

**THRESHOLDS OF CHANGE IN DECOMPOSITION RATE ALONG A
DUNE/SWALE TRANSECT ON A VIRGINIA BARRIER ISLAND**

by

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ABSTRACT

THRESHOLDS OF CHANGE IN DECOMPOSITION RATES ALONG A DUNE/SWALE TRANSECT ON A VIRGINIA BARRIER ISLAND

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Aboveground and belowground decomposition rates were determined along a barrier island dune/swale transect located on the Virginia Coast Reserve-Long Term Ecological Research Site using litterbags and wooden dowels. The objective was to determine the influence of fine scale changes in the environment on decomposition to identify any potential thresholds affecting decomposition rate. Wax myrtle (*Morella cerifera* L. Small) leaves and dowels of southern yellow pine wood were used as standard substrates to evaluate environmental influences on decay. Aboveground ($F=6.494$, $p < 0.0001$) and belowground ($F=5.705$, $p < 0.0001$) decay rates (yr^{-1}) showed significant variation among litterbag/dowel locations. Aboveground decay rates (yr^{-1}) ranged from 0.339 (Upper Dune station) to 0.699 (Marsh/Lower Dune Transition station) and belowground decay rates (yr^{-1}) ranged from 0.132 (Marsh station) to 0.411 (*Morella* Thicket Edge station). The Upper Dune station showed the lowest aboveground rates and the Marsh Edge and Marsh/Lower Dune transition station showed the highest decomposition rates (REGWF, $p = 0.05$). Surface elevation was highest at the Upper Dune station (2.411 m) and lowest at the Marsh Edge Station (1.324 m). As a result, annual mean distance to groundwater was highest at the Upper Dune station (1.486 m) and lowest in the marsh stations (0.421 m). Soil N (%) content was highest at the Lower Dune (marsh side) station and at the Marsh Edge station. Aboveground decay rate (yr^{-1})

showed a strong positive trend with increasing soil N content, and stations with significantly higher concentrations of soil N also demonstrated high aboveground decay rates. The inverse relationship between surface elevation (m) and soil N content (%) and the positive relationship between aboveground decay rate (yr^{-1}) and soil N (%) demonstrate predictive thresholds of aboveground decomposition rates. Belowground decay rates (yr^{-1}) only showed significant variation at the *Morella* thicket station, where the highest decay rates were recorded. Vegetation surveys conducted suggest that elevation is an important environmental driver of state change. Relatively small (approximately 0.25 - 0.5 m) increases or decreases in elevation dramatically affected species abundance and makeup. Elevation and distance to groundwater seem to provide a basis for identifying thresholds of ecosystem process rates and state change. The fine scale dynamics of ecosystem processes, aboveground and belowground production, and nutrient cycles, on barrier islands merit further investigation in order to determine areas where thresholds of change occur.

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TABLE OF CONTENTS

| | Page |
|----------------------------------|------|
| LIST OF TABLES | vi |
| LIST OF FIGURES | vii |
| INTRODUCTION | 1 |
| METHODS | 6 |
| STUDY AREA | 6 |
| ABOVEGROUND DECOMPOSITION | 9 |
| BELOWGROUND DECOMPOSITION..... | 10 |
| ENVIRONMENTAL MEASUREMENTS | 12 |
| SURFACE ELEVATION..... | 12 |
| GROUNDWATER | 12 |
| SOIL ANALYSIS..... | 12 |
| VEGETATION SAMPLING..... | 14 |
| DATA ANALYSIS..... | 14 |
| RESULTS | 16 |
| ABOVEGROUND DECOMPOSITION | 16 |
| BELOWGROUND DECOMPOSITION..... | 16 |
| STATE CHANGE THRESHOLDS | 30 |
| DISCUSSION | 37 |
| ABOVEGROUND DECOMPOSITION | 37 |
| BELOWGROUND DECOMPOSITION..... | 39 |
| ENVIRONMENTAL LANDSCAPE | 40 |
| STATE CHANGE THRESHOLDS | 42 |
| CONCLUSIONS..... | 44 |
| LITERATURE CITED | 46 |
| VITA | 50 |

LIST OF TABLES

| Table | Page |
|--|------|
| 1. Mean aboveground annual decay rate (yr ⁻¹), mean belowground annual decay rate (yr ⁻¹), mean soil % N content, mean elevation (m), mean distance to groundwater (m) and dominant vegetation type for all litterbag/dowel placement stations. | 18 |

LIST OF FIGURES

| Figure | Page |
|---|------|
| 1. The Delmarva Peninsula and its barrier islands..... | 7 |
| 2. Location of research site on northern Hog Island..... | 8 |
| 3. Example of a transect showing the nine litterbag/dowel placement stations..... | 11 |
| 4. 3.05 X 3.05 m raster resolution digital elevation model of the study area. | 13 |
| 5. Aboveground % mass remaining vs. # of days in the field. | 17 |
| 6. Mean aboveground decay rate (yr^{-1}) vs. mean surface elevation (m) ($r^2 = 0.10$, $p = 0.004$)..... | 19 |
| 7. Mean aboveground decay rate (yr^{-1}) vs. mean soil % N content ($r^2 = 0.25$, $p < 0.001$). | 20 |
| 8. Mean aboveground decay rate (yr^{-1}) vs. annual mean distance to groundwater (m) ($r^2 = 0.14$, $p = 0.032$)..... | 21 |
| 9. Belowground % mass remaining vs. # of days in the field..... | 22 |
| 10. Mean belowground decay rate (yr^{-1}) vs. mean surface elevation (m) ($r^2 < 0.001$, $p = 0.898$)..... | 24 |
| 11. Mean belowground decay rate (yr^{-1}) vs. annual mean distance to groundwater (m) ($r^2 < 0.001$, $p = .963$) | 25 |
| 12. Mean belowground decay rate (yr^{-1}) vs. mean soil N content (% N) ($r^2 = 0.044$, $p = 0.60$)..... | 26 |
| 13. Annual mean distance to groundwater for all litterbag/dowel placement stations throughout the study period..... | 27 |
| 14. Mean soil N content for all litterbag/dowel placement stations. | 28 |
| 15. Mean surface elevation (m) vs. mean soil N content (%) ($r^2 = 0.108$, $p = 0.002$). | 29 |
| 16. Example of a transect highlighting possible thresholds for changes in system state. | 31 |
| 17. Mean aboveground decay rate (yr^{-1}) vs. litterbag/dowel station dominant species... | 32 |
| 18. Mean belowground decay rate (yr^{-1}) vs. litterbag/dowel station dominant species... | 33 |
| 19. Mean distance to groundwater (m) vs. litterbag/dowel station dominant species.. ... | 34 |
| 20. Mean soil N content (%) vs. litterbag/dowel station dominant species..... | 36 |

