excluded from sampling. All sites showed the general characteristics of dunes at their respective age. Sandy parent material provided the soil for the youngest dunes. Increased leaching of nutrients and aerosols leads to an increasingly spodic soil farther inland, though the intermediate dunes sampled in this study were still fairly unleached, what can be called “yellow dunes”. The older dunes studied showed increased soil development due to the buildup of organic matter over time and the subsequent slowing of leaching, though incipient spodic horizon characteristics could still be seen at depth.

Table 2. Continued

	P-Y	P-I	P-O	H-Y	H-I	H-O	S-Y	S-I	S-O
<i>Eragrostis spectabilis</i> (Pursh) Steud.	x		x		x			x	x
<i>Eupatorium capillifolium</i> (Lam.) Small						x			
<i>Eupatorium hyssopifolium</i> L.	x	x	x		x	x		x	x
<i>Euthamia tenuifolia</i> (Pursh) Nutt.						x			
<i>Festuca rubra</i> L.		x	x		x	x		x	x
<i>Galium</i> sp.		x	x						
<i>Gnaphalium chilense</i> Spreng.						x			
<i>Hieracium greenii</i> L.						x			
<i>Juncus</i> sp.	x					x			
<i>Krigia virginica</i> L.		x	x		x				
<i>Lepidium virginicum</i> L.			x				x	x	x
<i>Melothria pendula</i> L.								x	
<i>Monarda punctata</i> L.			x					x	
<i>Morella pensylvanica</i> (Mirb.) Kartesz		x	x						
<i>Morella cerifera</i> L.						x			
<i>Opuntia compressa</i> J.F. Macbr.			x						x
<i>Panicum amarum</i> Elliot	x	x		x	x	x	x	x	x
<i>Panicum dichotomiflorum</i> Michx.						x			
<i>Panicum lanuginosum</i> Elliot			x				x		
<i>Physalis walteri</i> Nutt.	x						x	x	x
<i>Prunus serotina</i> Ehrh.			x						
<i>Pseudognaphalium obtusifolium</i> (L.) Hilliard & B.L. Burt								x	
<i>Pseudognaphalium stramineum</i> (Kunth) Anderb.					x				
<i>Rubus argutus</i> Link						x			
<i>Rumex acetosella</i> L.			x		x	x		x	
<i>Salicornia virginica</i> L.							x		
<i>Salsola kali</i> L.	x			x			x		
<i>Schizachyrium scoparium</i> (Michx.) Nash		x			x	x	x	x	x
<i>Smilax bona-nox</i> L.			x						x
<i>Smilax rotundifolia</i> L.			x						
<i>Solanum carolinense</i> L.			x				x		
<i>Spartina patens</i> (Aiton) Muhl.	x	x	x	x	x	x	x	x	x
<i>Strophostyles helvola</i> (L.) Elliott	x			x					x
<i>Teucrium canadense</i> L.			x				x	x	x
<i>Triplasis purpurea</i> (Walter) Chapm.							x		
<i>Uniola paniculata</i> L.	x						x	x	

Table 3. Plant family species counts across study area.

Asteraceae	14
Brassicaceae	2
Cactaceae	1
Chenopodiaceae	4
Cucurbitaceae	1
Cyperaceae	3
Euphorbiaceae	1
Fabaceae	1
Juncaceae	1
Lamiaceae	2
Myricaceae	2
Poaceae	13
Polygonaceae	1
Rosaceae	1
Rubiaceae	1
Smilacaceae	2
Solanaceae	2

The intermediate dune sites, in all cases one to two dunes behind the fore dune for this study, likewise showed little variation in morphology. Vegetation was found to be more variable in terms of dominant species. The dunes were all relatively tall, ranging from 2 m on Smith Island to around 3 m on Parramore Island. Dense, grassy vegetation was common with *Spartina patens* dominant on Hog and Parramore Islands. *Schizocyrium scoparium* Nash, and *P. ammarum* were also important parts of these two dune systems. *A. breviligulata* was the dominant graminoid at the intermediate dune sites sampled on Smith Island. While common species such as *S. patens* and *S. scoparium* were found across the sites sampled on this dune, several species, including *Uniola paniculata* L. and *Solidago sempervirens* L., were found only here among all the sites studied. The close proximity to the traffic of the Chesapeake Bay Bridge Tunnel, approximately three miles over open water, may create a pathway for the introduction of

exotic seeds which could provide an explanation for the increased diversity on Smith Island's dunes.

While the young and intermediate dunes displayed fairly similar morphology and vegetation, the old dunes studied on each island varied greatly. The dune studied on Smith Island was adjacent to the lagoon-side salt marsh. The dune rose to approximately 1 m and varied from relatively overgrown with shrubs and young trees, to open and grassy, though the dominant flora in most sample plots still consisted of *Spartina patens*. *Smilax bona-nox* L. was also prevalent at this site.

The old dune site studied on Hog Island was farther inland as all dunes closer to the back-barrier side of the island are densely covered in trees and shrubs. The study dune rises approximately 1.5 m from the surface of the surrounding freshwater wetlands. Though shrubs have filled in thickly along the dune-marsh ecotone, the ridge itself remains open. Dominant species included *Spartina patens* and *Schizocyrium scoparium*, though numerous other taxa were found across the site.

On Parramore Island the old dune site was located far from the back-barrier, separated from it by several older, forested dunes. As on Hog Island, older dunes are heavily forested. The site selected was the remnant of an old dune where the swales had largely filled in over time. Numerous depressions separate short dune ridges, rising to a height of approximately 3.5 m above the surrounding swales and beaches. Trees are scattered across the ridges and swale, though most of the ridges remain unshaded. Sampling here avoided the depressions and focused on three short, parallel ridges. As on Smith Island, dominant species include *S. patens* and *S. bona-nox*. Though not as thickly vegetated, many more species were found across the site in lower densities.

METHODS

SAMPLE COLLECTION AND PROCESSING. During the summer of 2007, line transects were created on each of the nine dune ridges identified for the study. To estimate peak biomass at the middle of the growing season, data were collected from late June through early August. Along each transect, 15 0.25 m² study plots were established using a stratified random approach (Dilustro and Day 1995). These plots ranged anywhere within 1 m to the right or left of the line transect along the top of the dune ridge. Any plot located in a depression or off the ridge was excluded and a new plot located randomly. These plots were used in collecting data on each dune for above- and belowground plant biomass, plant species diversity, soil and plant nitrogen levels, and the depth to the freshwater lens.

To estimate aboveground biomass, all materials were harvested to the soil surface. Dead material was separated from live. All live material was sorted by species, bagged and labeled. Both live and dead samples were dried at 70 degrees C for 48 hours. Mass of major species and standing dead material were determined on an analytical balance.

Belowground biomass was estimated by extracting a 7 cm diameter core in the center of each 0.25 m² plot, to a depth of 40 cm, in 10 cm increments. The cores were stored at 1-4 degrees C until processed. Roots were removed using a 2 mm sieve. Those roots that were obviously dead, based on brittleness and decay, were separated from the live. Any questionable roots were included as live. After drying for 48 hours at 70 degrees C, mass for live and dead roots was established using an analytical balance.

Species richness was determined by recording the species present in each plot and computing the species total for each dune. The Shannon index was used to estimate species diversity and to compare it among dunes and islands.

$$H' = - \sum_{i=1}^s p_i (\ln (p_i))$$

H' = Shannon diversity index

p_i = n_i / N

n_i = biomass of species "i"

N = biomass of all species

S = total number of species

the summer and the following year, voucher specimens of blooming and fruiting plants were collected from areas immediately around the plots, pressed, identified and stored in the Old Dominion University Herbarium.

Soil samples for N analysis were collected by extracting a 7-cm diameter core to a depth of 10 cm in each plot. The cores were air dried until processed. A 2-mm sieve was used to separate roots and coarse organic matter from the soil. The remaining soil and fine organic matter was ground to a fine powder using mortar and pestle. Soil nitrogen was determined using a Carlo Erba 1200 CHNS analyzer. 15-16 mg samples were used to determine soil nitrogen concentration, leading to an estimate of absolute soil nitrogen content.

To determine the depth to fresh groundwater beneath the dunes, a sand auger was used to extract soil down to a maximum depth of 2.5 m at each plot. The extracted soil was tested for saturation by squeezing until water was noticeably extruded. The depth of the hole was recorded once saturation was established. Where saturation was not found by the 2.5 m mark, the dune was noted to have a deep water table. For reference, auger

hole data on Hog Island were compared to data from continuously recording wells on Hog Island.

Dune distance from the ocean was measured using aerial photographs in ArcGIS software. Measurements were taken from several points along each ridge, within the study area, to a line identified as a mean high tide line along each seaward beach. The measurements were averaged to provide a value for each dune.

ANALYSIS. Two-Way Crossed ANOVAs were run to test for variation among islands and dunes. Significant interactions were found between main effects for most variables. To provide more precise results and rule out interaction effects, one-way ANOVAs were run for each variable among dunes on each island and among islands for each dune position. Split-plot ANOVAs were run to test for vertical variability in root biomass on each island. Correlations were determined for each set of variables on each island.

RESULTS

ABOVEGROUND BIOMASS. Mean total aboveground biomass (Fig. 5) was significantly different among dunes on Parramore and Smith Islands (Table 4), where the intermediate dune had greater biomass than the young or old dunes (Tukey, $P < 0.05$). The same trend was seen on Hog Island, though there was no significant difference (Table 4). Values for intermediate dunes ranged from 207 g/m^2 on Parramore Island to 379 g/m^2 on Smith Island. Young dunes had the lowest values across the study, ranging from 207 g/m^2 on Parramore Island to 379 g/m^2 on Smith Island (Fig. 5). Biomass was also different among islands (Table 5) on young dunes and on old dunes. At both dune positions total aboveground biomass was significantly higher on Hog than on Parramore Island (Tukey, $P < 0.05$).

Table 4. 1-way ANOVA results for aboveground biomass among dunes on each island. *indicates a significant difference at the 0.05 level.

Island	Variable	F	P
Parramore	Total Biomass	3.196	0.05*
Hog	Total Biomass	0.327	0.723
Smith	Total Biomass	11.003	< 0.001*
Parramore	Live Biomass	1.601	0.214
Hog	Live Biomass	< 0.001	1.000
Smith	Live Biomass	0.759	0.475
Parramore	Dead Biomass	3.248	0.049 *
Hog	Dead Biomass	1.222	0.305
Smith	Dead Biomass	16.162	< 0.001*

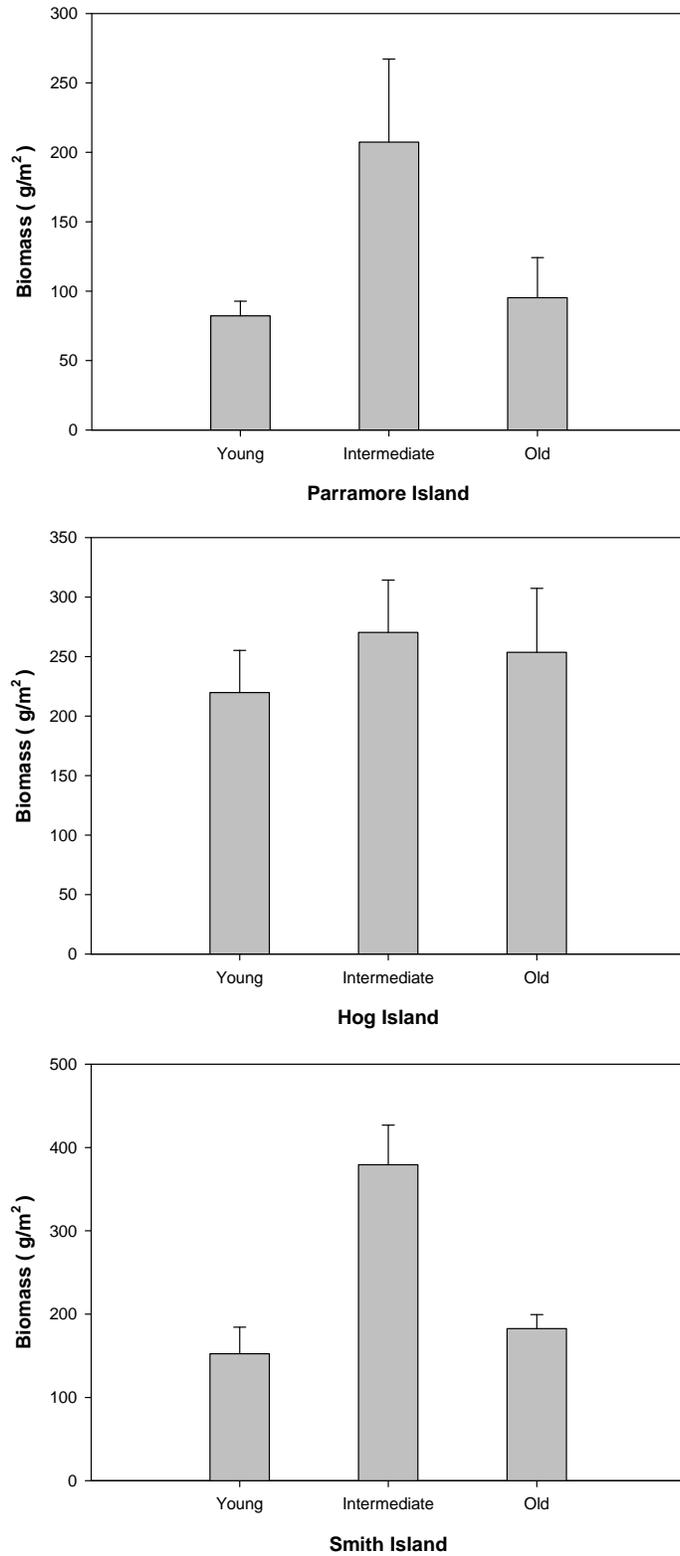


Fig. 5- Mean total aboveground biomass per dune on each island

Table 5. 1-way ANOVA results for aboveground biomass among islands on each dune. *indicates a significant difference at the 0.05 level.

