Inter-Island Variability in Above and Belowground Plant Biomass in Interior Marshes on the Virginia Barrier Islands

by
Staci B. Blecha
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Approved by:

Frank Day (Director)

G. Richard Whittecar (Member)

Rebecca D. Bray (Member)

ABSTRACT

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Staci B. Blecha
Old Dominion University, 2010
Director: Dr. Frank P. Day

The Virginia Coast Reserve's Long Term Ecological Research (LTER) site is of great interest because the barrier islands have been migrating, rapidly at times, and are exceptionally dynamic. The barrier islands have tidal saltwater marshes on the lagoon side and freshwater marshes on the island interiors. In these interior marshes on North Hog Island, South Smith Island, and North Parramore Island, salinity and depth to water table were measured to determine if these factors were influencing biomass and biomass allocation patterns in the marsh. Hog Island had the freshest interior marshes (0 and 0.7 ppm), and the most diverse (H'=0.84 and 1.026), but had the least aboveground biomass (36.69 and 161.92 g/m^2). Smith and Parramore Islands were more saline (18.6 and 19.8 ppm, respectively), less diverse (H'=0.504 and 0.745), and had higher aboveground biomass (406.86 and 563.32 g/m^2). The saltiest marsh, on Parramore Island, had the most aboveground biomass. Belowground biomass was primarily located in fine roots (less than 5 mm diameter). Depth did not have a significant effect on belowground biomass, though this could be due to a small sample size. Roots were found to be related to the vegetation type, and were located primarily in the top 20 cm of the soil, with the exception of Smith Island's marsh. Salinity, depth to water table, and soil nitrogen were all found to be different among marshes. Root: shoot ratios were highest in Hog Island's eastern marsh (0.5), and lowest in Parramore Island's marsh (0.12), and were significantly different. Correlation analysis suggests that salinity, nitrogen, and water table depth may have an influence on biomass and biomass allocation, though r values were not significant due to a low sample size. The results indicate that each island has a unique set of factors influencing the amount of belowground biomass and how biomass is allocated. The depth of the water table may be influencing root allocation in Smith Island's marsh, since its water table is deep, and causing other marshes to have anoxic soils that hinder root development and growth. Diversity and biomass were found to have an inverse relationship, with the most diverse marshes being the least productive. This relationship between diversity and biomass suggests heavy resource competition in these marshes. These barrier islands are different from each other and should be managed individually.

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I would also like to thank Robert Forgey for his continued support throughout this process. Most of all, I'd like to thank my mother, Lorie Blecha, for tolerating a little girl that loved to play in the mud, and whose love and patience has always carried me through any obstacle.

This thesis is dedicated to my mother who taught me that I could do and be anything I wanted to, as long as I worked hard.

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INTRODUCTION

Coastal barrier islands are dynamic ecosystems. Located on the fringes of mainland areas, it is believed that they were formed during the early Holocene. Melting glaciers caused sea level rise and formed areas behind beach ridges at the end of the Holocene. Barrier island systems have a unique role in ecosystems. They protect the mainland from storm damage, provide a unique habitat for wildlife, and are excellent habitats for studying succession, since they are constantly migrating and changing (Hayden et al. 1991).

Plants on barrier islands systems are subjected to many stressors. Physical events, like storms, can cause overwash, erosion, and accretion. These sudden abiotic changes often cause nutrients to be lost out of systems. Frequent storm events cause overwash events that salinize freshwater. Sometimes, these events are so severe that they can induce state changes and cause climax communities to shift (Ehrenfeld 1990).

Fresh water comes solely from the accumulation of rainwater into a lens. Lenses are zones of fresh groundwater that are highest at mid-island and can extend downward tens of meters below sea level (Figure 1). These lenses result only from rainfall since islands are too far from the mainland to be connected to any other ground water systems. Interior plant communities, therefore, depend on rain for the lens to form and build up. Dry seasons can reduce the height and volume of the lens, and lead to salt water intrusion beneath interior areas. This freshwater lens can be contaminated with salt water when [1]there is severe drought or when sea levels rise, subjecting the interior marsh communities to salt stress (Figure 1). The frequency and severity of salt water events

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*Thesis prepared in the style of Wetlands.

can influence the plant communities present (Nielson 1999).

(a)

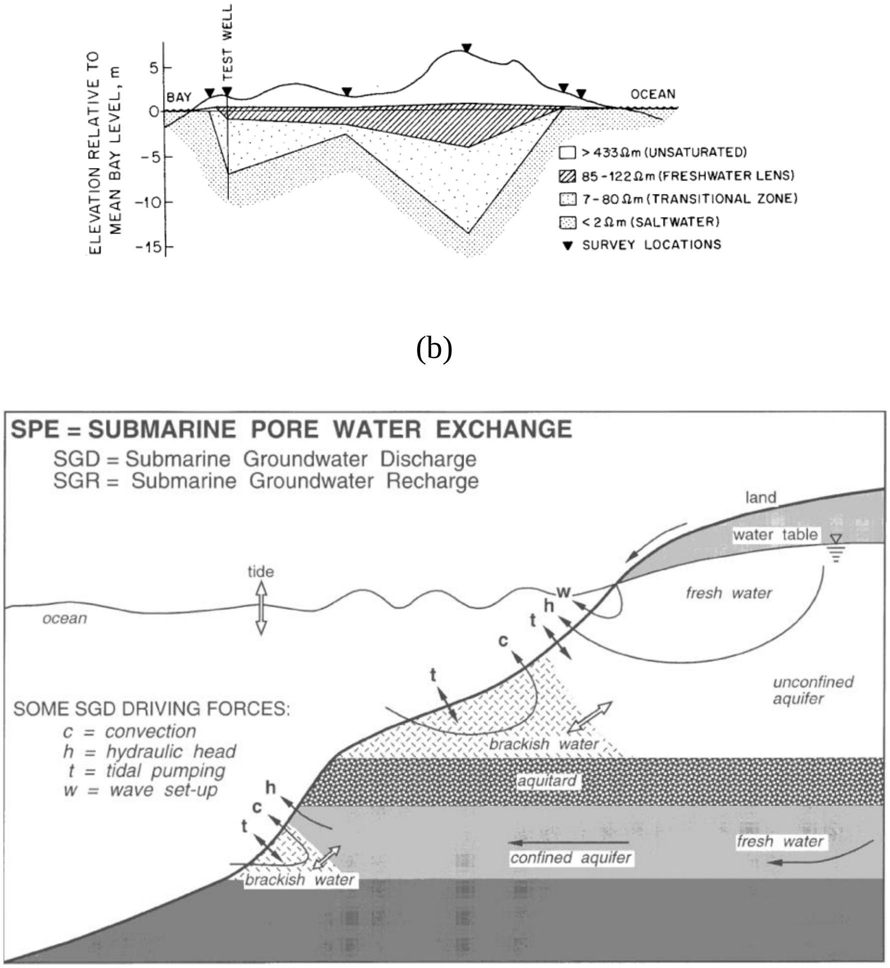


Figure 1. The dynamics of saline and freshwater in barrier island and coastal systems. A. shows the freshwater lens on barrier islands. Freshwater discharges from the lens into the surrounding salt water. Over wash events cause salinization of interior marshes (Bokuniewicz and Pavlik 1990). B. General groundwater dynamics for coastal systems showing outflow of freshwater lens into surrounding salt water (Burnett et al. 2003).

New factors, such as urbanization of coastal areas are further complicating this story. As areas are developed, wetlands are lost because of habitat destruction. Along with this problem, sea level rise due to climate change is resulting in more severe storm damage to coastal systems. More frequent storms are causing more over-wash events leading to the salinization of freshwater lenses and the decline of salt intolerant plant species (Herwitz and Wunderlin 1990).

Within a barrier island chain, both biotic and abiotic pressures can be quite different. Abiotic pressures, like salinization of freshwater, erosion, and accretion depend heavily on the size and shape of the island. Less substantial islands are able to shift quickly, while larger islands move much slower. Smaller islands also experience overwash more frequently than bigger islands (Hayden et al. 1991). Biotic changes, like plant species composition, are almost constant. In addition to species arrival and extinction, the physical setting is highly influential, since it changes frequently (Macarthur and Wilson 1967).

Individual barrier islands have unique habitat zones. Because of their constant migration, a series of dunes and swales form within the island (Figure 2). These series of dunes and swales differ in age, with youngest dunes being formed on the ocean side. Interior swales often contain freshwater marshes, while shrub thickets develop in older areas that are in the later stages of succession.