INTRODUCTION

Coastal barrier islands represent landscapes that probably have as much variation along environmental gradients as any in the biosphere. These landscapes are rapidly changing and are ideal locations for the study of the interaction between landscape dynamics, such as elevational gradients and ecosystem processes (Hayden *et al.*, 1991). Topography on barrier islands typically includes a conspicuously parallel sequence of dune ridges. The extreme rate of landscape change among dunes on a barrier island is a compelling focus for research. Hayden *et al.* (1991) stated that only the Chandeleur Islands, found on the east face of the Mississippi Delta, have a more dynamic barrier island coastline than those located along the Virginia coast.

The landscape on a barrier island can be quite varied in regard to the different transitional system states, consisting primarily of forested and grass dominated dunes, and interdunal swale marshes and shrub thickets. It is critically important to understand state transitions across the barrier island landscape, the processes (i.e. decomposition) that mediate the transitions, and environmental factors regulating these processes (Day, 1995).

Ecosystem state change, in most environments, occurs over decades or centuries as the ecosystem processes that cause it are often slow. The frequency of disturbance events is high along the Virginia coast and succession on the barrier islands is often set back to earlier stages or diverted along alternate paths, causing changes in system states. State change is also accelerated on barrier islands due to frequent and rapid changes in free surfaces across the islands. Ecosystem processes, landscape and successional

patterns are controlled by the ever changing free surfaces on barrier islands (the vertical positions of the land, sea level and the freshwater table). Research conducted on barrier islands at the Virginia Coast Reserve (VCR) has its foundations based on these constantly shifting free surfaces. Relatively small variations in distance to or height of the freshwater table, land or sea level surfaces can result in ecosystem and landscape changes that are equivalent to continental scale biome transitions, e.g. change from grassland to pine/hardwood forest. It is hypothesized that the dynamic free surfaces found on these islands are the cause of shifts in states across the island (Hayden *et al.*, 1995).

The decomposition of organic matter, including litter, and the amount of carbon returned to the atmosphere by decomposition are important components of the global carbon budget (Raich and Schlesinger, 1992). Aerts (1997) suggested that the three main levels of litter decomposition control operate in the following order: climate > litter chemistry > soil organisms. Environmental factors, such as temperature and moisture, have a direct effect on litter decomposition. However, because environmental conditions exert some influence on soil formation and nutrient cycling, it is hypothesized that they also indirectly influence litter composition as well (Swift *et al.*, 1979). Decomposition is an important functional aspect of ecosystems that should be influenced by abiotic thresholds and reflect state changes.

Coastal dunes are found at the boundary between land and sea, and are known to have extremely stressful environmental conditions (Tackett and Craft, 2010) resulting from disturbance events and the dynamics of the free surfaces. In all ecosystems, environmental gradients are important factors to consider when evaluating the impacts on litter decomposition rates. These gradients have been found to impact aboveground and

belowground decomposition rates (Day, 1995). The quantification of environmental effects on decomposition is complicated by many confounding factors in the complex of regulating factors. A frequently used method of separating out environmental effects is to quantify mass loss rates of a common substrate such as leaves from a single plant or wooden dowels (Vitousek *et al.*, 1994; Austin, 2002; Day, 1995).

Small changes in land surface elevation on barrier islands can have a dramatic effect on water availability and water quality, both of which directly influence decay rates (Hayden *et al.*, 1995; Lammerts *et al.*, 2001; Muñoz-Reinoso, 2001). Below barrier islands, a layer of freshwater, deposited by rainfall, permeates the soil and floats on denser saline ground water from the ocean. This freshwater layer wells up to form a convex lens under the island's soil surface. Therefore, any change in land surface elevation greatly magnifies the amount of freshwater available for use in the system (Hayden *et al.*, 1995). Dune swales have a lower elevation that results in increased moisture levels. The anoxic condition found in these soils inhibits the release of nutrients during decomposition and minimizes the effects of litter quality on decay (Conn and Day, 1997). Instead, nutrients are released in pulses as the soil dries out between rainfall events (Kushlan, 1990; Conn and Day, 1997).

Ecosystems on barrier islands are considered to be nutrient limited due to sandy soils which promote rapid decay and high nutrient leaching potential (Conn and Day, 1996). As a result, nutrients in barrier island soils have been shown to be tightly cycled (Kushlan, 1990; Conn and Day, 1996; Conn and Day, 1997); nutrient limited ecosystems often exhibit patterns which enhance nutrient conservation, such as increased nutrient immobilization (Bargali *et al.*, 1993; Hunt *et al.*, 1988; Vitousek *et al.*, 1994). This is

especially true on the barrier islands of the VCR where nitrogen has been shown to be a limiting factor (Day, 1996). The well-drained soils on the coastal dunes have high leaching rates of nitrate from the upper layers of the soil. Stressful conditions in dune soils, such as low fresh water availability, may also inhibit nitrification and nitrogen mineralization (Kachi and Hirose, 1983). Soil nitrogen availability may influence decay rates directly by affecting microbial populations or indirectly through influences on substrate quality (Hunt *et al.*, 1988).