Island	Variable	F	P
Young	Total Biomass	6.394	0.004*
Intermediate	Total Biomass	2.927	0.065
Old	Total Biomass	4.367	0.019*
Young	Live Biomass	3.826	0.030*
Intermediate	Live Biomass	0.640	0.532
Old	Live Biomass	3.519	0.039*
Young	Dead Biomass	3.782	0.031*
Intermediate	Dead Biomass	4.478	0.017*
Old	Dead Biomass	2.309	0.112

No significant differences in aboveground live biomass were found (Table 4), though slight variation was apparent (Fig. 6). Values for the intermediate dunes ranged from 115 g/m² on Parramore to 159 g/m² on Hog, though there were no significant differences among dunes (Table 4). The ranges of data for live biomass on the oldest and youngest dunes were more similar. Live aboveground biomass was significantly different among islands (Table 5) on young and old dunes. Values were significantly higher on Hog than on Parramore on both dunes (Tukey, P<0.05).

Results for mean dead aboveground biomass (Fig. 7) showed a similar pattern to that of total aboveground biomass. Mean dead aboveground biomass (Table 4) was significantly different among dunes on both Parramore and Smith Island. On Parramore dead aboveground biomass was significantly greater on the intermediate dune than on the youngest (Tukey, P<0.05), while on Smith Island the intermediate dune showed significantly more than either the old or young dunes (Tukey, P<0.05). Values for

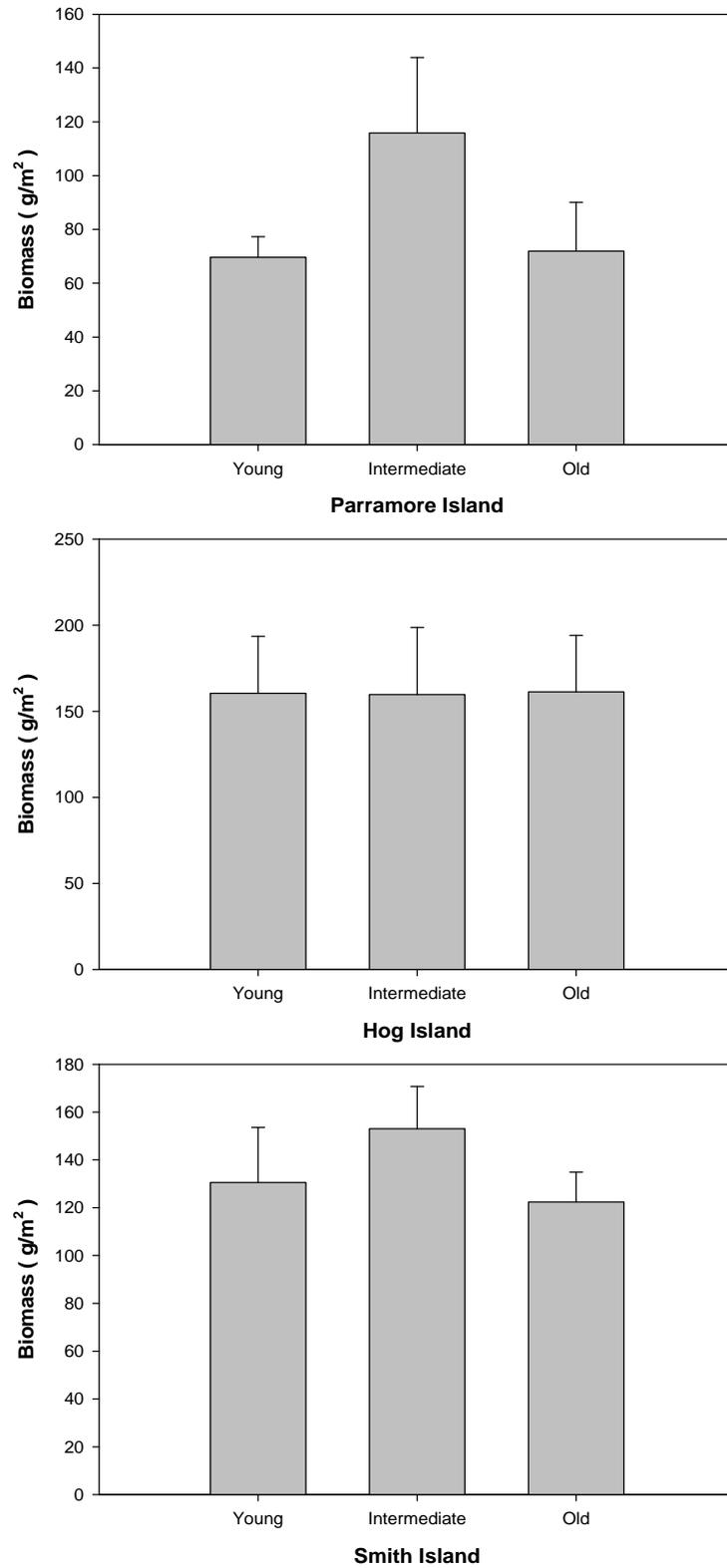


Fig. 6- Mean live aboveground biomass per dune on each island

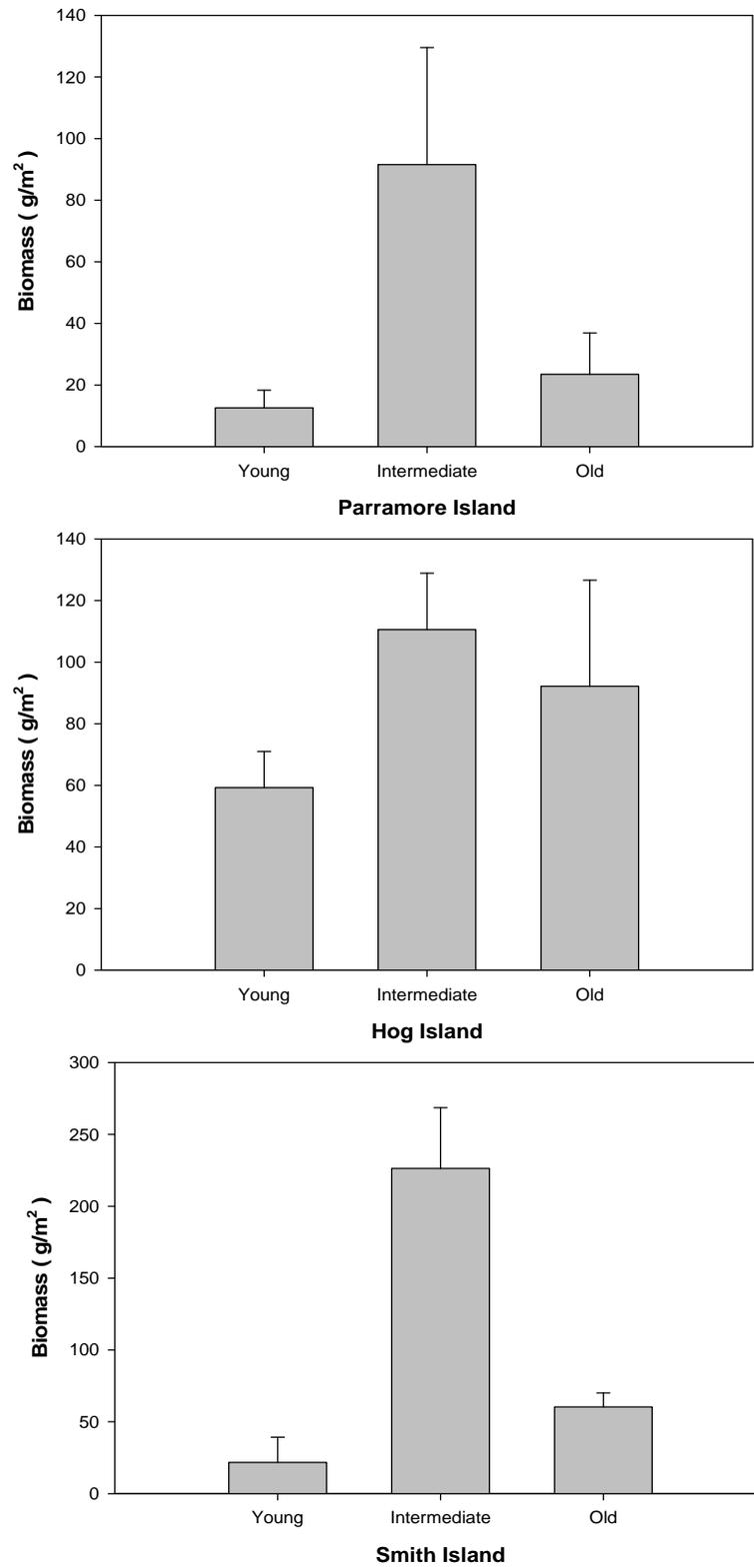


Fig. 7- Mean dead aboveground biomass per dune on each island

intermediate aged dunes ranged from 91 g/m² on Parramore to 226 g/m² on Smith. Values on the old dunes ranged from 23 g/m² on Parramore to 92 g/m² on Hog (Fig. 7).

Biomass was significantly different among islands (Table 5) on both young and intermediate dunes. On young dunes, dead aboveground biomass values were significantly greater on Hog Island than on Parramore (Tukey, $P < 0.05$), while on intermediate dunes values are higher on Smith than on Parramore Island (Tukey, $P < 0.05$).

On all three islands, the greatest live:dead ratio for aboveground biomass was found on the youngest dune (Table 6). The lowest value was found on the intermediate dunes, followed by the older dune. The greatest percent of total biomass was found on the young dune on Smith Island, where 86 percent of the total biomass was live. Parramore had a similarly high value of 85 percent live on the young dune. At 73 percent, the value was slightly lower on Hog. On the oldest dunes, values ranged from 64 percent live on Hog Island to 75 percent live on Parramore. The only dune with greater dead than live biomass was the intermediate dune on Smith Island, where 60 percent of the total biomass was dead. The intermediate dunes as a group had the most even ratio of live to dead biomass (Table 6).