Freshwater wetlands along the coast are also in danger because of the effects of sea level rise. As the rate of sea level continues to increase, coastal areas are subjected to a decrease in sediment deposition, habitat changes and loss, the inward retreat of wetlands, and aquifer contamination. This flooding causes increases in salinity and water

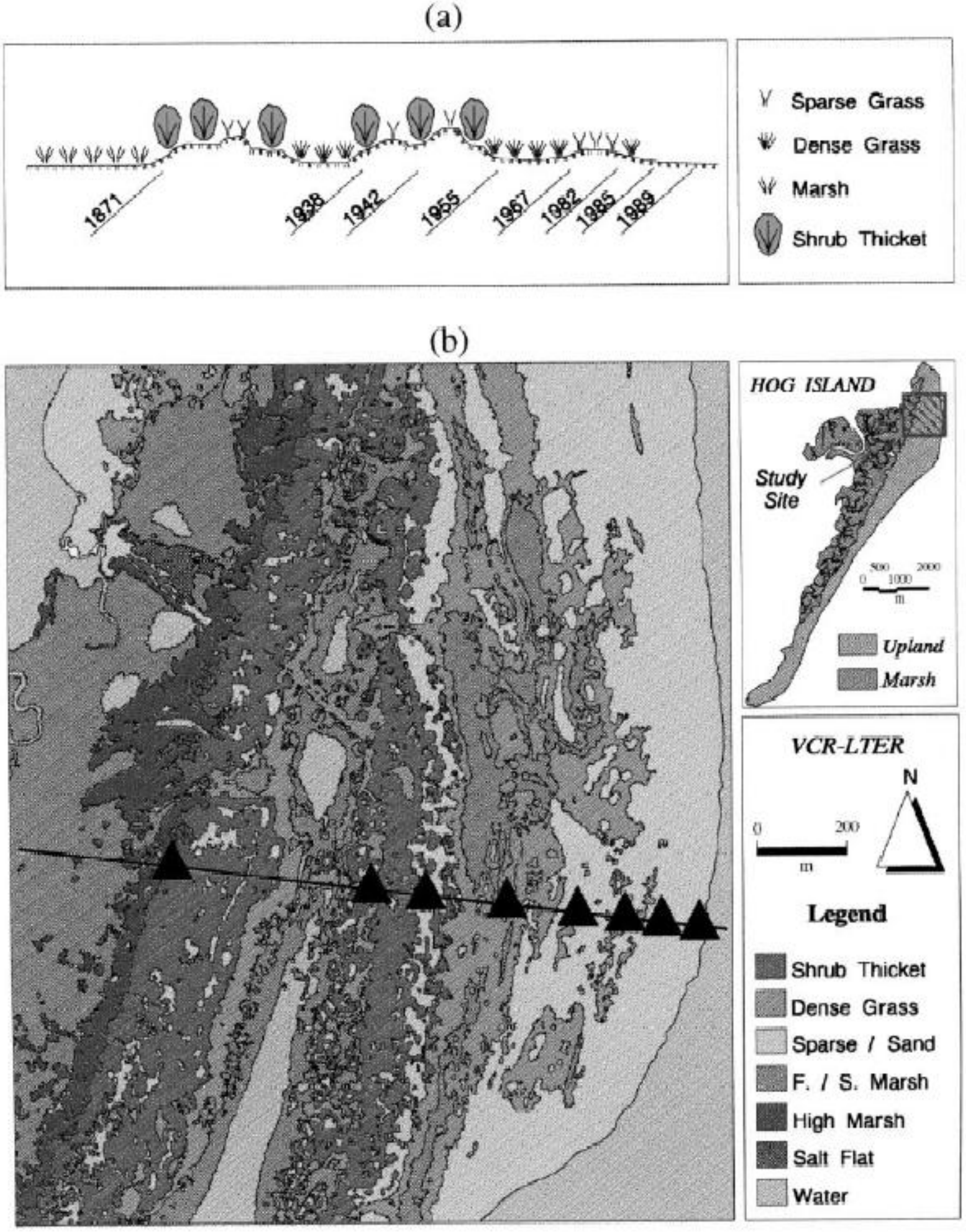


Figure 2. a. Typical barrier island cross section with dense grass areas representing interior marshes and sparse grasses representing dune areas. b. Aerial view of typical habitat types on barrier islands. (Hayden, personal communication).

logging, which leads to anaerobic conditions (Anderson 2002). Salinization of wetlands creates more salt water marshes on the coast with fresh water wetlands in further inland areas. With increase urbanization, these freshwater wetlands are left with less favorable areas to migrate to (Salinas et al. 1986).

Interior swales on the Virginia barrier islands are different depending on their location. Swales located on the center of the island experience less overwash events than marshes located toward the edges. Because the primary input of groundwater is rain, these marshes are often fresh and have been shown to have more root biomass than the dune ecosystems (Stevenson and Day 1996). Occasionally, salt water overwash and subsequent evaporation, along with the impermeability of some soils can cause a rise in the salinity of these marshes and the water table. Landscape topography and the direction of accretion and erosion directly influence how often these marshes experience salt water stress and physical state changes (Hayden et al. 1991).

Nitrogen availability in coastal systems can influence species richness, biomass and biomass allocation, succession and general community structure (Gleeson and Tilman 1990). This is especially true on the barrier islands of Virginia's eastern shore where nitrogen has been shown to be limiting (Day 1996). Nitrogen limitation in an ecosystem can decrease species richness and increase proportional allocation to belowground biomass (Wilson and Tilman 2002, Hilbert 1989). On Hog Island's dunes, the addition of artificial nitrogen has caused shifts in community structure, since these islands have been shown to have nutrient poor soils (Day 1996, Day et al. 2004). Biomass, or the amount of living plant tissue, has traditionally been used to estimate how productive an ecosystem is. Systems with nutrients that are readily available to plants are more productive.

Belowground biomass has been shown to play a vital role in ecosystem processes (McClaugherty et al 1982, Nadelhoffer et al. 1985, McKane et al. 1990), since it accounts for a significant percentage of a plant's total biomass (Vogt et al. 1982). Belowground portions of a plant's total biomass often exceed the amount of aboveground biomass, especially in nitrogen limited systems (Shaver and Billings 1975, Ovington 1963). The allocation of above and belowground biomass is extremely plastic. Allocation varies widely with changing environmental conditions, particularly with hydrology (Tilman et al. 1997). In soils that are nutrient limited, more biomass is allocated to roots to optimize nutrient uptake (Dennis 1977, Chapin 1980, Saterson and Vitousek 1984), but hydrologic factors such as duration of inundation and salt water intrusion can cause drastic changes in this pattern. Some studies show that with increasing salinity, total biomass decreases, and that allocation changes are species specific. These changes often result from the toxic effect of salt on intolerant species, while species adapted to salt stress can continue to thrive (Martin and Shaffer 2005, Pezeshki et al. 1999). The degree of inundation is also highly influential on root:shoot ratios. Megonigal and Day (1988) found that in swamps, flooded areas have more primary production than areas that were rarely flooded, but in areas rarely flooded, there was proportionately more belowground production. Other studies have found the same relationship (Keeley 1979, Donovan et al. 1988). One study of *Sagittaria* species concluded that flooding does not impact biomass or biomass allocation, but only when standing water was under 30 cm deep (Martin and Shaffer 2005). In flooded conditions, plants allocate more biomass into shoots, resulting in lower root:shoot ratios (Megonigal and Day 1992). This change may be an effort to obtain water in areas with a deep water table. It has been noted that this change in allocation could be due to an anoxic root zone with high water tables as well. Root production is less in saturated soils because soil conditions are unfavorable (Lieffers and Rothwell 1987, Armstrong et al. 1986).

The species richness of an area can influence how productive it is. The exact mechanism and predictive relationship are ecosystem dependent (Waide et al. 1999). Grasslands, for example, are more productive when there is high species richness (Drake 2003). Marshes, however, typically exhibit low diversity and are one of the most productive systems in the world (Theodose 1999). Chalcraft et al. (2004) found that the dissimilarity of species niches within a community is more influential than just the number of species in an area. Abiotic factors also influence productivity. The seasonal input of organics into a system, along with the seasonal drawdown of the water table in wetland systems have been suggested as reasons for higher productivity (Gomez and Day 1982, Day 1984).

Many studies of differing ecosystems have found opposing results. Some describe the relationship between diversity and productivity as unimodal (Tilman 1982, Wheeler and Giller 1982). Others have found diversity to be correlated with increasing productivity (Brown and Gibson 1983, Curie 1991). Diversity has also been shown to increase with decreasing productivity in some instances (Rosenzweig 1971, Huston 1980). Since diversity and productivity have different relationships in different environments, other studies have focused on environmental relationships. For example, heterogeneity in environmental factors can positively influence diversity (Pringle 1990, Scarsbrook and Townsend 1993, Harman 1972) allowing many species to fill different niches. Competition can be a major influence. In studies on competition and diversity, environmental factors such as nutrient and light availability can lead to competitive exclusion and consequently a decrease in diversity (Rajaniemi 2002). These disturbances can be slowed through periodic disturbances (Huston 1979). Many studies have found that increased productivity should result in an increased probability of local extinction of species already in a habitat (Tilman 1993). The resulting species richness is maintained through the dynamic equilibrium theory: that local extinction and local colonization influence the number of species that exist in an ecosystem (MacArthur and Wilson 1967). Increased production can lead to increased diversity if there is a high probability of successful colonization and/or a high probability of local extinction (Tilman 1993).