In contrast to dunes, nutrient availability in swales is limited by an overabundance of water. Excessive moisture availability sustained by prolonged periods of flooding induces anoxic conditions and consequently may result in decreased decay rates (Conn and Day, 1997). Flooding may directly limit the availability of some nutrients important to decomposition, such as nitrogen, through leaching or dilution (Jones and Etherington, 1971).

Belowground processes also play an important role in ecosystem dynamics, but have been studied less frequently (McClaugherty *et al.*, 1982; Nadelhoffer *et al.*, 1985) especially on barrier islands (Vogt *et al.*, 1986; Hendrick and Pregitzer, 1993; Day, 1995; Conn and Day, 1996; Conn and Day, 1997). Barrier islands are inherently nutrient poor and the contribution to soil organic matter and nutrient pools by root turnover can equal or exceed aboveground litter inputs (Ehrenfeld, 1990).

The only decomposition studies performed at the VCR have focused on belowground decomposition (Conn and Day, 1996; Conn and Day, 1997; Day, 1995). These studies found that litter quality alone, though important to decomposition, does not

explain trends in decomposition rates and that environmental variability between dune and swale environments strongly influence decay rates in swales (Conn and Day, 1997).

Not only is it important to observe the rates of litter decomposition at different points along the dune's topography, but it is also important to observe environmental thresholds (i.e. groundwater level, soil nutrient content, or vegetation cover) that might alter the rate of litter decay. The aforementioned studies attempted to observe trends in decomposition over a broad spatial scale, but the fine scale patterns of barrier island decomposition have not been studied. Determination of thresholds in the turnover rate of organic materials might lead to better understanding of the breakdown and recycling of litter on barrier islands and thresholds of state transitions. The objective for this study was to examine the fine spatial scale variation in decomposition rate over a dune/swale gradient and the ecosystem states associated with it in order to identify thresholds that might affect decomposition or state change.

METHODS

Study Area

The Virginia Coast Reserve (VCR) is owned by the Nature Conservancy and is a National Science Foundation (NSF) Long Term Ecological Research (LTER) site with the primary research program centered at the University of Virginia. The protected settings of the Virginia barrier islands provide an excellent location for the study of ecosystems associated with these islands, as well as the effects of global events such as climate change. The primary goals of the Virginia Coast Reserve LTER project focus on succession, disturbance, and system state change.

The study was conducted on the north end of Hog Island, a narrow low-lying barrier island 11.3 km in length, averaging 0.8 km in width and lying 14 km off the Virginia coastline of the Delmarva Peninsula (Dueser *et al.*, 1976) (Figure 1). The islands are part of The Nature Conservancy's Virginia Coast Reserve, a National Science Foundation Long Term Ecological Research site. The center of Hog Island is made up of large dune ridge "islands" surrounded by swales consisting of thickets of wax myrtle (*Morella cerifera* L.) or freshwater marsh (Dilustro, 1992). A 56 year old dune (Conn and Day, 1996) located in the center of Hog Island was selected for this study (Figure 2). Three similar transects, each approximately 85 m in length, incorporated a grass dominated dune ridge and the marsh to the east and wooded swales to the west. The upper ridges of Hog Island dunes typically support communities of