As expected, based on initial plant family assessments (Table 3), graminoids contributed more than 60% of the aboveground biomass on all dunes, ranging from high values of 97% and 93% on the young dunes on Hog Island and Smith Islands respectively, to lower values such as 60% on the intermediate dune on Parramore Island. As expected, dominant species (Table 7) varied among dune positions; however, the same species were not dominant at similar positions on different islands. *Spartina patens* was widely distributed and was one of the three most dominant species on seven of the

Table 6. Aboveground Biomass

Location	Mean Total Biomass (g/m ²)	Mean Live Biomass (g/m ²)	Mean Dead Biomass (g/m ²)	Percent of Total Biomass		Live : Dead Ratio
				Live	Dead	
Hog-Yng	219.65	160.45	59.21	73	27	2.71
Hog-Int	270.24	159.70	110.55	59	41	1.44
Hog-Old	253.43	161.25	92.19	64	36	1.75
Paramore-Yng	82.21	69.61	12.60	85	15	5.52
Paramore-Int	207.36	115.80	91.56	56	44	1.26
Paramore-Old	95.39	71.94	23.45	75	25	3.06
Smith-Yng	152.33	130.56	21.77	86	14	6.00
Smith-Int	379.37	153.05	226.32	40	60	0.68
Smith-Old	182.69	122.38	60.31	67	33	2.03

nine dunes. Of the most abundant species from each position, no others are nearly as dominant across all dunes as *S. patens*, though *Ammophila breviligulata* and *Panicum amarum* each occurred among the three most dominant species at four sites. There was no clear trend of increasing or decreasing biomass with dune age among any of the dominant species.

BELOWGROUND BIOMASS. There was no clear trend overall for mean total belowground biomass (Fig. 8). Highest and lowest means were found on a different dune on each island. Mean total belowground biomass (Table 8) was significantly different among dunes on Smith Island, where the oldest dune had greater biomass than other dunes (Tukey, $P < 0.05$), ranging from 100.95 g/m² on the young dune to 1522.25 on the old dune. Means on Hog ranged from 282.58 g/m² on the intermediate dune to 532.73 g/m² on the old dune, and on Parramore from 100.09 g/m² on the young dune to

Table 7. Dominant species per dune on each island. The three species with the highest dominance for each site were listed.

Dune	Species	Mean Live Biomass (g/m ²)	Dominance (%)	Frequency (%)
Hog- Yng	<i>S. patens</i>	209.64	33.8	40
	<i>A. breviligulata</i>	197.36	31.8	40
	<i>P. amarum</i>	195.67	31.5	87
Hog- Int	<i>S. scoparium</i>	200.6	31.5	13
	<i>S. patens</i>	153.94	24.2	47
	<i>C. spinosissimum</i>			40
Hog- Old	<i>S. patens</i>	229.19	41.8	60
	<i>S. scoparium</i>	131.38	23.9	27
	<i>C. spinosissimum</i>	35.28	6.4	40
Parramore- Yng	<i>P. amarum</i>	107.34	41.1	53
	<i>A. breviligulata</i>	68.3	26.2	60
	<i>C. edentula</i>	33.85	12.9	33
Parramore- Int	<i>S. patens</i>	178.08	44.9	40
	<i>P. amarum</i>	151.43	38.3	93
	<i>C. spinosissimum</i>	35.5	8.9	7
Parramore- Old	<i>S. patens</i>	96.33	35.3	20
	<i>S. bona-nox</i>	67.59	24.7	47
	<i>E. spectabilis</i>	31.47	11.5	27
Smith- Yng	<i>S. patens</i>	364.25	73.5	100
	<i>P. amarum</i>	54	10.9	47
	<i>A. breviligulata</i>	35.19	7.1	13
Smith- Int	<i>A. breviligulata</i>	240.78	41.9	67
	<i>P. walterii</i>	163.95	28.6	87
	<i>E. spectabilis</i>	58.61	10.2	20
Smith- Old	<i>S. patens</i>	281.44	61.1	100
	<i>S. bona-nox</i>	87.91	19.1	27
	<i>E. spectabilis</i>	21.48	4.7	13

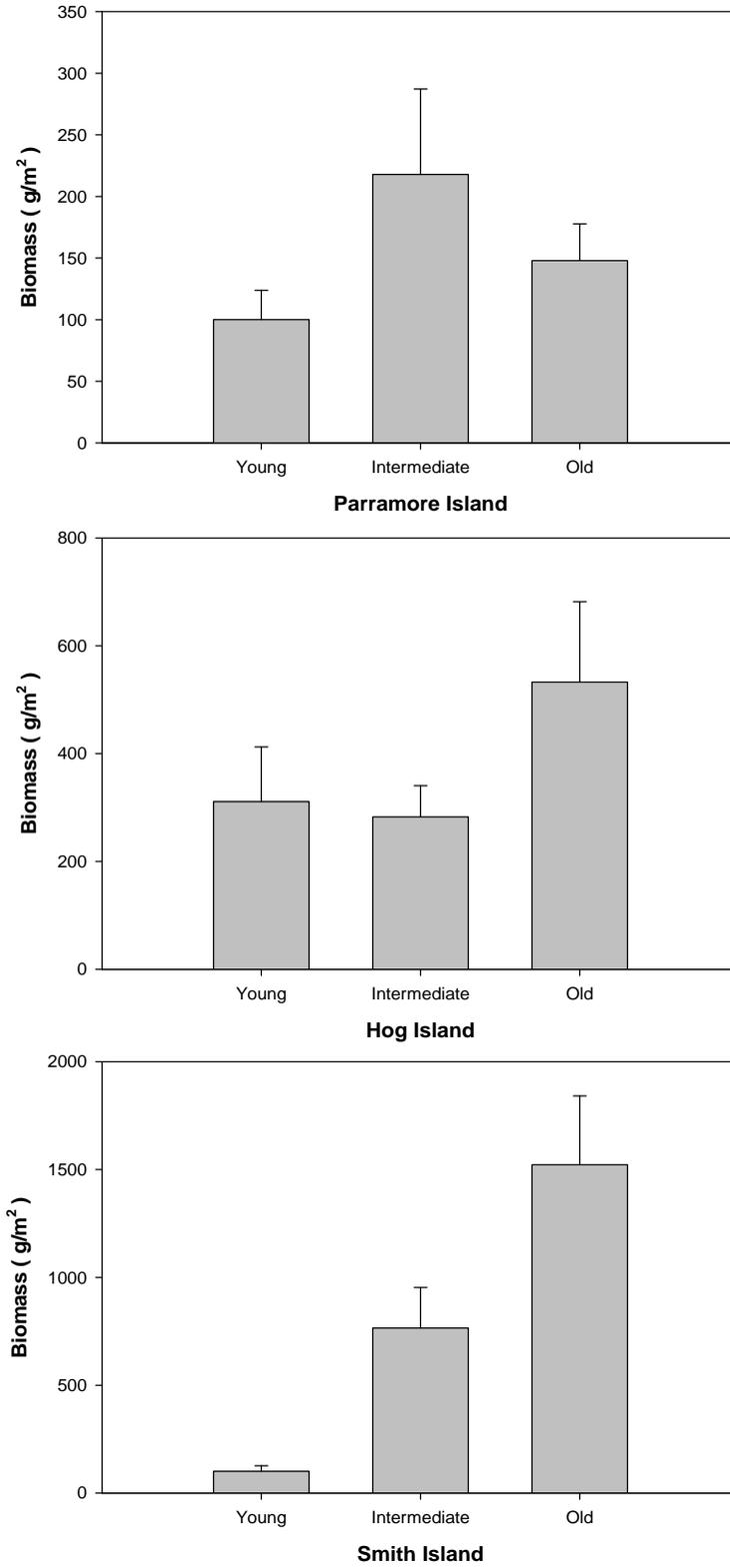


Fig. 8- Mean total belowground biomass per dune on each island.

217.82 g/m² on the intermediate dune (Fig. 8). The lack of a clear trend shows even more clearly among islands, where values were significantly different on all three dunes (Table 9). On young dunes, belowground total biomass is significantly higher on Hog than the other islands (Tukey, P<0.05). Values were greater on Smith than Hog or Parramore Islands on both intermediate and old dunes (Tukey, P<0.05).

Table 8. 1-way ANOVA results for belowground biomass among dunes on each island. *indicates a significant difference at the 0.05 level.

Island	Variable	F	P
Parramore	Total Biomass	1.679	0.199
Hog	Total Biomass	1.576	0.219
Smith	Total Biomass	11.003	< 0.001*
Parramore	Live Biomass	1.851	0.170
Hog	Live Biomass	1.338	0.273
Smith	Live Biomass	11.117	< 0.001*
Parramore	Dead Biomass	0.009	0.991
Hog	Dead Biomass	2.842	0.070
Smith	Dead Biomass	5.857	0.006*

Table 9. 1-way ANOVA results for belowground biomass among islands on each dune. *indicates a significant difference at the 0.05 level.

Island	Variable	F	P
Young	Total Biomass	3.858	0.029*
Intermediate	Total Biomass	6.174	0.004*
Old	Total Biomass	12.065	< 0.001*
Young	Live Biomass	3.832	0.030*
Intermediate	Live Biomass	5.226	0.009*
Old	Live Biomass	12.890	< 0.001*
Young	Dead Biomass	0.348	0.708
Intermediate	Dead Biomass	5.609	0.007*
Old	Dead Biomass	6.195	0.004*

Mean live belowground biomass (Fig. 9) showed a pattern similar to the total belowground biomass. The dunes on Smith Island varied significantly (Table 8) in mean belowground live biomass. The oldest dune was significantly different from the others (Tukey, $P < 0.05$), ranging from 97.79 g/m^2 on the young dune to 1335.92 g/m^2 on the old dune. Though not significant, differences were seen on Hog and Parramore Islands, where values ranged from 303.25 g/m^2 on the intermediate to 478.67 g/m^2 on the old and 91.14 g/m^2 on the young dune to 209.70 g/m^2 on the intermediate dune respectively (Fig. 9). Live belowground biomass was significantly different among islands on all dunes (Table 9). Values were greater on Smith than Hog or Parramore Islands on both intermediate and old dunes (Tukey, $P < 0.05$). On young dunes, belowground total biomass is significantly higher on Hog than on Parramore Island (Tukey, $P < 0.05$). On Smith and Hog Islands a trend was apparent for mean dead belowground biomass, increasing with dune age (Fig. 10). The differences were significant only on Smith Island where a difference was seen between the old and young, ranging from a low of 3.16 g/m^2 on the foredune to a high of 186.33 g/m^2 on the old dune, compared nearly significant difference on Hog, which ranged from 7.67 to 54.07 g/m^2 the same dunes (Table 8). Also nonsignificant, the pattern was reversed for Parramore Island, with less variability among dunes, ranging from 7.97 g/m^2 on the old dune to a value of 8.95 g/m^2 on the young dune. On the intermediate and old dunes, values were significantly different among islands (Table 9). Biomass is significantly greater on Smith Island than the others (Tukey, $P < 0.05$).

Vertical distribution of belowground biomass varied among islands and dunes (Table 10). Significant differences were found among depths for both live

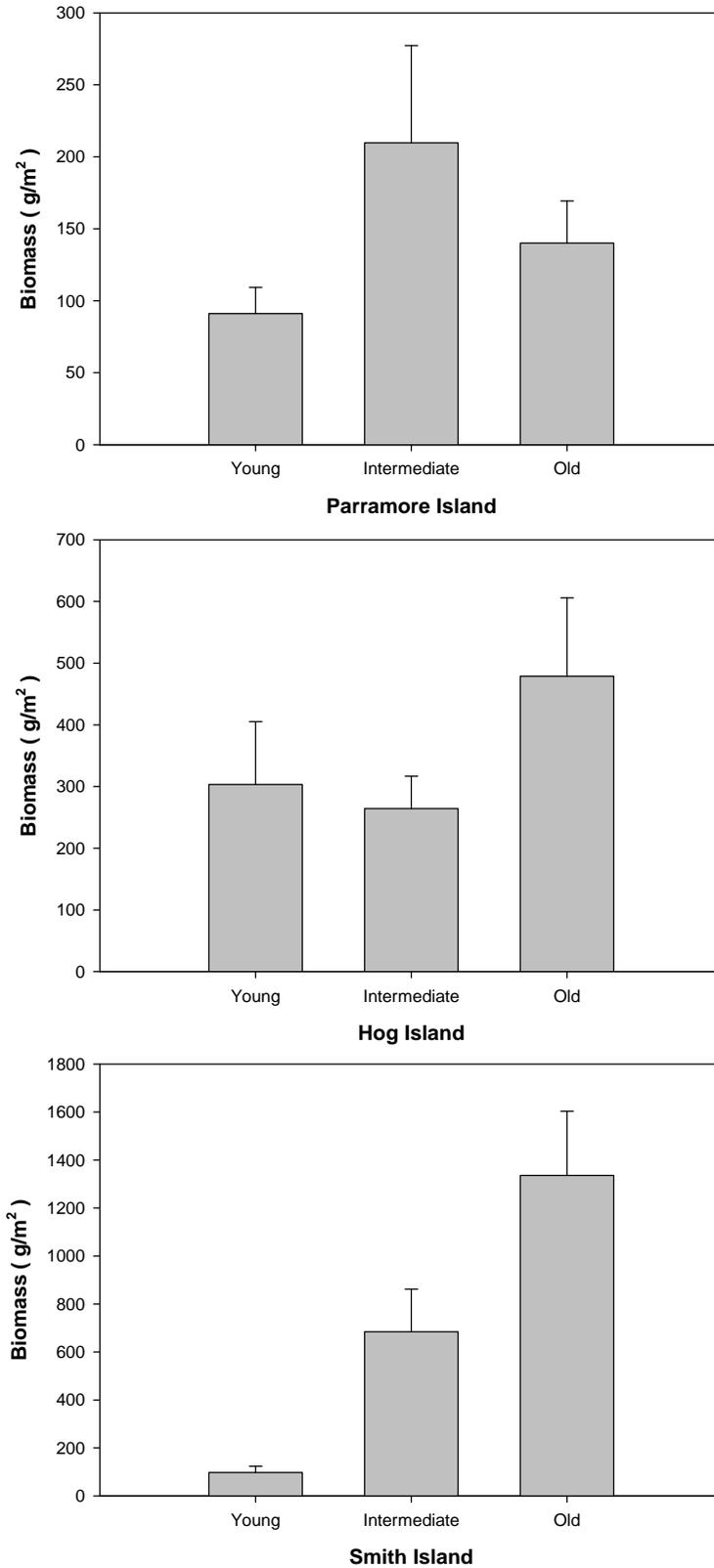


Fig. 9- Mean live belowground biomass per dune on each island.