Studies have shown that freshwater systems have more variability in plant biomass and above and belowground allocation than saltwater systems. The intrusion of salt water into the system can dramatically change those dynamics (Odum 1988), often causing a decrease in biomass (Whigham et al. 1989). Freshwater plants that are in close proximity to a source of salt water exhibit higher mortality than plants that are located in completely fresh water systems (Young et al. 1995) since some species are not able to deal with salt stress.

The degree and duration of innundation of marshes impacts species richness and biomass as well. The amount of soil saturation often determines what plant species can thrive since different plants respond differently to varied hydrologic conditions (Weltzin et al. 2000). Wetland communities that are completely flooded for a long period of time are less diverse and often have less total biomass (Casanova and Brock 2000), though this relationship is species specific.

The current study was conducted on the Virginia Coast Reserve’s (VCR) Long Term Ecological Research (LTER) site on Virginia's Eastern Shore. While much research has been conducted on Hog Island and its dune system, its interior grass dominated swales and variability among islands have not been studied. More specifically, how variable are these interior freshwater marshes among the islands and what factors drive this potential variability?

Because the freshwater marshes on the barrier islands can experience over wash events by storms, salinity was hypothesized to be a major factor in determining the variability in biomass and root:shoot allocation. Marshes that tended to be more brackish were expected to have less biomass. Areas that were less nitrogen limited were hypothesized to have less biomass allocated in their roots. Marshes that were less extensively inundated were predicted to have more biomass than those constantly saturated.

The objective of this study was to obtain an estimate of the variability in biomass, biomass allocation, and species richness that exists among these island swales. Abiotic soil influences were measured to determine which might be influencing differences in biomass and biomass allocation. Nitrogen in the soil, nitrogen in plant and root tissues, above and belowground biomass, salinity, and depth to the water table were quantified in this study. In addition, meteorological data were collected from nearby weather stations.

METHODS

Site Description

This study was conducted on the mid-Atlantic barrier islands of the Delmarva Penninsula. These 13 islands and their marshes constitiute The Nature Conservancy's (TNC) Virginia Coastal Reserve (VCR), which is a Long Term Ecological Research (LTER) site of the National Science Foundation (NSF). The islands in the barrier island chain are between 4 to 40 km in length and 1-5 km wide. They are separated from the mainland by lagoons and bays up to 48 km wide. There are both continuous barriers and discontinuous barriers in this chain (Hayden et al. 1995). The study sites included two interior marshes on northern Hog Island, one marsh on northern Parramore Island and one marsh on southern Smith Island (Figure 3). Parramore Island is the farthest north and Smith is the farthest south. These marshes were located at -75.62 W, 37.56 N (Parramore), -75.67 W, 37.45 N (Hog's 2nd marsh), -75.67 W 37.45 N (Hog's 1st marsh) and -75.91 W 37.12 N (Smith Island) (Figure 4).

The barrier islands of the Eastern Shore are subject to periods of severe weather and have unique soils. They have a humid mesothermal climate that experiences westerly winds and pressure systems that typically form from east to west. Winters are mild, but can bring intense weather systems in the form of rapid by moving storm fronts that introduce periods of cold, polar air. Northeasters are also common during the fall and winter bringing heavy rain, strong winds, high tides and rough seas. Summers are long and warm with stable pressure and occasional hurricanes (Hayden et al. 1991). Soils in these island sloughs are typically Corolla-Duckston soils with thermic aquic udepsamments, and thermic typic psammaquents. These soils are poorly drained with a seasonably high water table causing innundation (U.S. Soil Conservation Service 1975).

The marshes differ in plant composition. Parramore and both Hog Island marshes are dominated by *Spartina patens* while Smith's marsh is dominated by *Distichlis spicata*. All marshes had stands of *Phragmites australis* and *Typha angustifolia.*

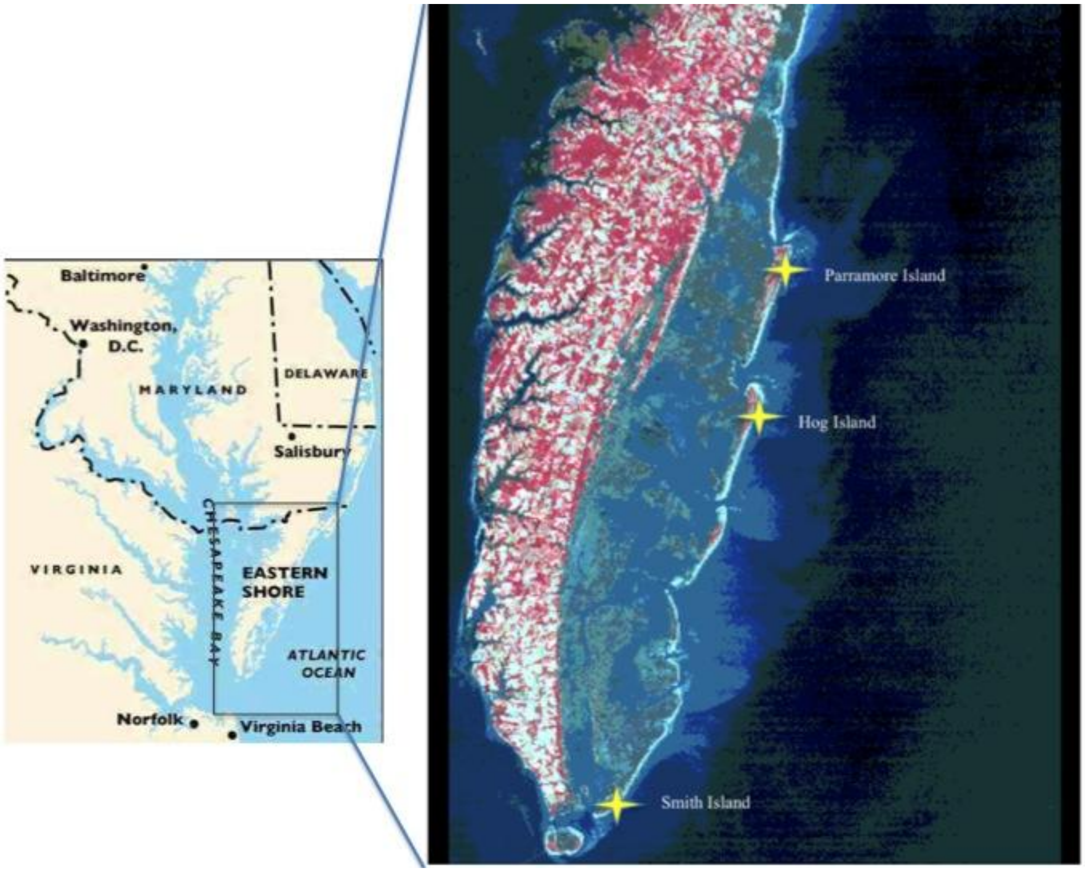


Figure 3. Location of Hog, Smith and Parramore Islands on the VCR LTER site on the Delmarva Peninnsula north of the mouth of the Chesapeake Bay.