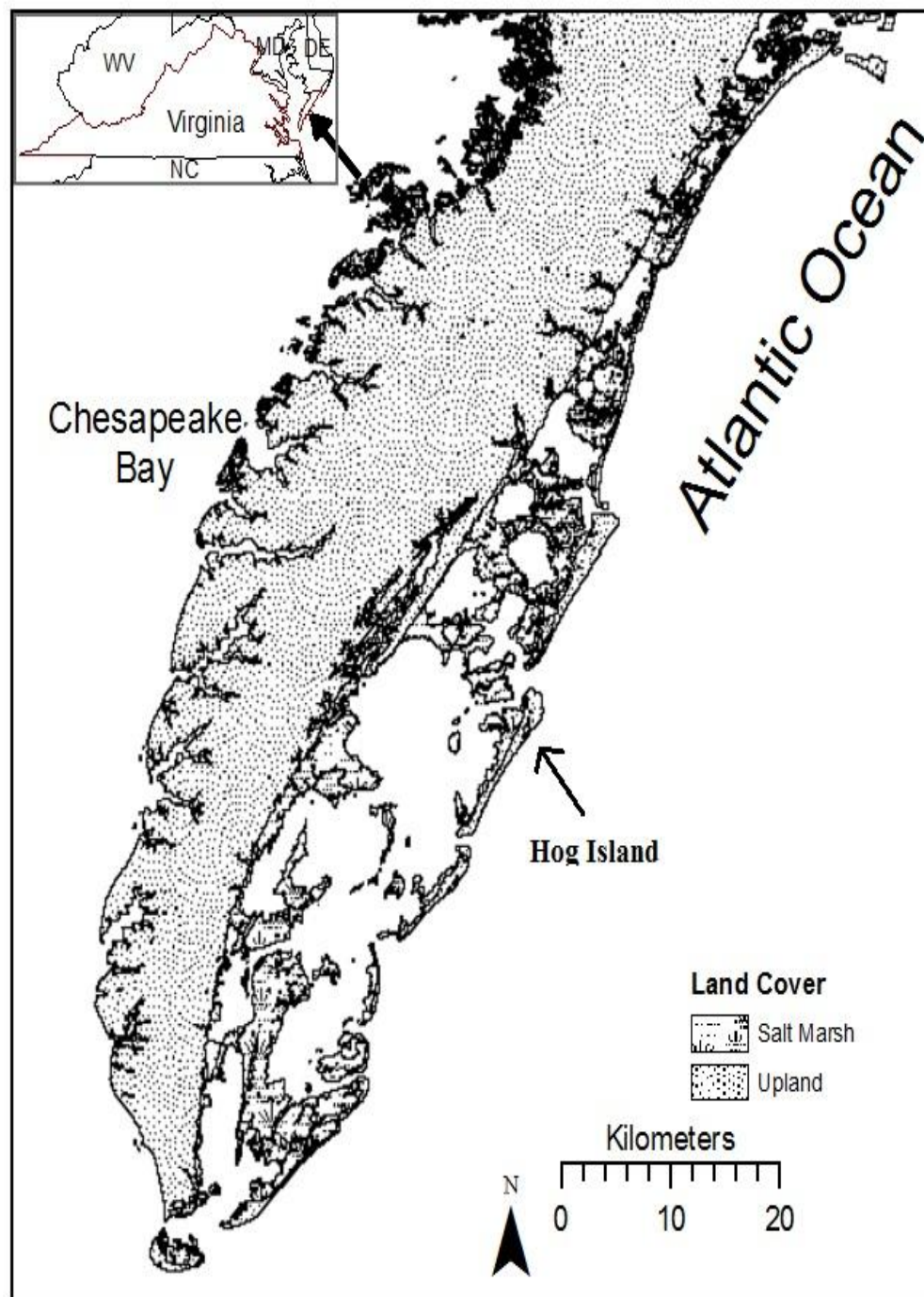


Figure 1. The Delmarva Peninsula and its barrier islands.

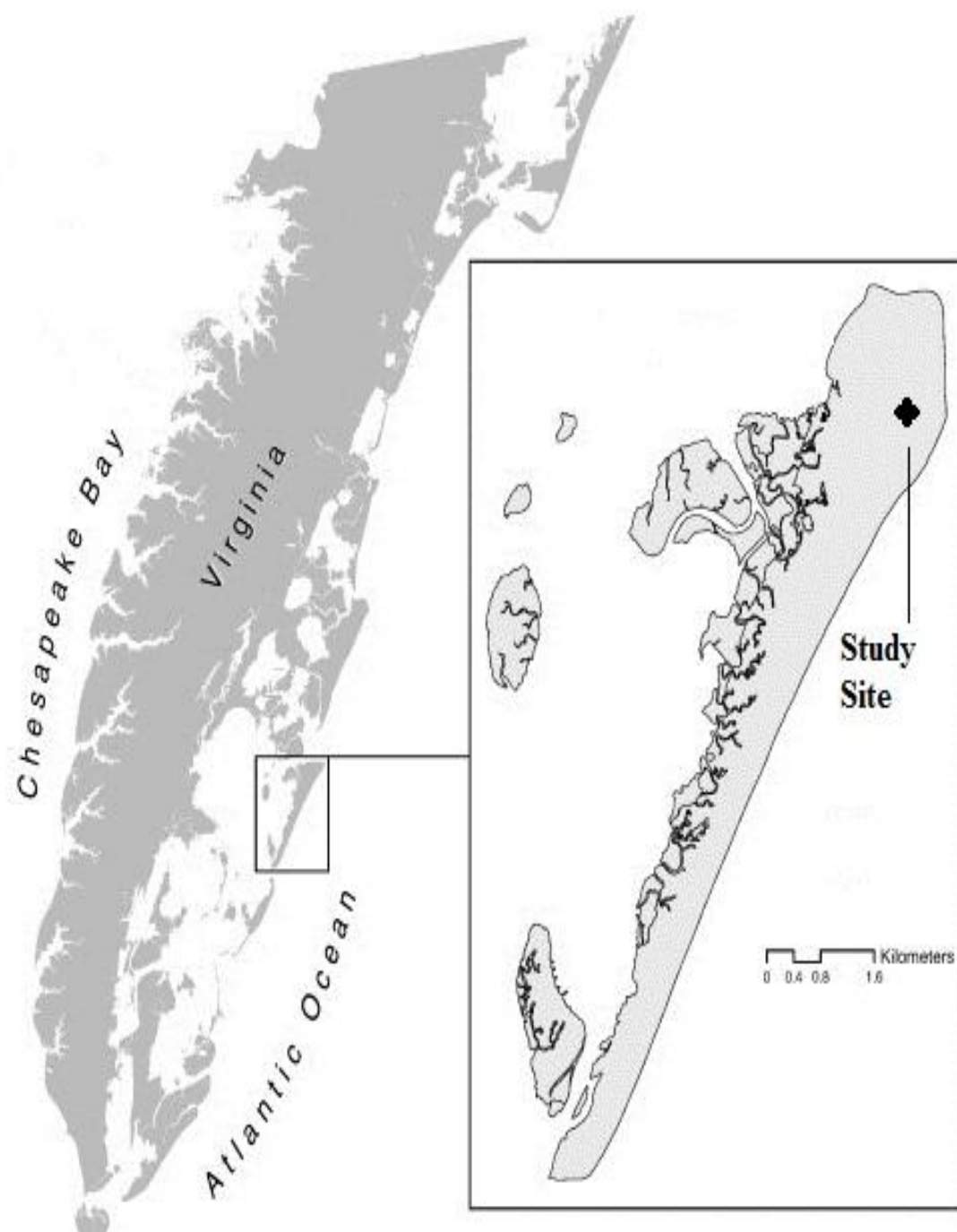


Figure 2. Location of research site on northern Hog Island.

graminoid species like *Spartina patens*, *Ammophila breviligulata* Fernald and *Schizachyrium scoparium* (Michx.). Marshes on Hog Island are typically dominated by salt meadow cordgrass (*Spartina patens* (Aiton) Muhl.). The dune ridge utilized during this study is dominated by little blue stem (*Schizachyrium scoparium*), while the western swale is dominated by wax myrtle (*Morella cerifera*), a woody shrub. The marsh swale in the east is not dominated by cord grass, but instead, the study locations and adjacent areas are dominated by sword grass (*Schoenoplectus pungens* (Vahl) Palla). Nine litterbag/dowel stations on each transect were marked with flags at similar elevations across the dune/swale transect (Figure 3).