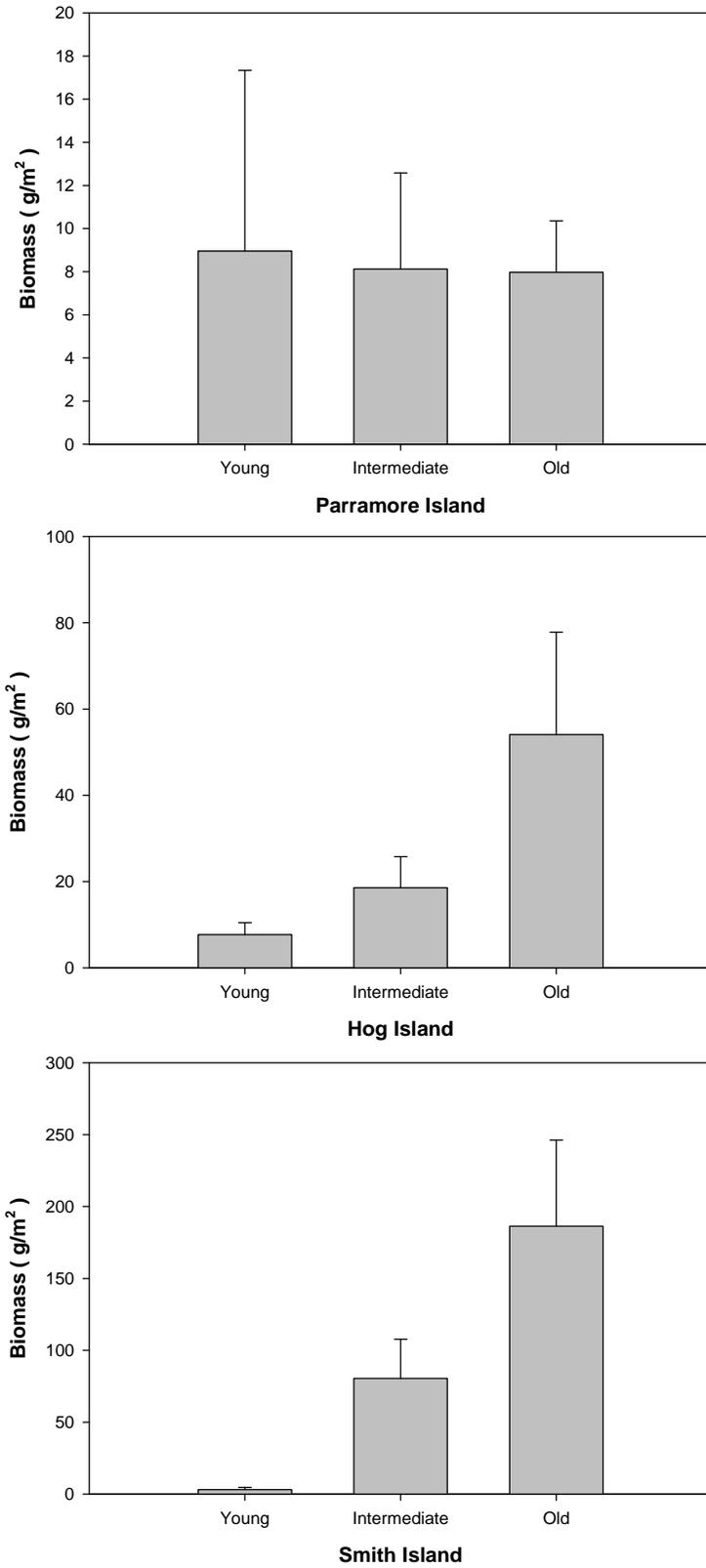


Fig. 10- Mean dead belowground biomass per dune on each island.

Table 10. Belowground biomass per dune on each island. Data are sorted by depth at 10 cm intervals.

Dune	Depth (cm)	Mean Total Biomass (g/m ²)	Mean Live Biomass (g/m ²)	Mean Dead Biomass (g/m ²)	Percent Total Biomass By Depth	Percent of Total Biomass Live	Percent of Total Biomass Dead
Hog- Yng	10	63.47	62.03	1.44	20.41	98	2
Hog- Yng	20	111.03	107.97	3.07	35.71	97	3
Hog- Yng	30	20.67	19.51	1.16	6.65	94	6
Hog- Yng	40	115.75	113.74	2.00	37.23	98	2
Hog- Int	10	158.14	145.01	13.13	55.96	92	8
Hog- Int	20	59.24	56.44	2.80	20.96	95	5
Hog- Int	30	43.82	42.24	1.58	15.51	96	4
Hog- Int	40	21.39	20.35	1.03	7.57	95	5
Hog- Old	10	422.10	376.09	46.02	79.23	89	11
Hog- Old	20	69.88	63.95	5.92	13.12	92	8
Hog- Old	30	29.01	27.35	1.66	5.45	94	6
Hog- Old	40	11.75	11.28	0.46	2.21	96	4
Parramore- Yng	10	21.25	16.16	5.09	21.23	76	24
Parramore- Yng	20	45.90	42.35	3.55	45.86	92	8
Parramore- Yng	30	18.58	18.27	0.31	18.56	98	2
Parramore- Yng	40	14.36	14.36	0.00	14.35	100	0
Parramore- Int	10	31.30	31.30	0.00	14.37	100	0
Parramore- Int	20	62.29	57.48	4.81	28.60	92	8
Parramore- Int	30	88.45	86.24	2.21	40.61	98	2
Parramore- Int	40	35.79	34.68	1.11	16.43	97	3
Parramore- Old	10	53.62	51.66	1.96	36.24	96	4
Parramore- Old	20	31.93	30.61	1.31	21.58	96	4
Parramore- Old	30	37.59	35.77	1.81	25.40	95	5
Parramore- Old	40	24.83	21.95	2.88	16.78	88	12
Smith- Yng	10	28.99	28.23	0.76	28.06	97	3
Smith- Yng	20	27.42	26.32	1.10	26.54	96	4
Smith- Yng	30	24.00	23.74	0.26	23.23	99	1
Smith- Yng	40	22.89	21.84	1.04	22.16	95	5
Smith- Int	10	527.41	479.63	47.79	68.96	91	9
Smith- Int	20	85.97	81.03	4.94	11.24	94	6
Smith- Int	30	105.91	85.48	20.43	13.85	81	19
Smith- Int	40	45.55	38.28	7.27	5.96	84	16
Smith- Old	10	914.08	782.92	131.16	60.05	86	14
Smith- Old	20	468.91	416.36	52.55	30.80	89	11
Smith- Old	30	93.26	90.91	2.35	6.13	97	3
Smith- Old	40	46.00	45.73	0.27	3.02	99	1

(Split-Plot ANOVA, $F= 4.490$, $P= 0.016$) and dead (Split-Plot ANOVA, $F= 3.360$, $P= 0.042$) biomass. On all three islands the oldest dune showed a significant amount of total biomass in the top 10 cm of the profile (Fig. 11), likely influencing the results. Across the study, live biomass in the top 10 cm was significantly greater than that found at the 20-30 cm and 30-40 cm depths (Tukey, $P<0.05$). Dead biomass at the 0-10 cm depth was significantly greater than that found at the 30-40 cm depth (Tukey, $P<0.05$).

ROOT : SHOOT BIOMASS RATIOS. On all three islands, the highest value for root:shoot ratio was found on the oldest dune (Fig. 12). The highest value (10.92) was found on Smith Island and the lowest (1.95) on Parramore. The location of the lowest root:shoot ratio varied among dunes. On Hog the lowest value (1.65) was found on the intermediate dune, while on Smith and Parramore it was found on the youngest dune (1.31 and 0.75 respectively). Root:shoot ratios were significantly different (Table 11) among dunes on Smith Island. Values for the youngest dune were significantly less than on the intermediate and oldest dunes (Tukey, $P<0.05$). Root:shoot ratio was significantly different among islands on the oldest dunes, where values were significantly greater on Smith Island than the others (Tukey, $P<0.05$)