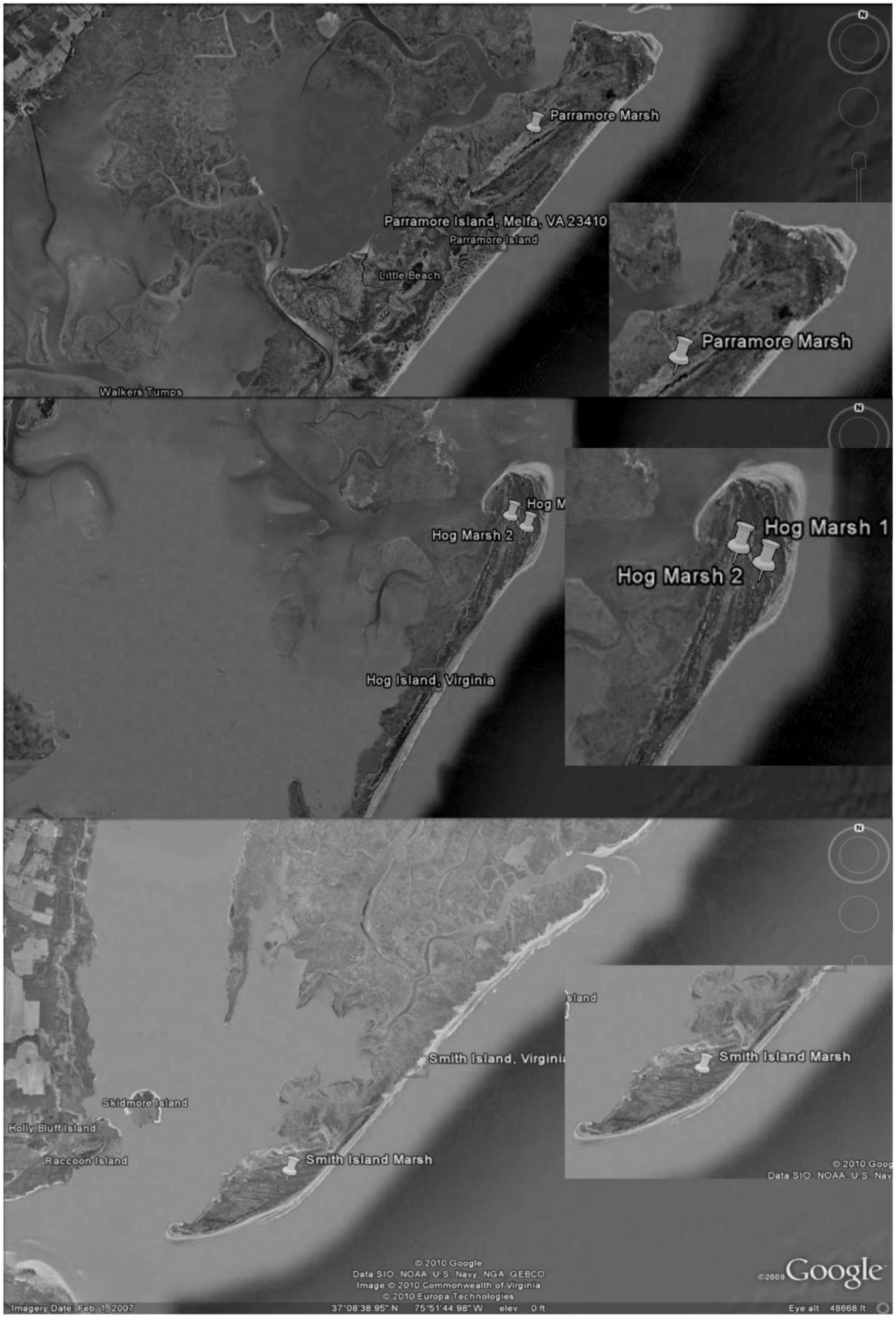


Figure 4. Location of Parramore Island, Smith Island and Hog Island’s marshes.

Sampling Methods

In each of the study marshes, fifteen 0.25 m^2 plots were randomly selected in late June to early August (the height of the growing season). Marsh boundaries were determined by locating tree and shrub lines outlining the marsh, along with major morphological features such as roads and open water. In these plots, all aboveground vegetation was harvested. The vegetation was sorted by species, dried in a 70° C drying oven for 48 hrs and weighed. These data were then converted to g/m^2.

To estimate belowground biomass, a 7-cm soil core was taken with a soil auger every 10 cm down to 40 cm depth. These cores were sieved with a 4-mm sieve. Roots were extracted, washed and separated by size. Roots less than 5 mm were considered to be fine, while those roots greater than 5 mm were considered coarse. The roots were dried at 70° C for 48 hours and weighed. Live roots were differentiated from dead roots based on color and brittleness. White, flexible roots were considered live, while darker, brittle roots were considered dead. From these data, root:shoot ratios were calculated for each site.

Nitrogen content was quantified for the soil along with salinity of the water table. The soil was dried and ground using a mortar and pestle (Heyel and Day 2006). Nitrogen analysis was completed using a Carlo Erba CN analyzer and reported as percent nitrogen in 10 mg of soil. Salinity of the groundwater was determined. To quantify salinity in each marsh, a refractometer was used. Measurements were taken in standing surface water where possible and from groundwater when the water table was below the surface. Salinity was recorded for each of the 15 plots in the marsh to determine if there was a natural gradient.

Depth of the water table, species richness, Shannon index of diversity, and meteorological events were all determined. The depth of the water table was quantified every time vegetation was collected, by digging a hole with soil auger. The depth of the water table was recorded as the depth below the surface at which water started pooling in the hole. Where water was above the surface, water table depth was measured as the height above the soil surface. Plant species were identified and used to calculate a Shannon index (H’) based on contribution to total biomass:

$H'=-\Sigma$ (pi ln pi)

pi=relative biomass (ni/N)

ni=aboveground biomass of species i (g/m^2)

N=total aboveground biomass for marsh (g/m^2)

Biomass values were used to obtain a proportion of the population made up by an individual species. Meteorological data were gathered to determine rainfall and storm events. These data were obtained from weather stations on the islands.

Data were then statistically analyzed for significant variability among marshes. ANOVAs were used to test for inter-site variability. Regression analysis was used to relate the independent variables to the variability in biomass.

RESULTS

Species Richness and Shannon Index

Marshes exhibited differences in plant species composition (Table 1). Hog Marsh 1 had 4 species, with *Spartina patens* being dominant and other species such as *Eleocharis parvula* and *Scirpus americanus* present. Hog Island's second marsh had 5 species, with *Spartina patens* being dominant. Smith and Parramore marshes had 3 species each. Parramore Island's dominant species was *Spartina patens* and Smith Island's dominant plant species was *Distichlis spicata.*

Hog Island's second marsh had the highest Shannon Index of diversity (1.026) (Table 2). Hog Island's first marsh was the next most diverse (0.842), with Parramore closely below that (0.745). Smith Island's marsh was the least diverse (0.504).

Aboveground Biomass

Marshes were significantly different from one another in the amount of live biomass (1 way ANOVA, $p=0.02$) and in the amount of dead biomass (1 way ANOVA, $p<0.05$). Parramore Island had the highest aboveground live biomass (563.32 g/m^2) (Tukey, $p<0.05$)(Table 1). Hog's first marsh was next (467.26 g/m^2). Smith Island's marsh had a lower value (406.86 g/m^2) and Hog Island's second marsh had the least (36.69 g/m^2). Parramore's marsh had the most dead aboveground biomass (592.45 g/ m^2) (Tukey, $p<0.05$). Other values for dead biomass ranged from 348.18 g/ m^2 to 288 g/m^2.

Table 1. Aboveground biomass by marsh and species

Island	Species	Biomass (g/m^2)
Hog Marsh 1	Dead	305.41
	Distichlis spicata (L.) Greene	19.08
	Eleocharis parvula (R. and S) Link	0.43
	Scirpus americanus Persoon	31.01
	Spartina patens (Aiton) Muhl.	111.34
	Total Live	161.92
Hog Marsh 2	Dead	349.18
	Distichlis spicata	1.28
	Polygonum hydropiperoides Michx.	4.37
	Scirpus americanus	1.37
	Spartina patens	26.86
	Typha angustifolia L.	2.81
	Total Live	36.69
Parramore	Dead	592.45
	Distichlis spicata	29.45
	Juncus scirpoides Lam.	137.08
	Spartina patens	396.78
	Total Live	563.32
Smith	Dead	288.62
	Distichlis spicata	331.69
	Spartina patens	72.80
	Typha angustifolia	2.37
	Total Live	406.86

Table 2. Shannon diversity index for marshes.

Marsh	H’
Hog Marsh 1	0.842
Hog Marsh 2	1.026
Parramore	0.745
Smith	0.504

Belowground Biomass

Belowground biomass was not significantly different among marshes (1 way ANOVA, p=0.188), probably due to a small sample size (Figure 5). Most biomass was allocated to fine roots (roots <5 mm diameter) (1 way ANOVA, p=0.00024). Biomass was not significantly different at different depths below the surface (1 way ANOVA, p=0.0646), though this is likely due to a low sample size. With the exception of Smith Island, other marshes tended to have fine roots that were located in the top 20 cm of soil. Coarse roots tended to be concentrated in the top 10 cm of soil. Smith Island tended to have the most belowground biomass (930.88 g/m^2), and it was equally distributed over the top 40 cm depth (Figure 6). Hog and Smith marshes had most of their fine root biomass in the top 10 cm.