Aboveground Decomposition

Decomposition rate was measured aboveground using litterbags filled with air dried leaves of wax myrtle. Wax myrtle is a dominant species on barrier islands throughout the southeastern United States, including Hog Island (Young *et al.*, 1995). As such, wax myrtle contributes to a majority of the litter found on the island. To estimate aboveground decomposition rates the litterbag method was implemented using fresh, mature leaves collected from a 2 m² area in close proximity to the study site. The leaves were air-dried, and 3 g (+/- 0.05 g) samples were placed into 15 X 15 cm nylon mesh litterbags with a mesh size of 1 mm. Twenty subsamples of leaves were dried in an oven at 70°C, and the mean correction factors (air-dried mass to oven-dried mass) were calculated. Each litterbag/dowel placement station had 21 bags total, allowing for three replicates for each collection event. Litterbags were randomly chosen, given a unique identification number, and set in place in May 2011. Three randomly assigned litter bags

were collected from each station along the three transects after 29, 60, 90, 120, 163, 184, and 386 days in the field. After collection, litterbags were oven-dried at 70°C. The leaves were removed from the bags and gently cleaned before weighing. Leaves were weighed to the nearest tenth of a gram.

Belowground Decomposition

Belowground decomposition rate was measured using commercial wooden dowels made of southern yellow pine wood. Species of pine, especially Loblolly pine (*Pinus taeda*), are found throughout the barrier islands in the Virginia Coast Reserve (Shao *et al.*, 1996). Wooden dowels have been used in other decomposition studies (Vitousek *et al.*, 1994; Austin, 2002) and were chosen because they allowed relatively easy insertion and recovery. Each dowel was 1.27 cm in diameter and was cut into 10 cm lengths. The dowels were air dried and weighed before placement into the field. For mass-loss analysis, ten subsamples of the dowels were dried in an oven at 70°C, and the mean air dry-oven dry mass correction factor was calculated. Randomly selected dowels were given unique identification numbers and were placed into the field behind litterbags with identical identification numbers. The dowels were driven into the ground 5 cm adjacent to each litter bag position along the three transects. Each station had 21 dowels total, allowing for three replicates for each collection event. Dowels were collected at the same time as the similarly numbered litterbags. Dowels were cleaned of any attached material and oven-dried at 70°C. Each dowel was weighed to the nearest tenth of a gram.

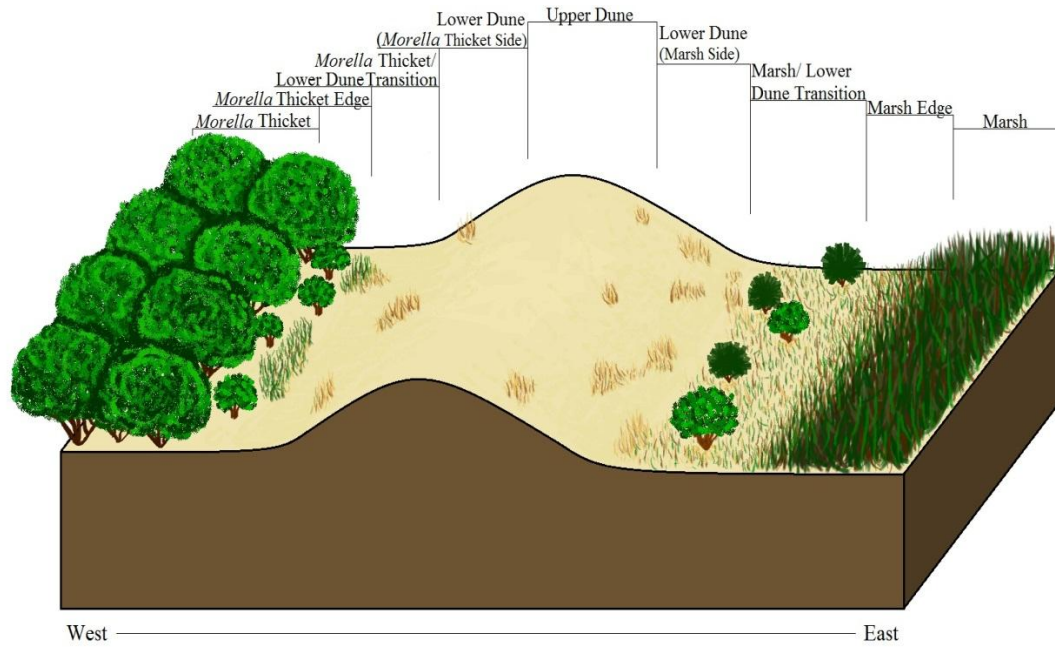


Figure 3. Example of a transect showing the nine litterbag/dowel placement stations.

Environmental Measurements

Surface Elevation

Ground elevation for the study area was determined using a 3.05 X 3.05 m raster resolution LIDAR derived Digital Elevation Model (DEM) of the study area (Figure 4). Coordinates for each litterbag/dowel site were gathered using a Garmin Montana 650t[®] handheld GPS unit. The coordinates were imported into ESRI Arc Map 10 (Spatial Analyst Toolbox) in order to determine elevation for each location.

Groundwater

Groundwater measurements on Hog Island are obtained with Campbell Scientific CS 450-L pressure transducers. Measurements are made every 15 minutes, then statistically summarized and reported hourly. Two groundwater wells are located approximately 100 m south of the southernmost transect and data from these wells were gathered from Anheuser Busch Coastal Research Center (ABCRC) website databanks. Mean depth to groundwater over the study period was calculated using the difference of mean height of groundwater above sea level minus the mean elevation data obtained from a 3.05 X 3.05 m raster resolution LIDAR derived digital elevation model (DEM) of the litterbag/dowel stations (Figure 4).