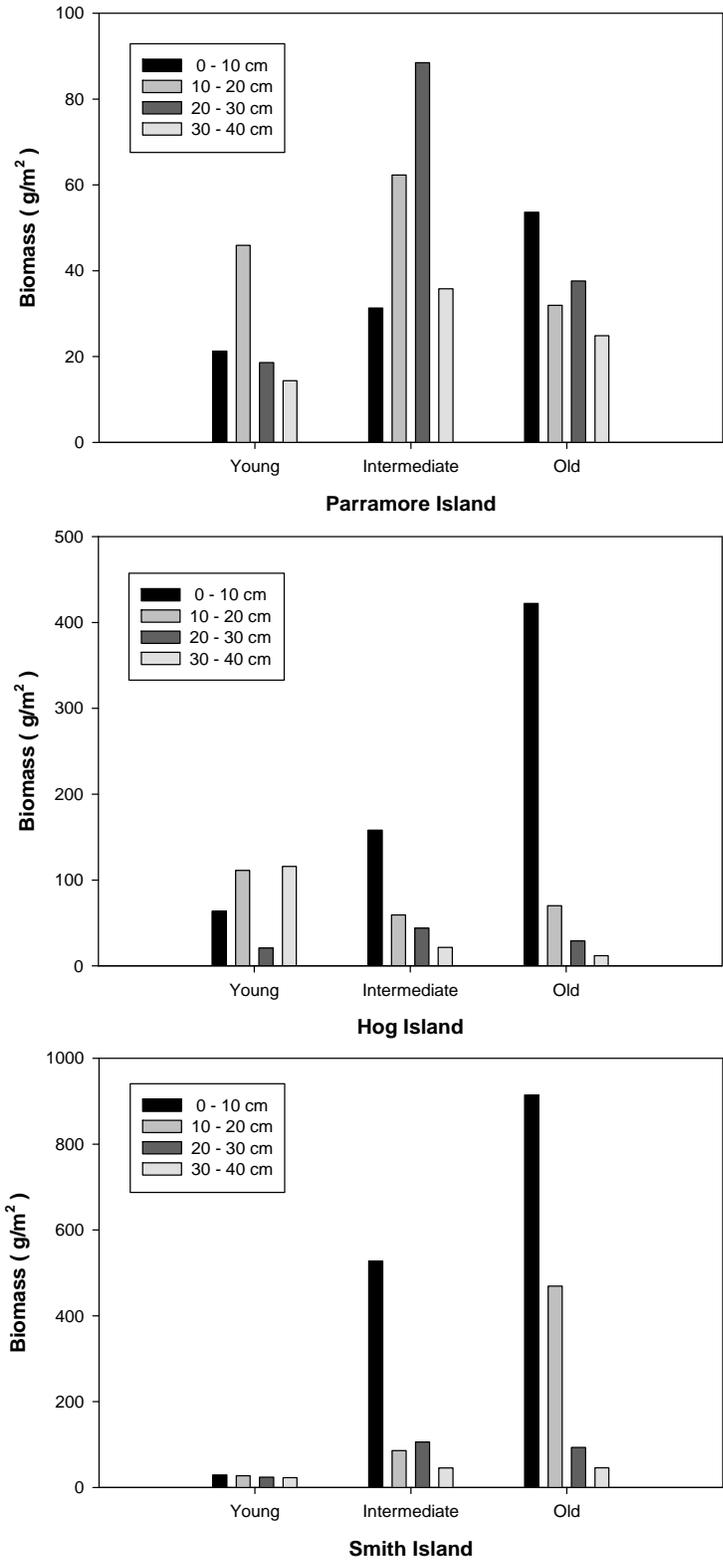


Fig. 11- Belowground total biomass distribution by depth

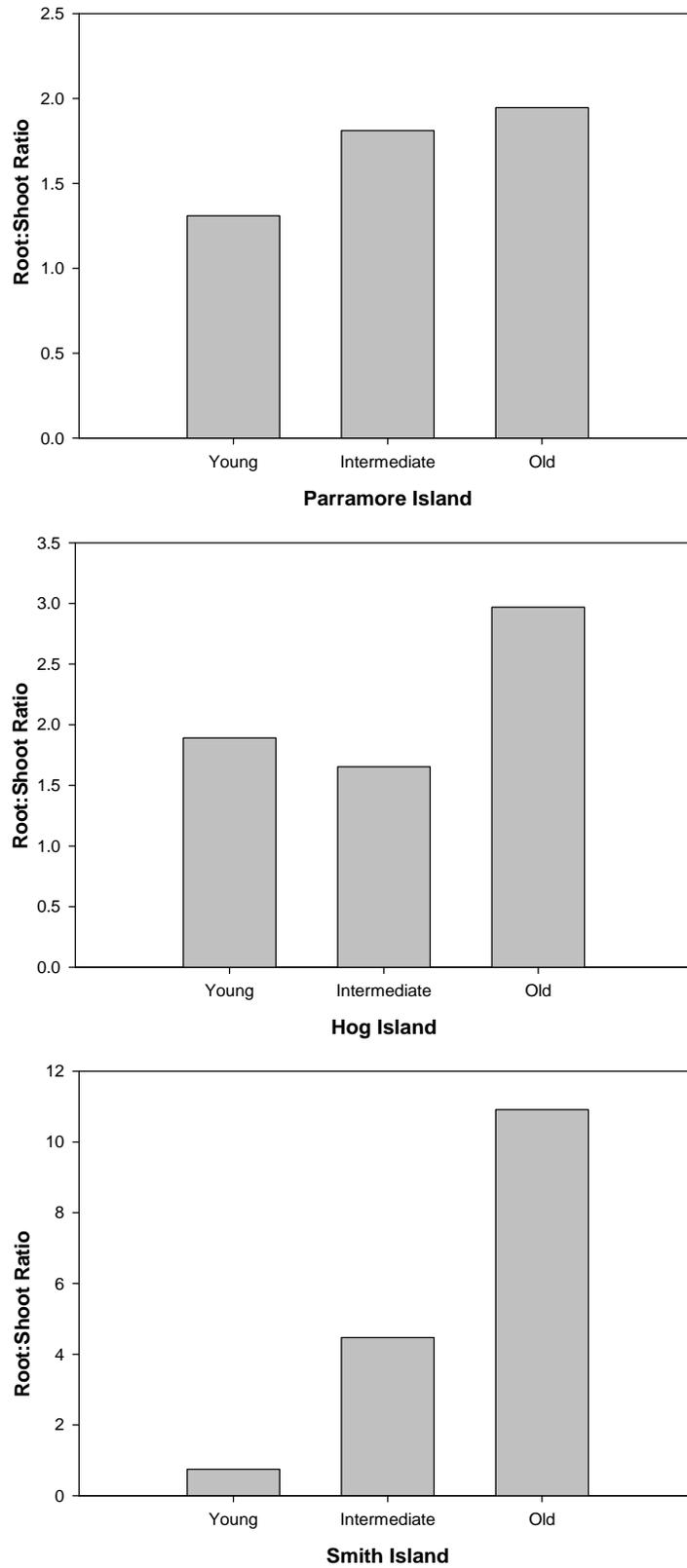


Fig. 12- Root:shoot ratios on each dune on each island

Table 11. 1-way ANOVA results for root:shoot ratio among dunes on each island and among islands on each dune. *indicates a significant difference at the 0.05 level.

Island	F	P
Parramore	1.117	0.337
Hog	0.363	0.698
Smith	8.650	0.001*
Young	0.949	0.395
Intermediate	1.294	0.285
Old	13.112	< 0.001*

SPECIES RICHNESS AND DIVERSITY. Estimates of species richness (Fig. 13) are based on the 40 species collected in sample plots during the study. Ten additional species were collected from the dunes throughout the study, but not found in any plots (Table 2). The older, more mature dune communities exhibited the greatest species richness, varying from 15 species on Smith to 19 species on Parramore. Results varied on young and intermediate dunes, ranging from 6 species on the young dune on Hog and the intermediate dune on Parramore, to 13 species on the intermediate dune on Smith. Both Hog and Smith Islands showed a trend of increasing richness with dune age, while Parramore broke this pattern with a low number of species on the intermediate dune. Shannon index (Fig. 14) values ranged from 6 on the intermediate dune of Parramore and young dune on Hog, to a high value of 19 on Parramore Island. Significant differences (Table 12) in species richness were found among dunes on Smith Island, where the youngest dune had fewer species than the intermediate dune (Tukey, $P < 0.05$). Significant differences were seen among islands (Table 12) on the intermediate dunes, where values for Smith Island were significantly greater than on Hog or Parramore Islands (Tukey, $P < 0.05$).

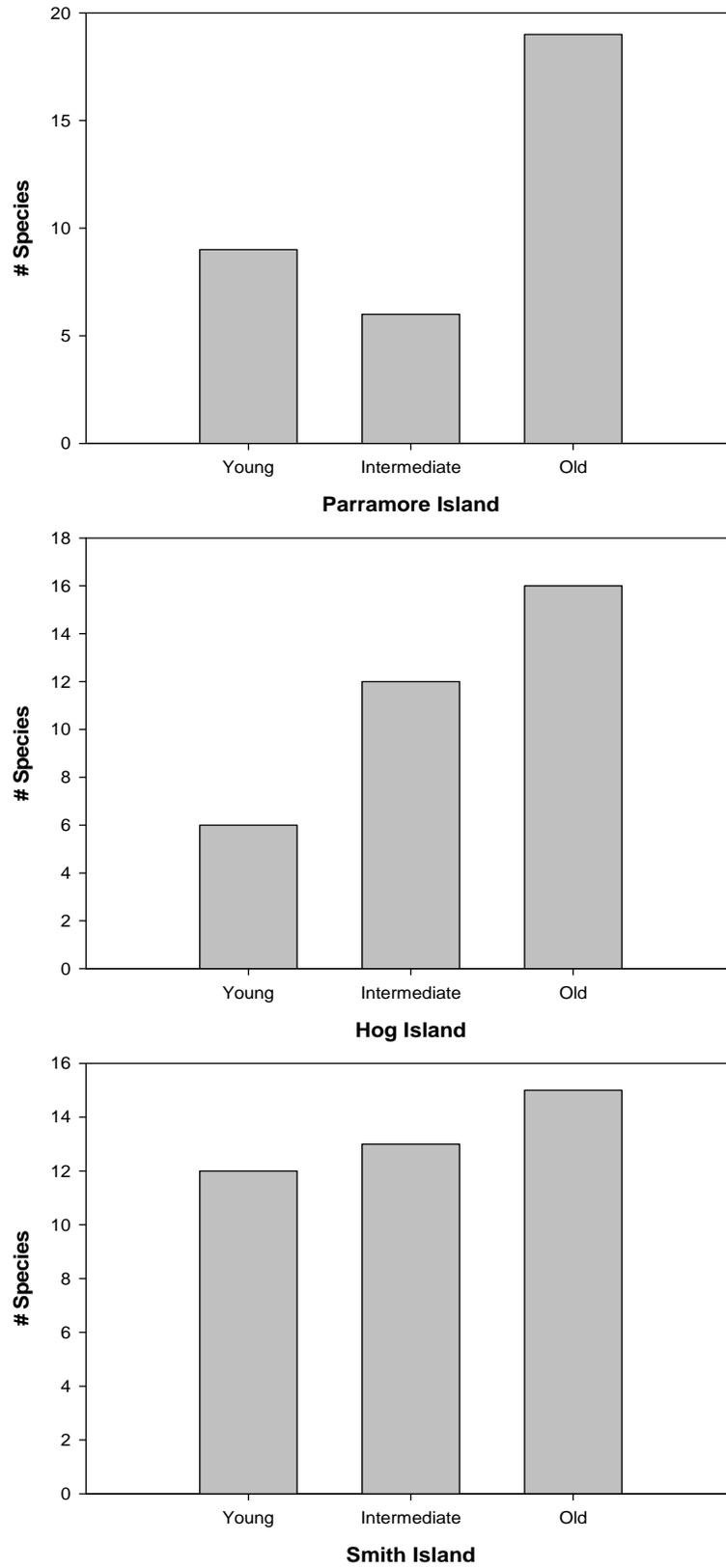


Fig. 13- Species richness on each dune on each island

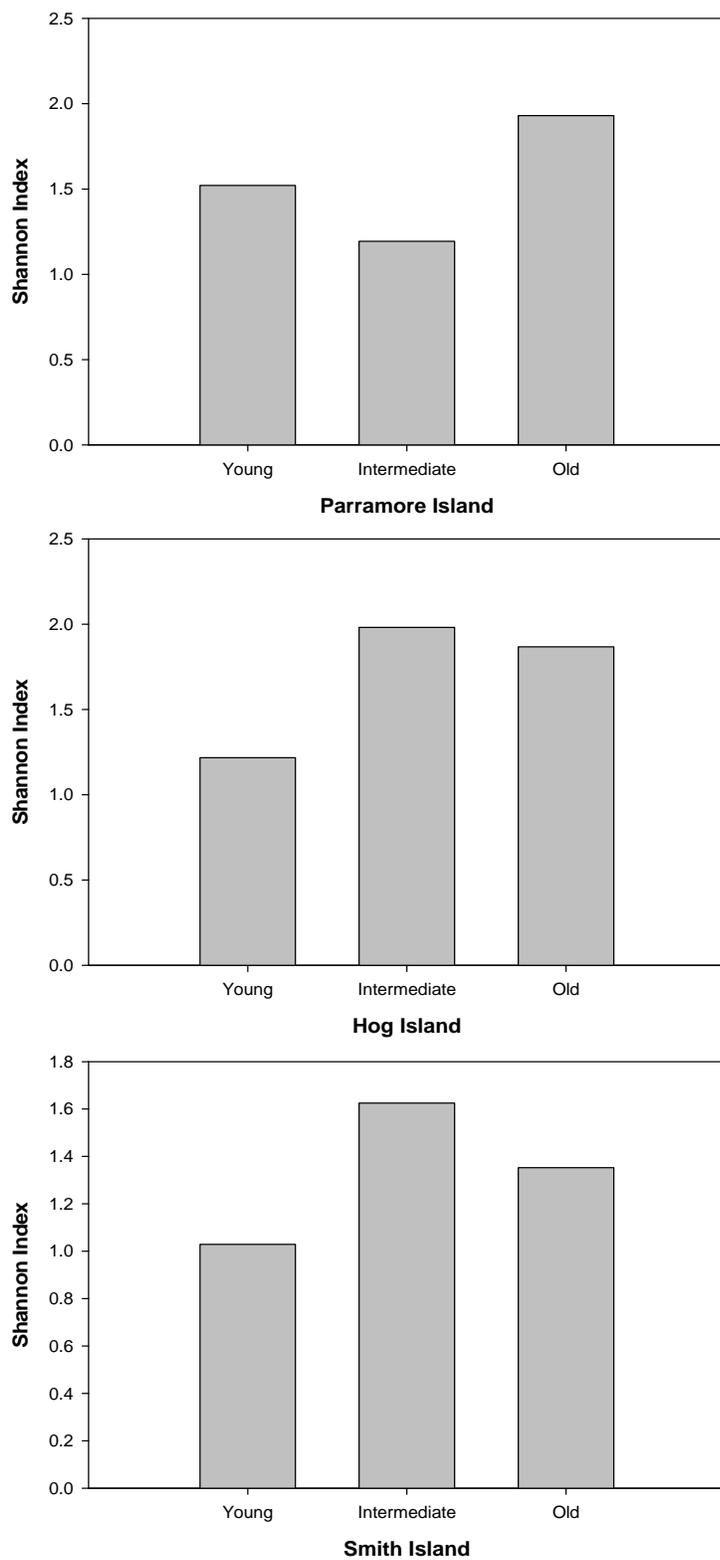


Fig. 14- Shannon Index on each dune on each island

Table 12. 1-way ANOVA results for species richness among dunes on each island and among islands for each dune. *indicates a significant difference at the 0.05 level.