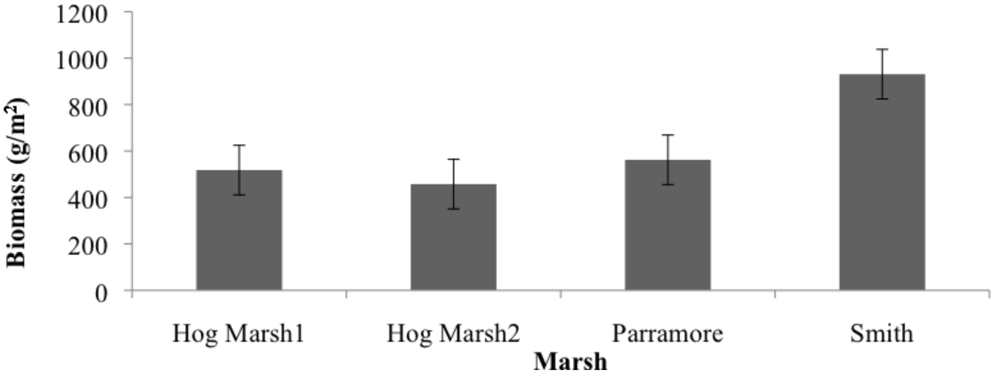


Figure 5. Total belowground biomass (g/m^2)

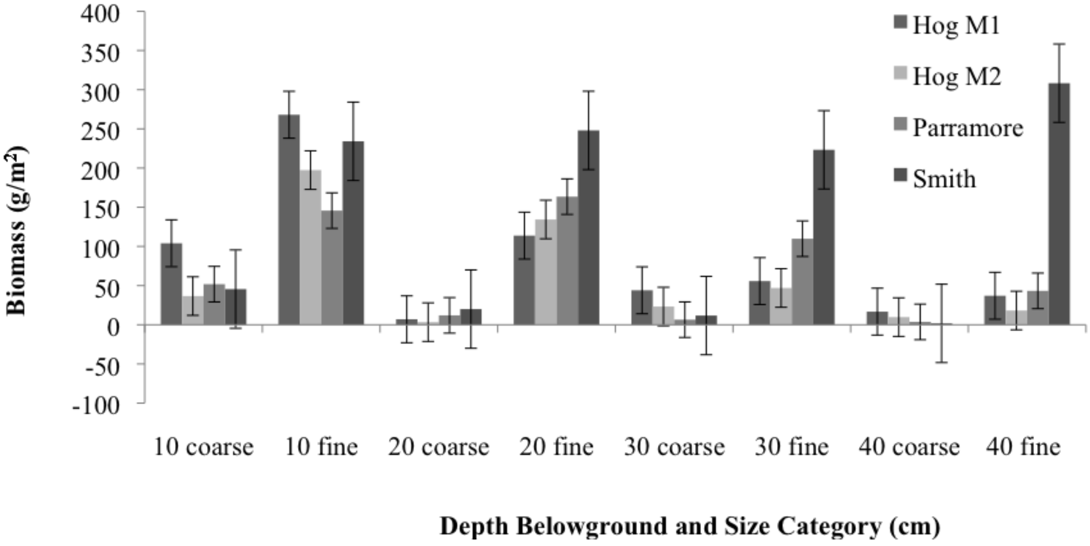


Figure 6. Belowground biomass by depth and size category. Coarse roots are roots >5 mm in diameter, while fine roots are <5 mm in diameter.

Root:shoot Ratios

Root:shoot ratios were significantly different among marshes (1 way ANOVA, p=0.007) (Figure 7). Hog Island's second marsh had the highest root:shoot ratio of almost 0.5 (Tukey, $p<0.05$), while Parramore had the lowest ratio of 0.05. Hog Island's first marsh and Smith Island's marsh had similar values of around 0.12. This indicates that Smith Island's marsh had proportionately less biomass belowground, while Hog's second marsh had proportionately more biomass belowground.

Soil Nitrogen

Soil nitrogen was found to be significantly different among marshes (1 way ANOVA, $p<0.0005$). Smith Island had the most nitrogen with 1.372% N/10 mg of soil (Tukey, $p<0.005$), which was well above the other islands (0.064, 0.140, and 0.151 %N/10 mg soil) (Table 3). There was a trend of greater biomass with higher soil nitrogen for both above and belowground biomass (Figure 8), but the relationship was not significant due to low sample size (1 way ANOVA, aboveground biomass p=0.52, belowground biomass p=0.17).

Salinity

Salinity was significantly different among marshes (1 way ANOVA, $p<0.0005$). Hog Island's second marsh tended to be the freshest with an average salinity of 0 (Table 3). Hog Island's first marsh was saltier with a mean salinity of 0.73 ppt. Parramore and Smith marshes were the most saline, with values of 19.80 and 18.60, respectively (Tukey, $p<0.05$). Correlation analysis revealed a trend of higher aboveground biomass with increasing salinity (p=0.22), and a weaker trend for belowground biomass (p=0.57) (Figure 9).

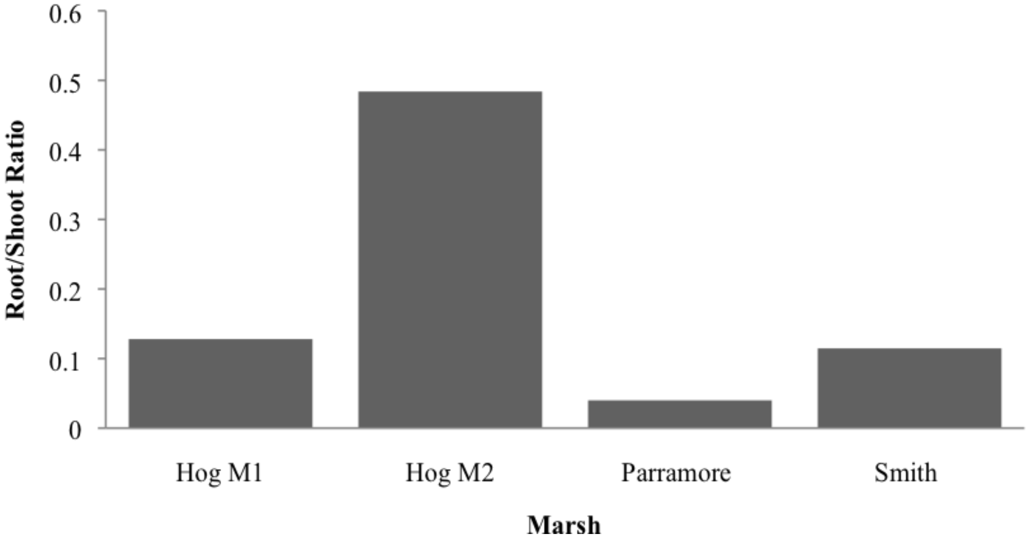
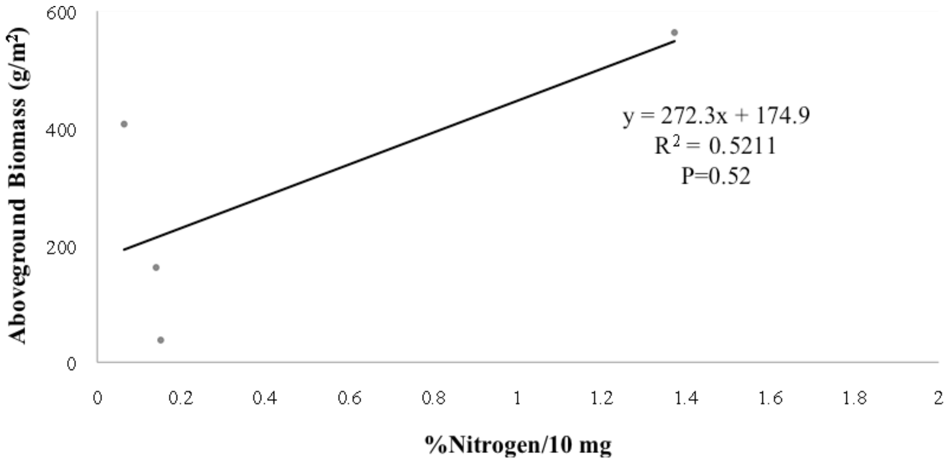


Figure 7. Root:shoot ratios by marsh.

Table 3. Mean percent nitrogen per 10 mg of soil, salinity and water table depth in each marsh.