Soil Analysis

Three soil samples from each litterbag/dowel station were collected in September of 2011 by extracting a 7 cm diameter core to a depth of 10 cm. The

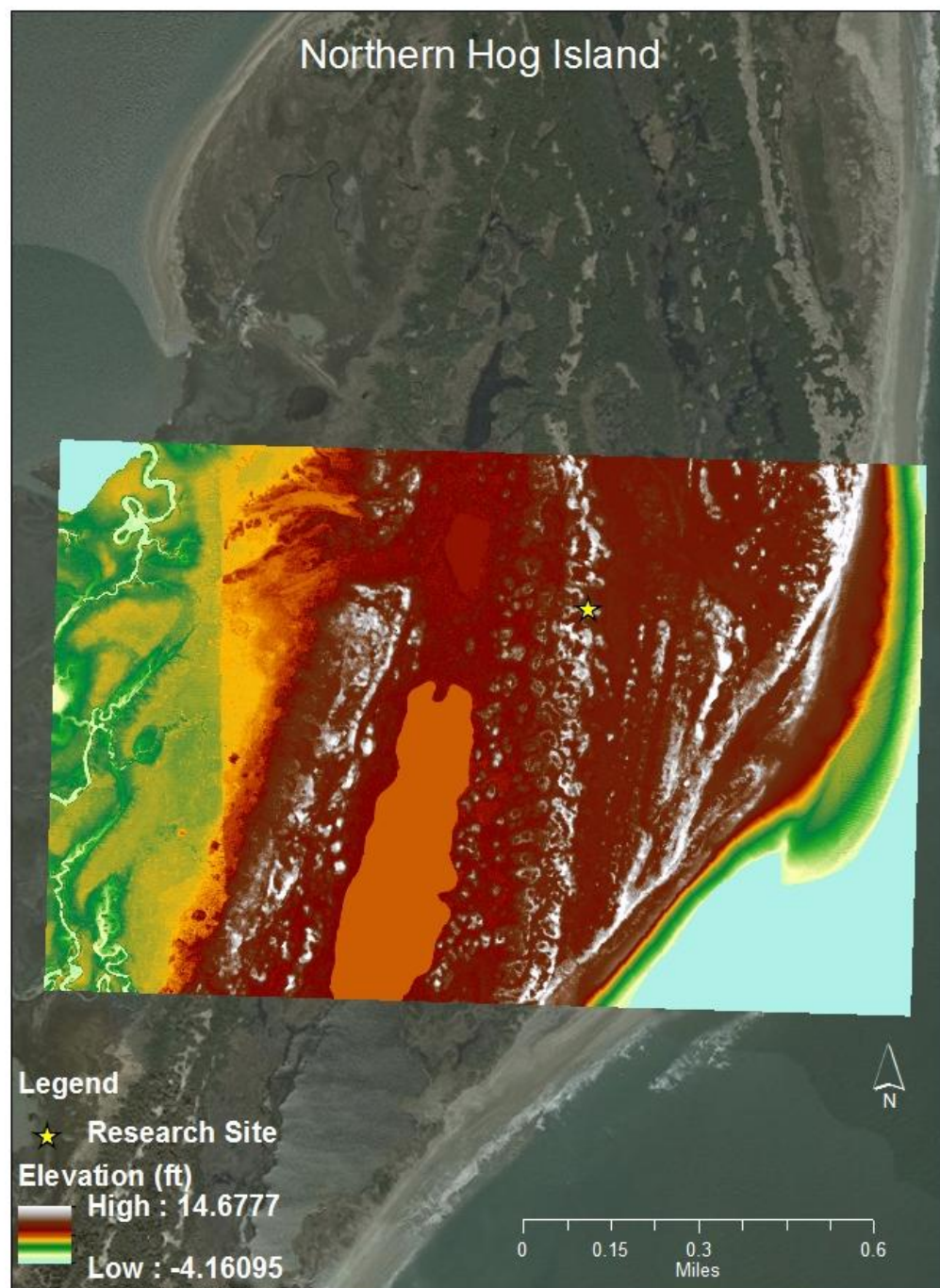


Figure 4. 3.05 X 3.05 m raster resolution digital elevation model of the study area.

soil samples were oven dried at 70°C for 48 hours. 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 in the Old Dominion University OEAS lab via techniques utilized by Cutter and Radford-Knoery (1991). Ten mg samples were used to determine soil percent carbon and nitrogen.

Vegetation Sampling

Vegetation sampling of each line transect was conducted using a 0.5 m wide belt transect running through the middle of each station along each transect. The belt transect was broken into 0.25 m² quadrats within which the density of each plant species was recorded. Individual samples of each unique plant species were gathered in October 2011 and were identified using the Manual of the Vascular Flora of the Carolinas (Radford *et al.*, 1981). Nomenclature was verified using Flora of the Southern and Mid Atlantic States, working draft of September, 2012 (Weakley, 2012).

Data Analysis

Aboveground and belowground decay rates (k) (yr^{-1}) were determined from a fixed-intercept negative exponential model (Wieder and Lang, 1982) corresponding to the following equation: $X = e^{-kt}$ where $X = \frac{X_t}{X_o}$ = proportion of initial mass (X_o) remaining at time t (years). One way analysis of variance (ANOVA) was used to analyze variation in decomposition rate (yr^{-1}) and environmental variables among stations. Significant differences in mean decay rate and environmental measurement ($p = 0.05$)

between stations were identified using the Ryan-Einot-Gabriel-Welsch F (REGWF) multiple comparison test for groups with an equal replication. Data for soil % N content were log transformed to meet assumptions for normality and homogeneity of variance. Regression equations were used to determine if predictive relationships existed between dependent (yr^{-1}) and independent (environmental) variables (Zar, 2010).