Island	F	P
Parramore	1.560	0.222
Hog	0.781	0.465
Smith	8.650	0.001*
Young	0.352	0.706
Intermediate	12.497	<0.001*
Old	0.075	0.928

HYDROLOGY. As was expected of the tallest dunes, the intermediate sites showed the greatest depth to water. The groundwater surface was not found above a depth of 2.23 m, equal to the length of the auger used in measurement, on both Parramore and Smith islands, as well as at the old dune on Parramore. The shorter, young dunes possessed the shallowest depth to fresh water, ranging from 1.02 m on Parramore to 1.16 m on Hog (Fig. 15). Significant differences (Table 13) in depth to fresh water among dunes were found on all three islands. On Smith the depth to freshwater varied significantly among dunes, with the highest value on the intermediate dune and the lowest on the young (Tukey, $P < 0.05$). Depth to fresh water under the young dune on Hog Island was significantly less than under the others (Tukey, $P < 0.05$). The same difference in dunes was found on Parramore (Tukey, $P < 0.05$). Significant differences in depth to fresh water were found among islands on all dunes (Table 13). Parramore Island had a significantly shallower depth than Hog (Tukey, $P < 0.05$) on young dunes. On intermediate dunes, Hog Island had a significantly shallower depth than Parramore or Smith Islands (Tukey, $P < 0.05$), while on old dunes Parramore Island had a significantly greater depth than the other islands (Tukey, $P < 0.05$).

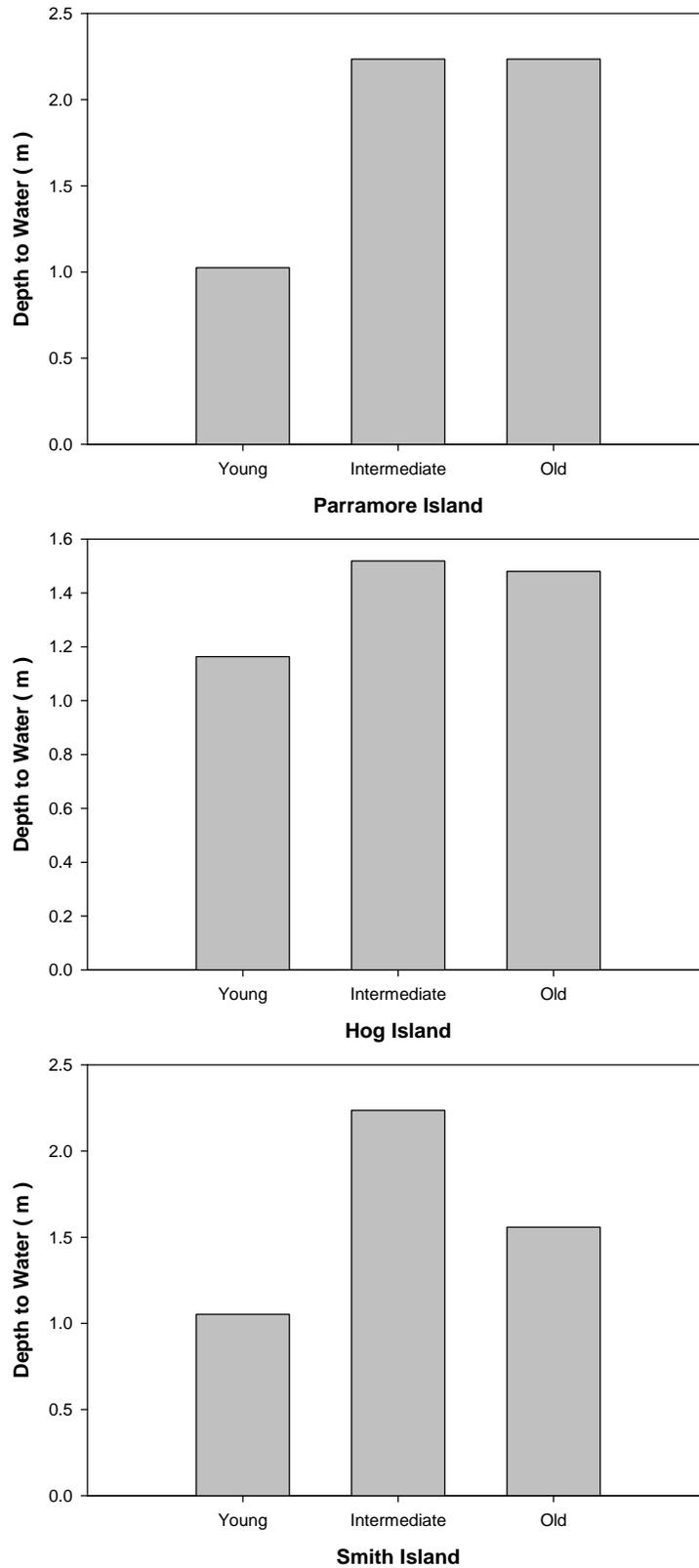


Fig. 15- Mean depth to fresh water on each dune on each island.

Table 13. 1-way ANOVA results for depth to fresh water among dunes on each island and among islands for each dune.

* indicates a significant difference at the 0.05 level.

Island	F	P
Parramore	1029.806	< 0.001*
Hog	3.351	0.045*
Smith	41.761	< 0.001*
Young	3.595	0.036*
Intermediate	24.249	<0.001*
Old	17.190	<0.001*

SOIL NITROGEN. A clear pattern was apparent of increasing total soil nitrogen from young to older dunes on all three islands. Values on young dunes ranged from 0.004 % on Parramore Island to 0.023 % on Smith Island. On old dunes they ranged from 0.017 % on Parramore Island to 0.27 % on Smith Island (Fig. 16). Significant differences in total soil N (Table 14) were found among islands. Values were higher on Smith Island than on Hog or Parramore (Tukey, $P < 0.05$). Among dunes (Table 14) there was also a significant difference in soil nitrogen, where old dunes had significantly more soil N than young or intermediate dunes (Tukey, $P < 0.05$).

Table 14. 1-way ANOVA results for average soil nitrogen, distance inland and dune height among dunes islands and among dunes.

* indicates a significant difference at the 0.05 level.

Variable	Factor	F	P
Soil Nitrogen	Dune	21.238	< 0.001*
	Island	51.080	< 0.001*
Distance Inland	Dune	182.165	< 0.001*
	Island	9.740	< 0.001*
Dune Height	Dune	78.000	< 0.001*
	Island	14.542	< 0.001*

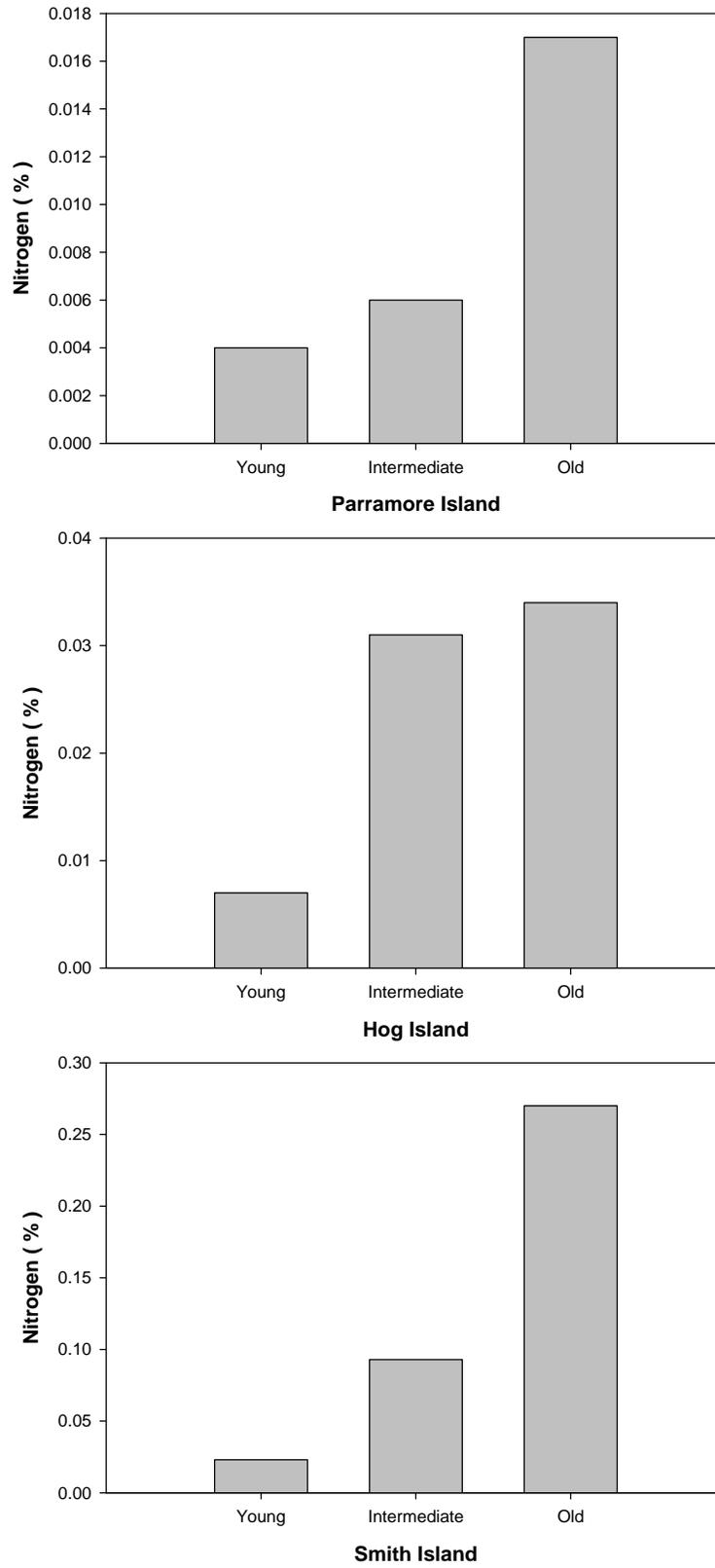


Fig. 16- Percent total soil nitrogen on each dune on each island.

DUNE POSITION. Significant differences in the distance of dunes from the ocean (Table 14) were found among islands and among dunes. All three dunes showed significantly different distance inland from one another (Tukey, $P < 0.05$). Among islands, dunes on Hog Island were significantly further from the ocean on average than those on Parramore or Smith Islands (Tukey, $P < 0.05$).

DUNE HEIGHT. The average height of dunes was significantly different (Table 14) among islands and among dunes. Among islands, Parramore had significantly higher dunes on average than the other islands (Tukey, $P < 0.05$) and among dunes all were significantly different from one another (Tukey, $P < 0.05$), with the highest values on intermediate dunes and the lowest on young dunes.

CORRELATIONS WITH ENVIRONMENTAL VARIABLES. Individual islands exhibited several significant correlations between community structure characteristics and environmental factors. On Hog Island (Table 15) the depth to groundwater was correlated with both aboveground and belowground live biomass. The distance of the dune from mean high tide along the ocean was correlated with depth to fresh water, belowground dead biomass, Shannon Index, and soil N. Dune height correlated with Shannon Index and soil N. A correlation was also found between Shannon Index and soil N.

On Parramore Island, soil N and Shannon Index both correlated with dune position. A relationship was also found between soil N and dune height, depth to fresh water, and the Shannon Index (Table 16). On both Parramore and Smith Islands data for

Table 15. Pearson correlations coefficients (top number) and P values (bottom number) on Hog Island. Depth to water- n= 42, All other factors- n= 45.