Marsh	Mean % N/10 mg	Mean Salinity (ppt)	Mean Depth of WT (cm)
Hog Marsh 1	0.140	0.73	5.41
Hog Marsh 2	0.151	0.00	19.60
Parramore	1.372	19.80	8.80
Smith	0.064	18.60	30.56



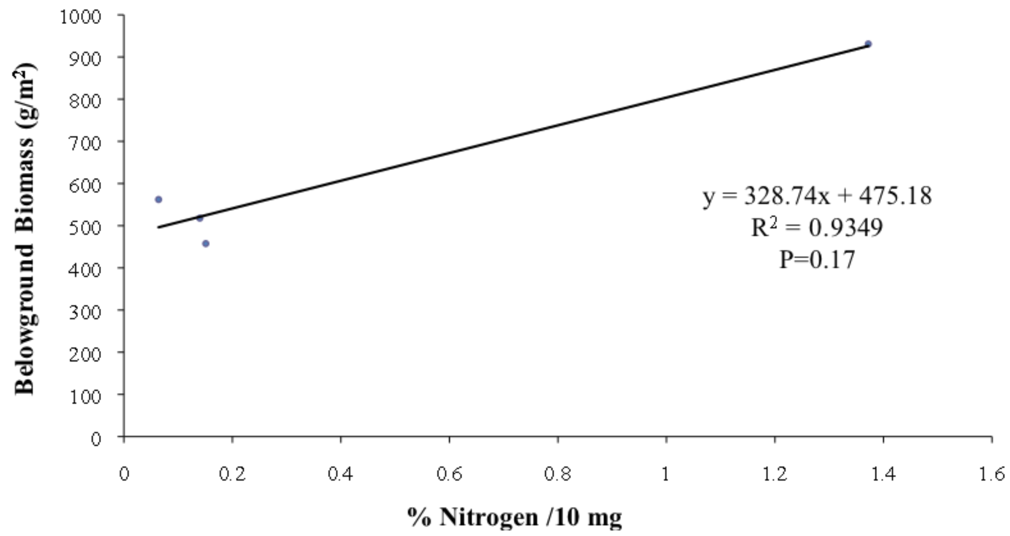


Figure 8. Correlation results for amount of nitrogen of marshes and above and belowground biomass of marshes.

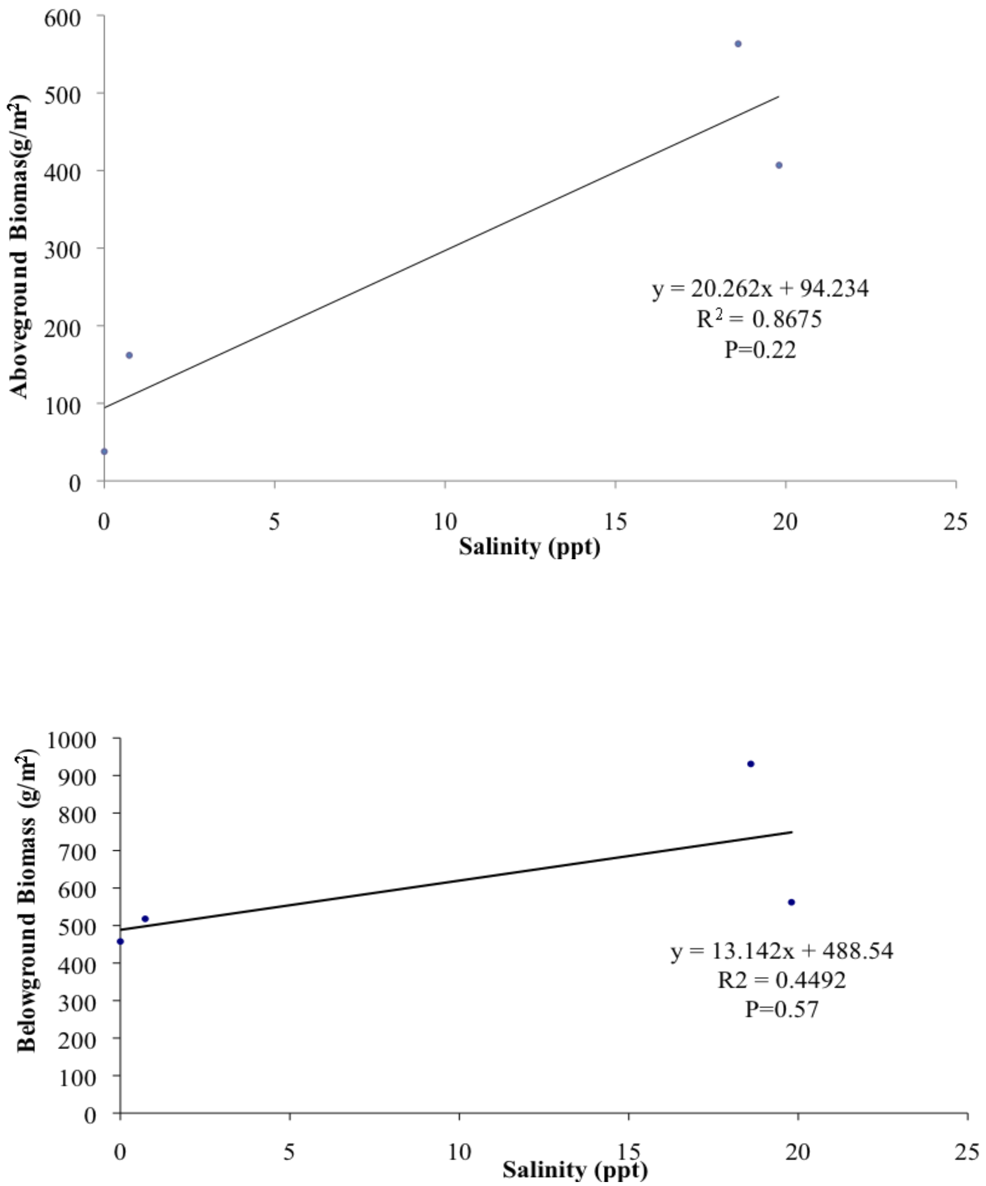


Figure 9. Correlation results for water table salinity of marshes and above and belowground biomass of marshes.

Depth of Water Table

The depth of the water table was significantly different among marshes (1 way ANOVA, $p<0.0005$). Smith Island was dry, with a water table depth of 30.56 cm on average (Table 3). The water table was 8.80 cm below the surface in Parramore's marsh. Hog Island's first marsh was the wettest, with an average water table depth of 5.41 cm below the surface (Tukey, $p<0.05$). Hog Island's second marsh was drier, with an average depth of 19.6 cm. There was no predictive relationship between depth of water table and biomass (Figure 10).

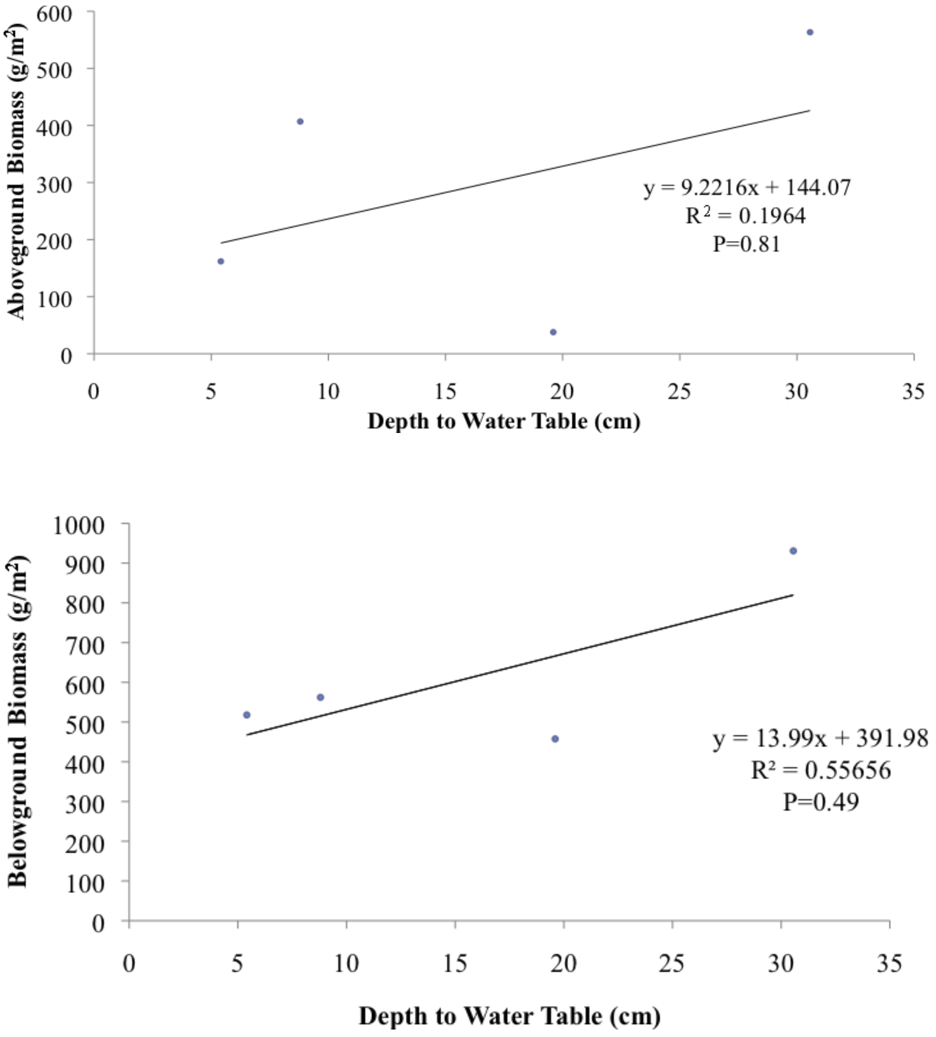


Figure 10. Correlation results for depth to water table of marshes and above and belowground biomass of marshes.