RESULTS

Aboveground Decomposition

Aboveground ($F=6.494$, $p < 0.001$) decay rates (yr^{-1}) varied significantly among litterbag/dowel stations. Mean aboveground decay rate (yr^{-1}) ranged from 0.339 (Upper Dune station) to 0.699 (Marsh/Lower Dune Transition station) (Figure 5). The Upper Dune, Marsh and Lower Dune (*Morella* thicket side) stations showed the lowest aboveground rates. The Marsh Edge, Marsh/Lower Dune transition and *Morella* Thicket stations showed the highest decomposition rates (REGWF, $p = 0.05$) (Table 1). Mean aboveground decay rate (yr^{-1}) exhibited a significant negative relationship with elevation ($r^2 = 0.10$, $p = 0.004$) (Figure 6) and a significant positive relationship with soil N content ($r^2 = 0.25$, $p < 0.001$) (Figure 7). Mean aboveground decay rate (yr^{-1}) demonstrated a significant negative relationship with annual mean distance to groundwater ($r^2 = .14$, $p = .032$) (Figure 8).

Belowground Decomposition

Belowground decay rates (yr^{-1}) varied significantly among stations ($F = 5.705$, $p < 0.001$). Mean belowground decay rate (yr^{-1}) ranged from 0.132 (Marsh station) to 0.411 (*Morella* Thicket Edge station) (Table 1). The Marsh and both Lower Dune stations (marsh side and *Morella* thicket side) exhibited the lowest annual decomposition rate and the *Morella* Thicket station had the highest annual decomposition rate (Figure 9) (Table 1). Belowground decomposition rate (yr^{-1}) at the *Morella* Thicket station was 59% higher than the next highest decomposition rate and was the only station that

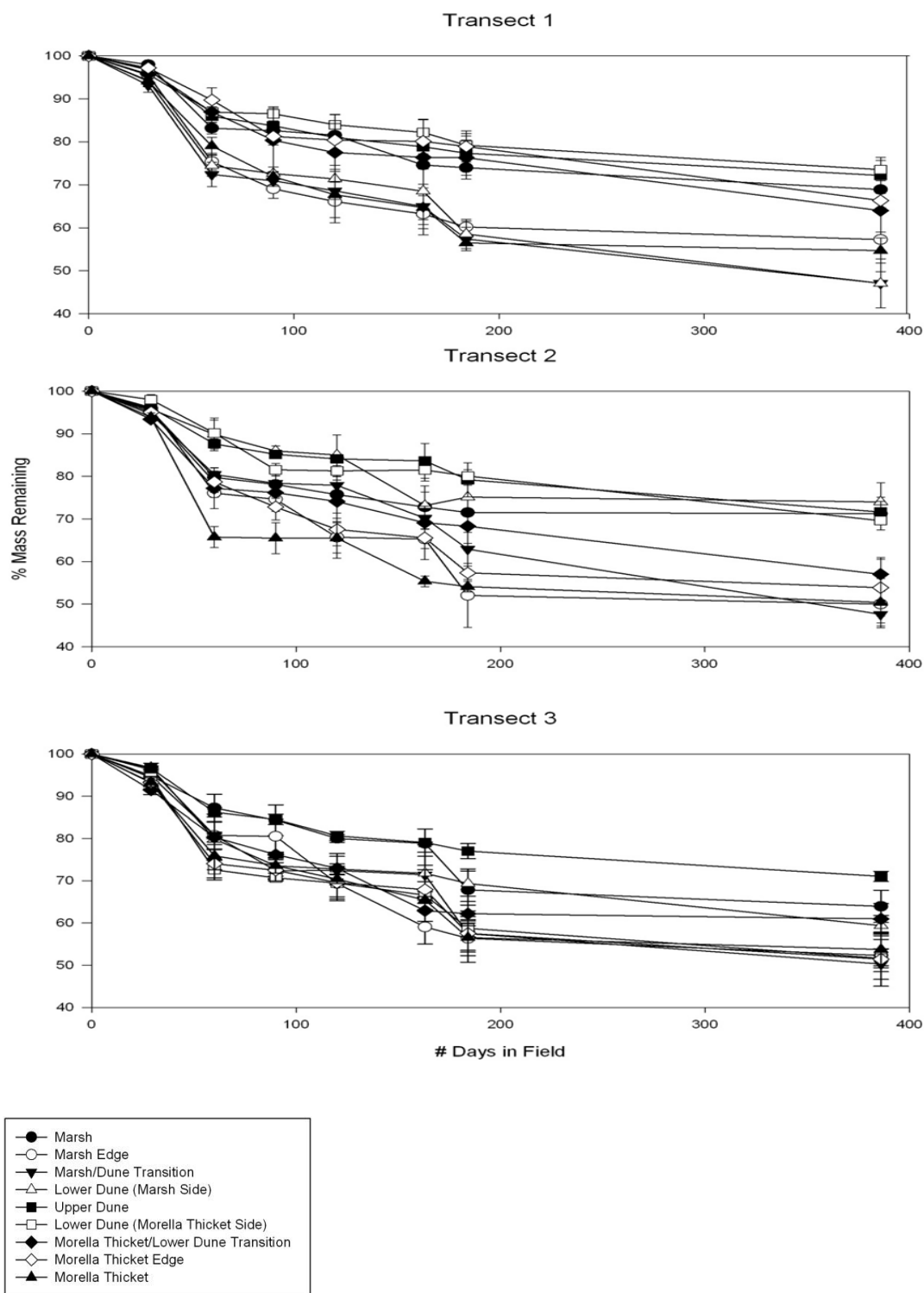


Figure 5. Aboveground % mass remaining vs. # of days in the field. Transect 1 is the southernmost transect and Transect 3 is northernmost. Figure legend for litterbag/dowel stations is in order from East (Marsh) to West (*Morella* Thicket).