	Species Richness	Shannon Index	Depth to Fresh Water	Soil Nitrogen	Dune Height	Distance Inland
Aboveground Total Biomass	-.007 .963	.121 .427	-.298 .056	.112 .463	.119 .436	.046 .765
Aboveground Live Biomass	.004 .980	-.001 .997	-.326* .035	.001 .997	-.003 .986	.004 .981
Aboveground Dead Biomass	-.019 .901	.229 .131	-.084 .599	.210 .166	.227 .133	.081 .598
Belowground Total Biomass	.083 .587	.074 .627	-.300 .054	.132 .389	-.049 .750	.253 .094
Belowground Live Biomass	.079 .606	.053 .731	-.318* .040	.107 .484	-.062 .687	.229 .130
Belowground Dead Biomass	.088 .566	.199 .189	-.097 .541	.260 .085	.049 .747	.345* .020
Root:Shoot Ratio	-.031 .841	-.045 .769	-.264 .091	-.015 .921	-.096 .532	.078 .611
Species Richness	--	.170 .264	-.098 .539	.146 .338	.189 .213	.024 .878
Shannon Index	.170 .264	--	.300 .054	.972** < .001	.891** < .001	.727** < .001
Depth to Fresh Water	-.098 .539	.300 .054	--	.334* .031	.300 .054	.327* .034
Soil Nitrogen	.146 .338	.972** < .001	.334* .031	--	.760** < .001	.546** < .001

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

Table 16. Pearson correlations coefficients (top number) and P values (bottom number) on Parramore Island. Depth to water- n= 15, All other factors- n= 45.

	Species Richness	Shannon Index	Depth to Fresh Water	Soil Nitrogen	Dune Height	Distance Inland
Aboveground Total Biomass	.039 .801	-.264 .080	.368 .177	-.075 .623	.187 .220	-.119 .437
Aboveground Live Biomass	.199 .190	-.203 .180	.135 .632	-.070 .648	.123 .419	-.101 .508
Aboveground Dead Biomass	-.057 .710	-.273 .070	.102 .719	-.085 .577	.179 .238	-.129 .399
Belowground Total Biomass	-.019 .901	-.147 .337	.207 .460	.010 .949	.192 .206	-.024 .875
Belowground Live Biomass	-.004 .978	-.152 .320	.159 .571	.012 .938	.202 .183	-.023 .879
Belowground Dead Biomass	-.127 .406	-.004 .978	.243 .383	-.015 .923	-.020 .894	-.013 .932
Root:Shoot Ratio	-.160 .295	-.158 .300	.031 .912	-.039 .799	.122 .425	-.066 .666
Species Richness	--	.257 .089	-.289 .297	.244 .107	.111 .467	.254 .092
Shannon Index	.257 .089	--	a.	.823** < .001	.217 .153	.887** < .001
Depth to Fresh Water	-.289 .297	a.	--	a.	a.	a.
Soil Nitrogen	.111 .467	.823** < .001	a.	--	.733** < .001	.992** < .001

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

a. not enough data to calculate correlation

depth to water could not be fully measured due to dune height, leading to limited results in calculating correlations.

On Smith Island (Table 17), dune position correlated with all measures of belowground biomass, as well as root:shoot ratio and soil N. Correlations with species richness were revealed for total and live belowground biomass, root:shoot ratio and Shannon Index. Shannon Index was correlated with total and dead aboveground biomass, live belowground biomass, root:shoot ratio, and soil N. All measures of belowground biomass, as well as root:shoot ratio, were correlated with soil nitrogen. Dune height was correlated with total and dead aboveground biomass, species richness and Shannon Index.

Table 17. Pearson correlations coefficients (top number) and P values (bottom number) on Smith Island. Depth to water- n= 26, All other factors- n= 45.

	Species Richness	Shannon Index	Depth to Fresh Water	Soil Nitrogen	Dune Height	Distance Inland
Aboveground Total Biomass	.365* .014	.558** < .001	.021 .920	-.075 .626	.611** < .001	-.112 .463
Aboveground Live Biomass	.506** < .001	.127 .406	-.013 .949	-.090 .555	.180 .236	-.100 .512
Aboveground Dead Biomass	.182 .231	.611** < .001	.052 .799	-.044 .774	.649** < .001	-.084 .581
Belowground Total Biomass	.086 .576	.293 .050	.263 .195	.574** < .001	-.022 .885	.565** < .001
Belowground Live Biomass	.089 .562	.298* .047	.284 .160	.575** < .001	-.018 .908	.566** < .001
Belowground Dead Biomass	.052 .733	.212 .161	.052 .802	.461** .001	-.042 .784	.456** .002
Root:Shoot Ratio	.506** < .001	.371* .012	.261 .198	.489** .001	.104 .496	.474** .001
Species Richness	--	.396** .007	.110 .594	-.013 .930	.411** .005	-.039 .798
Shannon Index	.396** .007	--	.363 .068	.312* .037	.846** < .001	.253 .094
Depth to Fresh Water	.110 .594	.363 .068	--	.363 .068	a.	.363 .068
Soil Nitrogen	-.013 .930	.312* .037	.363 .068	--	-.243 .108	.998** < .001

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

a. not enough data to calculate correlation

DISCUSSION

ABOVEGROUND BIOMASS. The pattern of aboveground biomass seen across the study area suggests there may be both similarities and differences in the functioning of the dune systems. The trend of highest total biomass on intermediate dunes is similar to that found in past studies on Hog Island (Day et al. 2001) and coincides with high Shannon Index values on those ridges. Many studies have found that increased diversity leads to an increase in biomass. The young foredunes showed the lowest biomass, likely due to the higher stress at these locations. Values for this dune on Hog Island were lower than those determined in previous studies (Day et al. 2001), possibly due to increased storm activity (Hayden et al. 1991). Numerous studies have shown factors such as salt spray, overwash and blowouts, all more common on foredunes, to be detrimental to plants, thus leading to decreased biomass (Ehrenfeld 1990, Hesp 1991, Houle 1997). Such factors would be increased by local storms such as hurricanes and northeasters. The oldest dune on Hog Island, similar to Smith and Parramore Islands, showed increased aboveground biomass compared to recent studies (Day et al. 2001), possibly suggesting continued succession as the less dense biomass slowly modifies soil characteristics and topography.

This pattern was also found for dead aboveground biomass on all islands. It seems reasonable that there would be little dead biomass on the young foredunes as these are commonly impacted by storm waves, washing away dead biomass. The high values on the intermediate dunes are a result of the lack of flooding, in addition to high amounts of live biomass and the resulting seasonal die-off. A correlation between dune height and

dead biomass on Smith Island, where the intermediate dune is significantly taller than those around it, supports this idea that more dead material is left intact since flooding is less common on the taller dunes. Though not significant, a similar relationship was found on Hog Island, which is less exposed relative to the dunes on Smith.

Results for total and live aboveground biomass on individual islands indicate that the systems on different islands may be controlled by different factors. As shown in other studies on Hog (Day et al. 2001) and other grassland sites (Hesp 1991, Davy and Pigueron 1993), the availability of water is a major factor controlling biomass on barrier islands. Contrary to past results on Hog Island (Day et al. 2001), the positive relationship between depth to water and aboveground live biomass seen there suggests other factors may be more influential. Some studies suggest water may not be as limiting as it would logically seem since plants can adapt via lower biomass and leaf area, while increasing their root system. In such situations, soil nutrients may be more limiting (Ripley and Pammenter 2004). Research has also found that while nutrients and water are common limiting factors, other factors such as salt spray, overwash and soil salinity may influence plant growth in some situations (Houle 1997). Water was not shown to be a significant factor on either Smith or Parramore Islands, though lack of complete data due to dune height surely influenced these results.

No other direct correlations were found on Parramore or Hog Islands to explain what may be controlling aboveground biomass, but on Smith Island a positive correlation with species richness was found. Some effect of diversity may be stabilizing the plant community, allowing the available resources to be better used and maintaining high biomass values even on tall, water stressed dunes. Research on other plant communities

and assemblages has shown that, under drought conditions, increased species richness leads to increased biomass (Mulder et al. 2001). Diversity was shown to increase with dune age on both Hog and Parramore Islands, suggesting a similar, though weaker, relationship is likely. This also suggests that it is other, unmeasured factors associated with the age of the dune that are ultimately controlling aboveground biomass on the islands. Factors such as increased organic matter, reduced soil salinity and salt spray, and increased soil nutrients, all associated with dune community succession, could have more impact than the depth to a fresh water table.

BELOWGROUND BIOMASS. There were no easily identifiable gradients of belowground biomass when the study area as a whole was considered. Total belowground biomass values varied greatly among the islands. The root mass on Parramore Island may be a result of increased stress. The young dune had clearly been recently overwashed and had built up little elevation since. The intermediate dune was the tallest of any across the entire study area. As Ehrenfeld (1990) suggested, small changes in elevation can lead to significantly more stress on the plant community. The high root mass on Smith Island may be a result of increased resources. Backbarrier flooding onto the dunes may deposit larger amounts of nutrients than are made available to the less exposed dunes on Hog and Parramore Islands. The old dune on Smith also showed a deeper organic layer, likely making more soil N available for root growth (Houle and Imbert 2001). The importance of soil nutrients, including nitrogen, on coastal plant community structure and biomass patterns has been shown in numerous studies (Ehrenfeld 1990, Bowman et al. 1993, Day 1996, Jones et al 2004). Even on Smith

Island, soil nitrogen values are still low compared to other systems, to the point of being limiting (Hayden et al. 1991).

Each island showed high and low means on different dunes. Stevenson and Day (1996) found similar results in their study of fine root biomass on Hog Island, where values were highest on the intermediate dune and decreased inland with age. The foredune was also found to be lower than the intermediate, but higher than the oldest dune. Results on Hog Island from the current study are counter to the findings of lower biomass on the intermediate dune, followed by the young and old dune. Further complicating an effort to determine a trend, the other islands each showed high and low means on different dunes. The young dunes on Smith and Parramore Islands had the lowest values for total belowground biomass, while on Hog Island the intermediate dune was lowest. Like Hog, values were highest at the old dunes on Smith Island, but on the intermediate dune on Parramore. Belowground dead biomass values increased with age on Hog and Smith, but decreased on Parramore, while values for live biomass followed the trends for total biomass. Changes in species composition such as the decline in *Ammophila breviligulata* and increase in *Schizocyrium scoparium* could account for the change in belowground biomass across Hog Island. Among islands, a more identifiable trend was expected. The lack thereof could be a result of different species combinations, though further analysis would be required.

The vertical distribution of roots on Hog Island was similar to that found in previous studies (Stevenson and Day 1996). On the older, taller dunes the majority of fine roots were located within the first 20 cm, dropping off quickly after that point. Other studies suggest that roots remain at a shallow depth on dune systems due to greater

nutrient supply (Schubauer and Hopkinson 1984, Houle and Imbert 2001) or to more rapidly absorb surface water if the fresh water lens is too deep for use (Ripley and Pammenter 2004). In contrast, the foredune showed a more even distribution of roots, possibly due to the shallower water table.

As with aboveground biomass, correlation results varied among the islands. The relationship between depth to water and belowground biomass on Hog Island varies from past results that found biomass increasing with decreasing depth to water, a negative correlation. Too little data was available to judge the results of this relationship on Smith and Parramore Islands. Increased biomass with increasing depth to water suggests another factor may be more strongly influencing roots. The positive relationships with increasing dune age on Smith and Hog may indicate that root biomass is increasing as dune systems become more established. Studies in other systems have found increased belowground biomass in older habitats or in those further along in succession. The correlations found between dune position and both soil N and Shannon Index lend support to this. Though a significant relationship between these values and measures of belowground biomass were only found on Smith Island, studies have clearly shown the positive effect of increased soil nutrients and diversity, in stressful conditions, on root biomass (Day 1996, Mulder et al. 2001).

ROOT:SHOOT RATIO. The high root:shoot ratio on the oldest dunes of all islands studied is likely a result of increased organic matter accumulation associated with older, more developed dunes. In relatively nutrient poor habitats such as this, organic matter mineralization may provide a significant source of available nutrients, leading to

more shallow surface roots and an overall increase in root biomass (Houle and Imbert 2001).