DISCUSSION

Diversity

Parramore and Smith Island's marshes had only three species. This level of diversity is comparable to marshes in the northeastern United States (Judd and Lonard 2002), but is much less diverse than *Spartina* dominated marshes in other parts of the United States, particularly the southwest, where marshes frequently have 22-32 species (Fell et al. 2003). These differences in diversity do not coincide with biomass results. Hog Island's second marsh was the most diverse, but had the lowest total live aboveground biomass. Smith Island was the least diverse, but had the second highest aboveground biomass. This pattern is also true for belowground biomass—Smith Island was the least diverse, but had high belowground biomass values. The least diverse marsh had the most belowground biomass, and the most diverse had the least amount. For this system, diversity seems to increase with decreasing productivity, supporting Rosenweig and Huston's findings (1971, 1980), and Grume's hypothesis that increased productivity can lead to lower diversity because of more intense resource competition (1973). Rajaniemi (2002) also suggested this trend may be due to the scarcity of nutrients and the resulting intense competition among species. This idea is contrary to what most plant ecologists expect to find (Tilman 1993). In this ecosystem, disturbances may be a driving factor. Heterogeneity of environmental factors has been associated with increasing diversity (Pringle 1990, Scarsbrook and Townsend 1993, Harman 1972), which means that disturbances may be a driving factor in diversity. Disturbances would result in intense competition for resources, which can be a major influence. The frequency and severity of disturbances differ from marsh to marsh and can therefore impact islands differently. For example, Smith Island's marsh had the most belowground and the second highest aboveground biomass, but also had only 3 species, and a deep, salty water table. Therefore, the plant species located there are able to deal with the frequent salinization of the ground water without any effect on productivity.

This pattern was found with root:shoot ratios as well. Typically, more diverse systems have more root and shoot biomass, and more constant root:shoot ratios than systems with only one species (Callaway et al. 2003). Hog's second marsh was the most diverse and had the highest root: shoot ratio. This marsh was also the freshest and had an intermediate amount of soil nitrogen. The lack of salt water and the availability of soil nitrogen may indicate salinity as a contributing factor to diversity and that competitive exclusion belowground may be playing a role in diversity as some research has suggested (Rajaniemi 2002, Grime 1973). Hog's second marsh also had the least live biomass. Smith Island's marsh was the least diverse, but had one of the higher live aboveground biomass values. In this case, diversity does not seem to influence biomass.

Biomass

The amount of biomass varied among marshes. The amount of biomass was around the same as other *Spartina* dominated marshes (Gross et al. 1986, Fell et al. 2003), but lower than inland, non-coastal marshes (Dwire et al. 2004). Belowground biomass values were lower than inland marshes (Dwire et al.2004, Fell et al. 2003), but similar to other east coast marshes (De la Cruz and Hackney 1977, Gross et al. 1986).

The amount of biomass seems to correlate most strongly with nitrogen availability, especially belowground. Nitrogen availability has been found to increase belowground biomass in dune systems on the barrier island systems (Heyel and Day 2006). Salinity seems to have more of an effect on aboveground biomass. In systems dominated by *Typha spp.,* aboveground biomass was found to increase with salinity (Whigham et al. 1989). This pattern only happens in marshes that have salt tolerant species. This appears to be the trend in these marshes as well, although they are dominated by *Spartina* and *Distichilis* spp.

Community structure

The community structure of these marshes was similar to other marshes in the Virginia area that are subjected to seasonal inundation (Perry and Atkinson 1997), but differed from other barrier island ecosystems, since conditions on barrier island systems vary greatly. In other marshes, when there is an increasing availability of fresh water, halophytes often decline and other species such as *Typha* move in. These species are able to persist with increasing salinity (Zedler and Beare 1986). *Eloarcharis* spp. and *Scirpus* spp. frequently are found in marshes that have freshwater inputs, with occasional salinity fluctuations (Ewing 1986). This was also true for the marshes we studied, since Hog Island's marshes are the freshest and had both species.

Salinity and influences on biomass

Salinity varied among marshes. The range of 0-34 ppt has been reported on other barrier island ecosystems as well. Salinity has been shown to be a function of depth below the surface in many cases. Marshes with a surface water table are more likely to be fresh, while marshes with deeper water tables experience more salt water intrusion

(Bokuniewicz and Pavlik 1990). This relationship did not seem to be the case on the Virginia islands, since Hog Island's second marsh was completely fresh and had a water table depth of 19.60 cm.

More likely, the width of the islands and the marsh location influence salinity. Since wider islands would build up a larger freshwater lens, marshes close to the center would be fresher. Marshes on the fringe of the interior would be more susceptible to salt water intrusion from the bay and oceans. This has been shown to be the case in small barrier islands like the Florida Keys (Meadows et al. 2004).

Salinity did appear to influence biomass. Although results were not significant due to a small sample size, there is an apparent relationship between salinity and aboveground biomass. Belowground biomass showed a weaker relationship. This might be due to the presence of salt tolerant species in marshes. These more tolerant species would be better adapted to dealing with salt stress than plants that require freshwater only.

Salinity can also influence root allocation. Whigham et al. (1989) found that with increasing salinity, root allocation switches to being dominated by shallower, fine roots. All of the marshes on Virginia's barrier islands are subjected to varying degrees of salt stress. Most of the belowground biomass was allocated in fine roots in the top 10 cm of soil, with the exception of Smith's marsh, which is consistent with salt water intrusion into the water table. Smith Island's marsh had the lowest water table depth which would cause a shift to deeper fine roots.

Nitrogen and influences on biomass

Soil nitrogen was also significantly different among marshes, and was below ranges for most freshwater systems (Morse et al. 2004), but within ranges for nitrogen limited barrier islands (Conn and Day 1993). These numbers also fit in with marshes that were found to have high organic content and sediment deposits (Godfrey and Godfrey 1976). This difference was obvious since Parramore Island's marsh had a deep brown soil in it's A horizon. This may have been due to Parramore's large amount of dead biomass (592 g/m ^{2}) (Vituosek 1997). This availability of nutrients due to dead organic matter may occur in marshes since it has been shown to influence nutrient availability in dunes on the barrier islands (Heyel and Day 2006). However, other marshes had a large amount of dead biomass and lower nitrogen values. This suggests that another mechanism, such as long term soil inundation may be affecting the rate of decomposition. Another reason Parramore Islands marsh has the most available soil nitrogen might be that the fire that took place on Parramore Island in 2002 added organics back into the system.

Nitrogen also seemed to influence biomass, though it correlated more strongly with belowground biomass. The more nitrogen available, the more productive the belowground portion was. Again, more samples would have allowed this trend to be more robustly evaluated. Some studies have shown that there is temporal variation in nitrogen availability as well. Sampling throughout the year for averages would give more accurate results (Cain et al. 1999).

Root: shoot allocation and nitrogen seemed to have a relationship. Parramore Island's marsh had the lowest root: shoot ratio, but the highest available soil nitrogen. Smith Island's marsh had a low root: shoot ratio and had the lowest available soil nitrogen. These results follow the trend that biomass allocation decreases with increasing nitrogen availability (Reynolds and D'Antonio 1996). In the other marshes, nitrogen availability may have been causing competition among plants, which can decrease diversity (Rajaniemi 2002).

Depth of water table and influences on biomass

Water table depth differed significantly among marshes, but did not seem to have a significant effect on biomass, above or belowground. All islands contained gleyed sands, indicating soil saturation at different points throughout the year. The lack of effect of water table depth on biomass may have been due to the depth of the water table being a snapshot in time while the islands were being sampled. Water table depth varies daily because of weather. Certainly, continuously recorded well data from each site would be more useful in making these comparisons.

Water table depth could have been influential on root allocation. Smith Island's marsh had the lowest water table depth, and also had fine roots distributed down to 40 cm deep. This pattern is typical for hydrophytes. As the soil becomes more continuously saturated, the root zone can become anoxic, reducing root biomass (Lieffers and Rothwell 1987, Armstrong et al. 1986). Along with this pattern, the deeper the water table is, the deeper roots go belowground to obtain water (Imada et al. 2008, Lewis and Burgy 1964). In wetland soils, plants allocate most of their root biomass above 50 cm depth, with mostly fine roots (Jackson et al. 1996). This could be due to anoxic conditions deeper in the soil that inhibit root growth (Rothwell 1987, Armstrong et al. 1986). This appeared to be the case with our study sites as the three more extensively inundated marshes had the most roots in the top 20 cm of soil. Smith Island's marsh, which was drier, had deeper fine roots. More extensive data on water table depth would be useful to compare long term water table patterns and root allocation and to identify the frequency of inundation or saturation.

Biomass allocation

Hog Island's second marsh had the highest root:shoot ratio. This marsh was also the freshest. Freshwater marshes are reported to have root:shoot ratios of around one, meaning that most biomass is equally distributed (Mitsch et al. 2009). It also had a deeper water table, which may have led to the formation of more biomass belowground. This change in allocation necessarily reduces the productivity aboveground (Megonigal and Day 1992).

The other marshes had lower root:shoot ratios. This is typical of nutrient limited systems (Hilbert 1990), and for plants early in the growing season. Systems that are nutrient or water limited have lower root: shoot ratios, while systems that are limited in sunlight or carbon dioxide have higher root: shoot ratios (McConnaughay and Coleman 1999). This suggests that Hog Island's first marsh, Smith Island's marsh, and Parramore Island's marsh are all more nutrient or water limited than Hog Island's second marsh. But, since Hog Island's second marsh had low nitrogen, some other factor must be influencing allocation. The depth of the water table might be a contributing factor. Hog Island's marshes and Parramore's marsh had a higher water table, which may be causing an anoxic zone in the soil, which would inhibit root growth (Lieffers and Rothwell 1987). Smith Island's marsh had a deeper water table and consequently more root biomass. This marsh had a high amount of aboveground biomass, resulting in a lower root: shoot ratio. Since this marsh is also one of the saltier marshes, and had low nitrogen, some other environmental factor must be influencing allocation.

Cumulative influences on biomass

Not surprisingly, these marshes exhibited differences. Species composition, above and belowground biomass, root:shoot ratios, nitrogen availability and salinity were all different, even though these marshes are located within the same barrier island chain. Other barrier island systems exhibit similar variability (Art et al. 1974).

Parramore's marsh had an interesting relationship between nitrogen and biomass. This marsh had the highest available nitrogen. It also had the highest aboveground biomass. In this marsh, the availability of nitrogen could allow more productivity. Parramore had the lowest root:shoot ratio. This may suggest that the availability of nitrogen does not require the plants to produce proportionally more root biomass, since nitrogen availability is a major determining factor on belowground biomass (Cain et al. 1999).

Smith Island, however, must have had other factors influencing biomass. Smith Island's marsh had the second highest aboveground biomass values, but the lowest soil nitrogen. The species composition between Smith and Parramore Island was quite different. Smith was dominated by *Distichilis spicata*, while Parramore's marsh was dominated by *Spartina patens*. The water table was deeper on Smith Island. This may be because *Distichilis* is better adapted to drier environments, or that it is better adapted for nitrogen limitation.

CONCLUSIONS

Overall, these marshes were quite different. Salinity, amount of soil nitrogen available, depth of water table, and root: shoot ratios were variable among marshes. Above and belowground biomass and allocation were different among marshes (Figure 11). Each marsh had differing species compositions and had different diversity indices.

Environmental factors that differ among marshes seemed to have varying degrees of influence as well. Salinity, soil nitrogen availability and water table depth appeared to have an influential relationship on the amount of biomass present both above and belowground, although these correlations were not significant. A larger sample size would help to statistically verify which conditions influence biomass and biomass allocation in marshes. Adding additional interior marshes to this study would help broaden results to the barrier island chain.

The variability among these marshes should be taken into consideration when attempting to manage barrier islands and their systems. Their various habitats are different, even within the same island, and should be treated as such. Further research should focus on each habitat zone as a separate entity, since freshwater marshes are different from the salt marshes and the dunes.

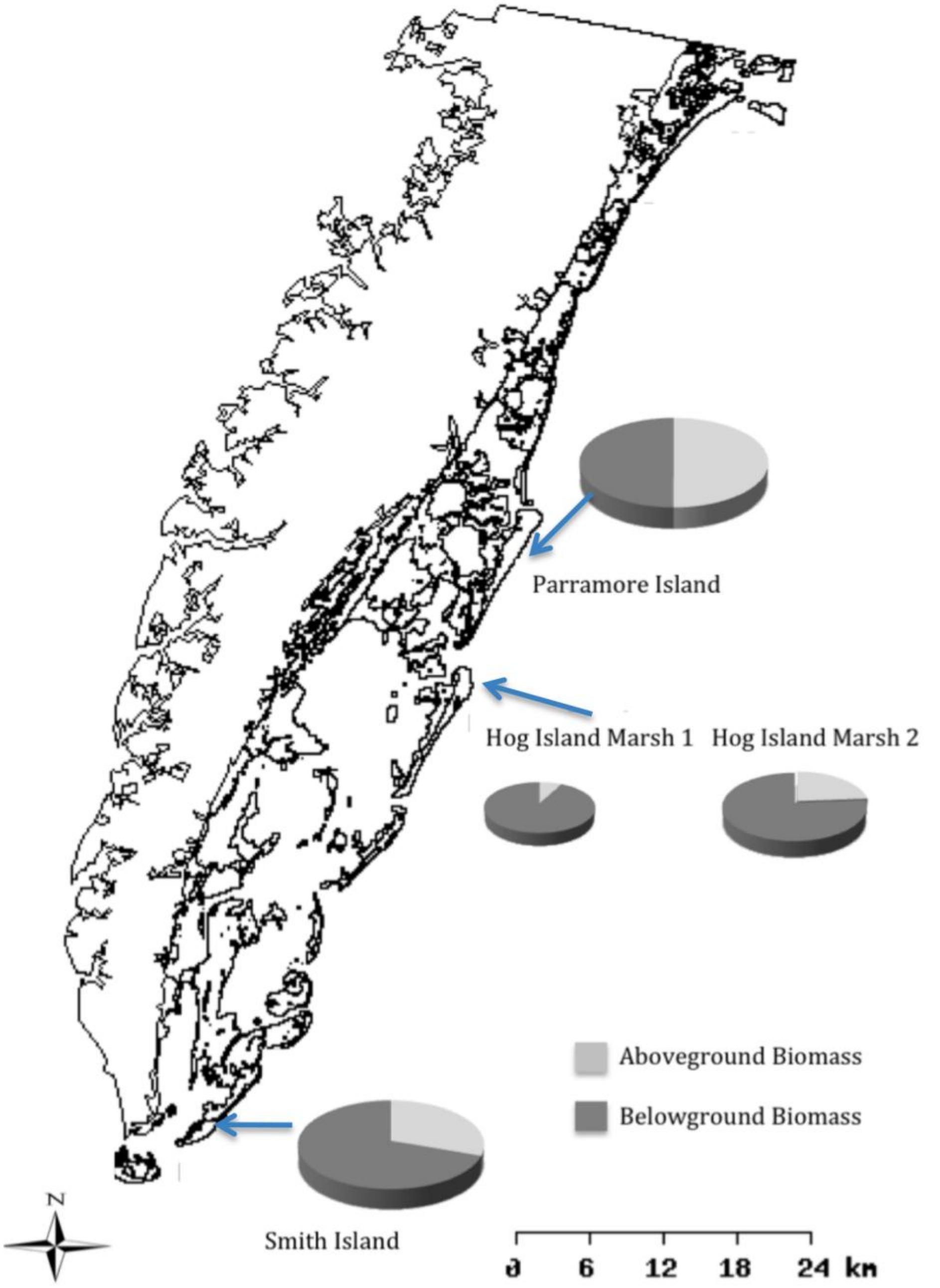


Figure 11. Interisland variation of above and belowground marsh biomass.

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VITAE

Staci B. Blecha

Adjunct Biology Instructor
Tidewater Community College, Portsmouth
120 Campus Drive
Portsmouth, VA 23701
(757) 803-6103
sblecha@tcc.edu

EDUCATION

B.S. Biology 2006
Niagara University, Lewiston New York

RELATED EXPERIENCE

Adjunct Biology Professor, Tidewater Community College, Suffolk, VA: 2009
Education Specialist, Nauticus Maritime Museum, Norfolk, VA: 2008-2009
Research Assistant, Old Dominion University, Norfolk, VA : 2007
Teaching Assistant, Old Dominion University, Norfolk, VA: 2006-2008
Research Assistant, Niagara University, Lewiston, NY: 2006
Teaching Assistant, Niagara University, Lewiston, NY: 2003-2006
Internship-U.S. Fish and Wildlife Service, Amherst, NY: 2005

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