The correlation between root:shoot ratio and N on Smith Island indicates that the increasing availability of nitrogen with dune age is having an effect on biomass allocation. Though many studies have shown that plant biomass allocation to roots tends to decrease with increased soil nutrients (Bowman et al. 1993, Chapin 1991, Day et al. 2004), it is possible a threshold at which this trend begins is not reached in the barrier island habitat. Though soil total nitrogen increased with dune age, the concentrations are still low compared to other sites, as is common on coastal dunes (Ehrenfeld 1990). With a greater available supply of soil nitrogen, allocation would likely shift aboveground, but in this situation it appears increased nitrogen availability may be promoting increased root biomass. Alternatively, some other factor also related to increasing dune age and development may be causing the observed pattern. Higher organic matter may be promoting the growth of roots at shallower depths and of belowground biomass overall.

On Hog Island, root:shoot ratio is higher on the young dune than the intermediate, counter to the pattern seen on other islands. Among the three islands, the foredune on Hog Island was the most developed, based on height and width. Plant species evolved to survive on foredunes have extensive root systems which maintain dunes during storm events, creating a more stable environment for the plant. These larger, more established dunes on Hog may, as a result, have increased root structure.

COMMUNITY COMPOSITION. The community composition varied somewhat from recent studies on Hog Island. The contribution of *Ammophila breviligulata*

decreased through the late 1990s (Day 2001). While it has long been considered a key species in coastal dune communities, the east coast has seen a significant decrease in *A. breviligulata* over the last few decades. It has been proposed that the species has suffered from increased herbivory from a pathogenic nematode (Seliskar and Huettel 1993).

Where once it was the major contributor to biomass on Hog Island dunes, it is no longer the dominant species on any of the dunes sampled, though it does account for one-third of the biomass on the young foredune. The species' dominance there is a change from past studies, which found little *A. breviligulata* on the foredunes, possibly due to the slower accretion of sand because of the expansive width of the beach (Day et al. 2001). More frequent storms since the last studies on Hog Island's dunes may account for an increase in sand accretion and the resulting improvement of conditions for *A. breviligulata*.

Though not as much as on Hog, *A. breviligulata* contributes a substantial proportion to the biomass of the foredunes on both Parramore and Smith Islands. The only other site across the entire study area on which it was a significant contributor was the intermediate dune on Smith Island where it accounted for nearly fifty percent of the biomass. Located on the southern tip of the island, this site is subject to frequent overwash, providing ideal conditions for *A. breviligulata* growth. Overall, this trend may be a return to more traditional habitat patterns for the species, as past studies have found it to decrease in importance with dune age (Wallen 1980, Ehrenfeld 1990) and dominate on nearshore dunes. Alternatively, as suggested by Day (2001), it may be part of a regular cycle of die off and community composition change resulting from extensive droughts and state change events, such as the tropical storms and northeasters that affect the islands of the VCR on a yearly basis (Hayden et al. 1991).

Spartina patens remained the single most frequently occurring and most common dominant species among all sampled sites. The pattern of decreasing biomass with dune age noted by Dilustro and Day (1997) held mostly true for all three islands. Biomass values for *S. patens* on the oldest dune of Hog Island were slightly greater than on the youngest, though this can likely be explained by the continuing decline of *A. breviligulata*. On Hog and Smith Islands, *S. patens* remained dominant over *A. breviligulata* as noted in past studies (Dilustro and Day 1997). On Parramore, *Panicum amarum* has replaced *S. patens* as the dominant foredune species, again followed by *A. breviligulata*. The foredune here was weakly established with a low elevation and appeared prone to overwash. Repeated burial represents a situation for which *S. patens* is poorly adapted, providing a possible explanation for the difference at this site (Ehrenfield 1990).

As noted by Day (2001), the graminoid species *Schizachyrium scoparium* continued to increase in importance on the older dunes of Hog Island. Though *S. patens* was the dominant species, *S. scoparium* accounted for nearly a quarter of the biomass on the oldest dune. On the intermediate dune it was the dominant species, with forty percent of the biomass. Day (2001) proposed the increasing frequency and dominance of this graminoid species may indicate a movement towards the next phase of succession on the dunes. Other studies have found *S. scoparium* to be important on coastal secondary dunes (Stalter and Odum 1993). The plant was not nearly as important on either Smith or Parramore Islands; however, on both, *Eragrostis spectabilis* was an important component of the community on older dunes. *S. scoparium* and *E. spectabilis* are both large 'clump' forming graminoids that can contribute to more rapid development of organic matter in

the soil. Such development is essential for the growth of shrubs and, later, maritime forests in the process of succession on coastal dune systems (Stalter and Odum 1993).

SPECIES RICHNESS AND DIVERSITY. On Hog and Smith Islands, species richness increased with dune age as is commonly the case along chronosequences with increasing nutrient levels and system maturity, until the system reaches a point at which specialization and dominance of particular species take over, reducing diversity (Tillman 1982). The intermediate dune on Parramore Island exhibited the lowest richness of the study area. This change in the expected pattern may be explained by the large height of the dune, combined with its narrow ridge width and a greatly diminished foredune, relative to the other islands. All of these factors, along with low soil nitrogen and a water table below 2.2 m, led to an even more stressful environment where only a few suitably hardy species could survive. Where positive correlations between increasing height and diversity, measured through the Shannon Index, were found on Hog and Smith Islands, these were not significant on Parramore. Ehrenfeld (1990) found that small changes in dune height could have significant ecological effects as numerous stresses increased. Accepting this abnormality, Parramore Island shows the same pattern of increasing species richness with dune age as the other islands. Similar to the stressed, tall dunes of Parramore Island, the young dunes on Smith and Hog Islands had low Shannon Index values, likely due to the constant stress of the environment there, where fewer species have adapted for survival. The high richness values on old dunes across the entire study area are linked to increasing diversity with system age. The correlation between Shannon

Index and dune position on Hog and Parramore Islands further supports this. A positive, but not significant, correlation is also seen between the factors on Smith Island.

CONCLUSIONS

Important for their many functions including protection of the mainland from large storms, habitat for numerous species, and economically important recreational and commercial uses, barrier islands can be found across the globe. An understanding of the structure and function of the communities and ecosystems on them is essential for the survival of these islands in an increasingly developed world. The results of this study reveal that there are significant differences in biomass (Fig. 17) and diversity among both the islands and the different age dunes. These differences likely relate to variations in dune age and morphology, plus the effect on and interaction with environmental factors such as depth to water and soil nutrient content. Islands such as Parramore, where conditions were found to be relatively more stressful, exhibited different trends in biomass than did Hog and Smith Islands, which were more similar in their geomorphology. Though the system as a whole is highly stressed and resource limited, small changes in factors such as dune height, dune position or the availability of water and nutrients can lead to significant differences when comparing among islands. Adaptations to low soil nutrients and water availability are seen as root biomass remains high close to the surface where organic matter is higher and water accumulation after rains and in pore spaces can be most effectively utilized. Increased allocation of biomass to roots with increased dune age also indicates nitrogen remains a limiting factor across the study area. Correlations between morphological characteristics, such as dune position and height, and diversity suggest that in this stressed system, biomass and diversity are both increasing with dune age or development.

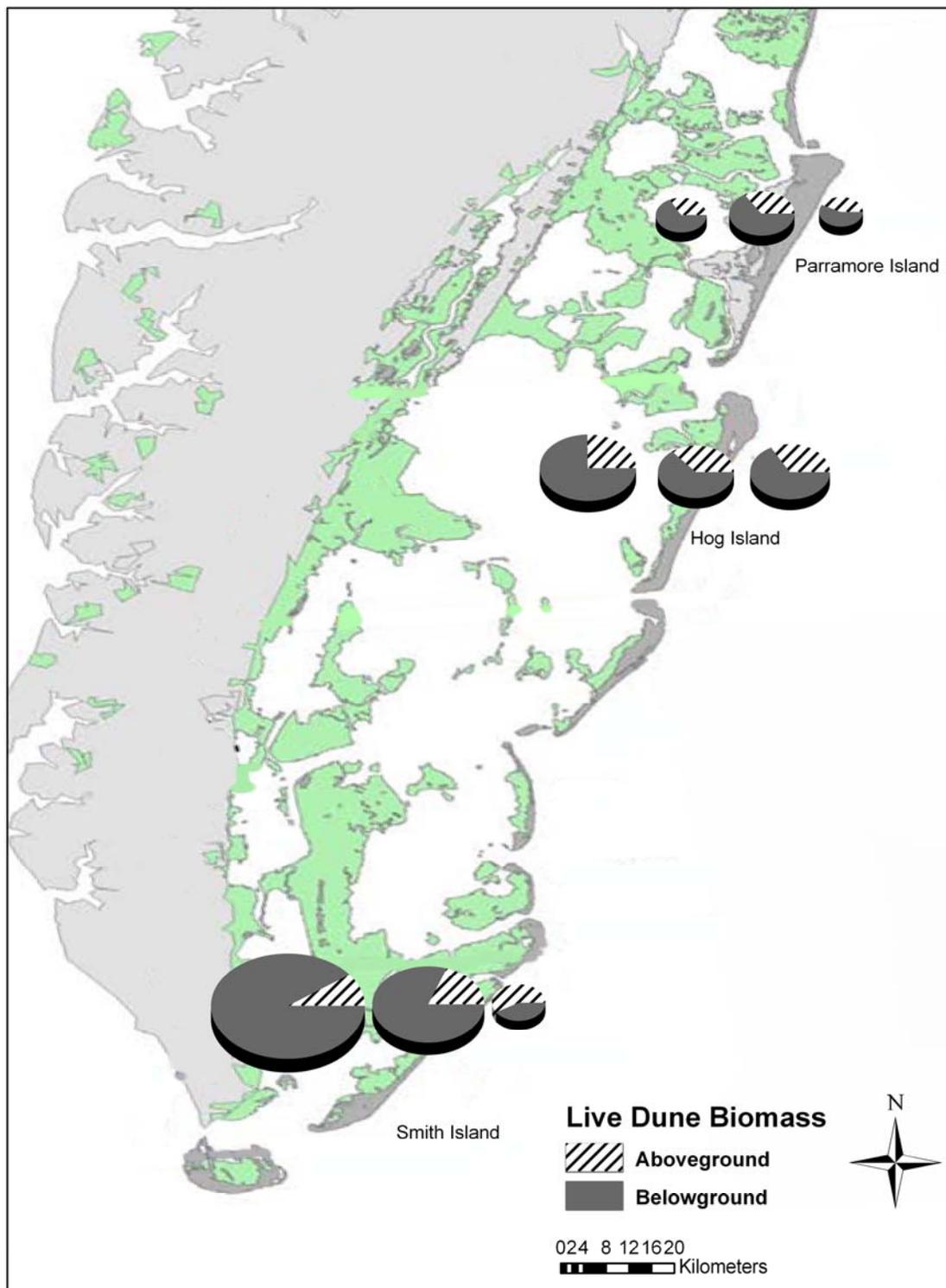


Fig. 17- Total live biomass values across the study area.

Similarities on all islands in the pattern of biomass and diversity allocation among dunes suggest that different islands may be looked at the same way. However, results indicating that the factors controlling these patterns differ among islands and dunes create the need for more research to better understand them. Long term conservation, or use, of these islands will require such understanding if they are to be maintained in the stressful conditions under which they exist.

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Holsinger, J.R., J. Shafer, D.W. Fong, and D.C. Culver. 2008. *Gammarus cohabitus*, a new species of subterranean amphipod crustacean (Gammaridae) from groundwater habitats in central Pennsylvania, USA. *Subterranean Biology* 6: 31-41.

RESEARCH SUBMITTED AND IN PREPARATION:

- Interisland variability of dune plant community structure on Virginia's barrier islands
- GIS analysis of range and habitat characteristics of the amphipod crustacean genera *Stygobromus* and *Bactrurus*

SCIENTIFIC PRESENTATIONS:

Shafer, Justin and F. Day. 2009. Interisland variability of dune plant community structure on Virginia's barrier islands. Long-Term Ecological Research All Scientists Meeting, Estes Park, CO.

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Shafer, Justin. 2003. GIS Application in the Development of a Comprehensive Conservation Plan: Great Dismal Swamp National Wildlife Refuge. Virginia GIS Users Conference, Richmond, VA.

GRANTS RECEIVED:

- Assisted John Holsinger in writing of GIS aspects of Cave Conservancy of the Virginia grant and extension for work on the creation of a database for the study of the amphipod genera *Stygobromus* and *Bactrurus*.