Table 1. Mean decay rate (yr^{-1}) and measured environmental variables for all litterbag/dowel placement stations.

| Station Name (East – West) | Mean Aboveground Annual Decay Rate (yr^{-1}) | Mean Belowground Annual Decay Rate (yr^{-1}) | Mean Soil N- Content (% N by weight) | Mean Elevation (m) | Mean Distance to Ground water (m) | Dominant Vegetation Type |
|---|---|---|--|--------------------------|--|---|
| Marsh | 0.388 ^{ab} | 0.132 ^a | 0.101 ^{ab} | 1.346 ^a | 0.426 | <i>Schoenoplectus pungens</i> (Vahl) Palla |
| Marsh Edge | 0.640 ^{cd} | 0.241 ^a | 1.651 ^{de} | 1.324 ^a | 0.416 | <i>Schoenoplectus pungens</i> (Vahl) Palla |
| Marsh/Lower Dune Transition | 0.699 ^{bcd} | 0.214 ^a | 0.261 ^{cd} | 1.909 ^c | 0.606 | <i>Morella cerifera</i> L. Small |
| Lower Dune (Marsh Side) | 0.526 ^d | 0.210 ^a | 1.664 ^{cde} | 1.841 ^c | 0.996 | <i>Schizachyrium scoparius</i> (Michx.) Nash |
| Upper Dune | 0.339 ^a | 0.210 ^a | 0.089 ^a | 2.411 ^d | 1.486 | <i>Schizachyrium scoparius</i> (Michx.) Nash |
| Lower Dune (<i>Morella</i> Thicket Side) | 0.442 ^{abcd} | 0.202 ^a | 0.282 ^{bc} | 1.759 ^{bc} | 0.846 | <i>Schizachyrium scoparius</i> (Michx.) Nash |
| <i>Morella</i> Thicket/Lower Dune Transition | 0.501 ^{abc} | 0.244 ^a | 0.429 ^{abc} | 1.861 ^c | 0.926 | <i>Morella cerifera</i> L. Small |
| <i>Morella</i> Thicket Edge | 0.564 ^{bcd} | 0.221 ^b | 1.034 ^e | 1.802 ^c | 0.886 | <i>Morella cerifera</i> L. Small |
| <i>Morella</i> Thicket | 0.629 ^d | 0.411 ^{ab} | 0.799 ^{cde} | 1.582 ^b | 0.656 | <i>Morella cerifera</i> L. Small |

Different lowercase letters between rows indicate significant differences ($p = 0.05$) between sites.

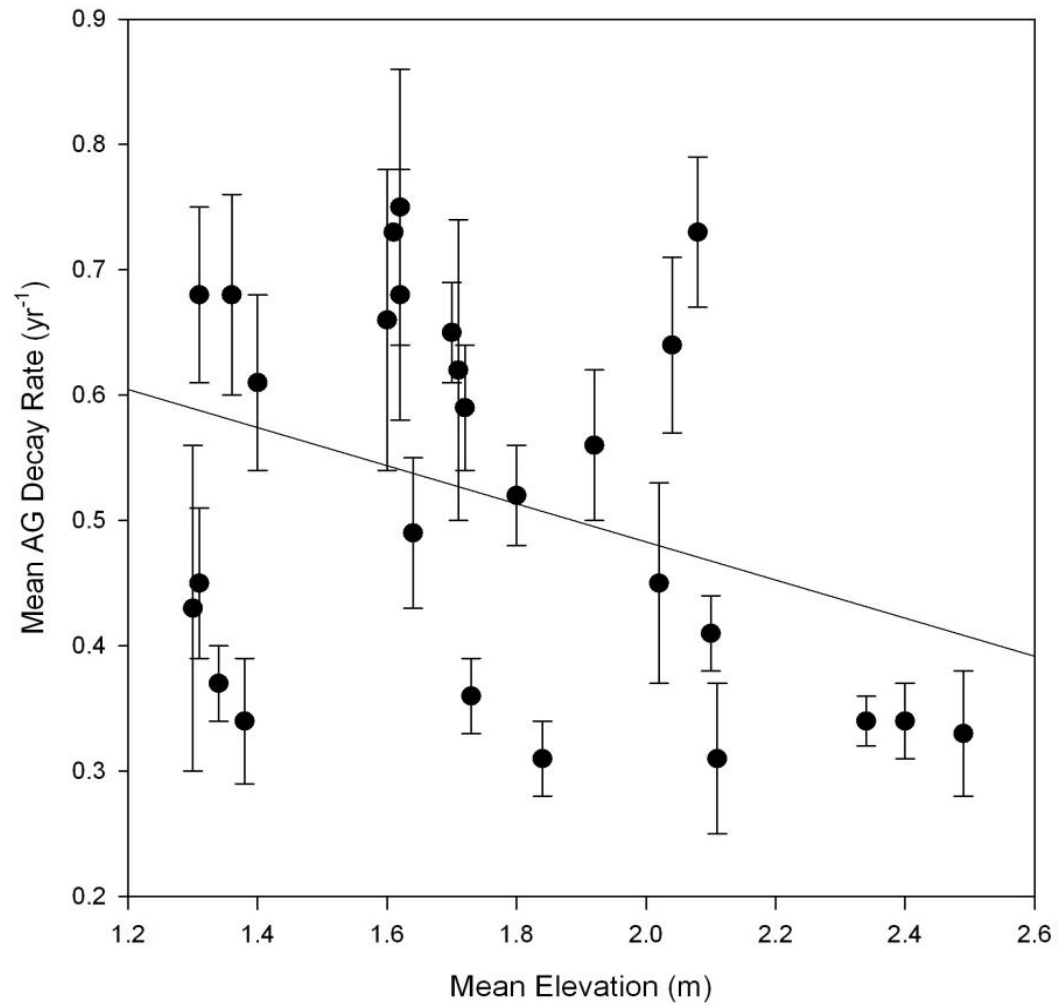


Figure 6. Mean aboveground decay rate (yr⁻¹) vs. mean surface elevation (m) ($r^2 = 0.10$, $p = 0.004$).

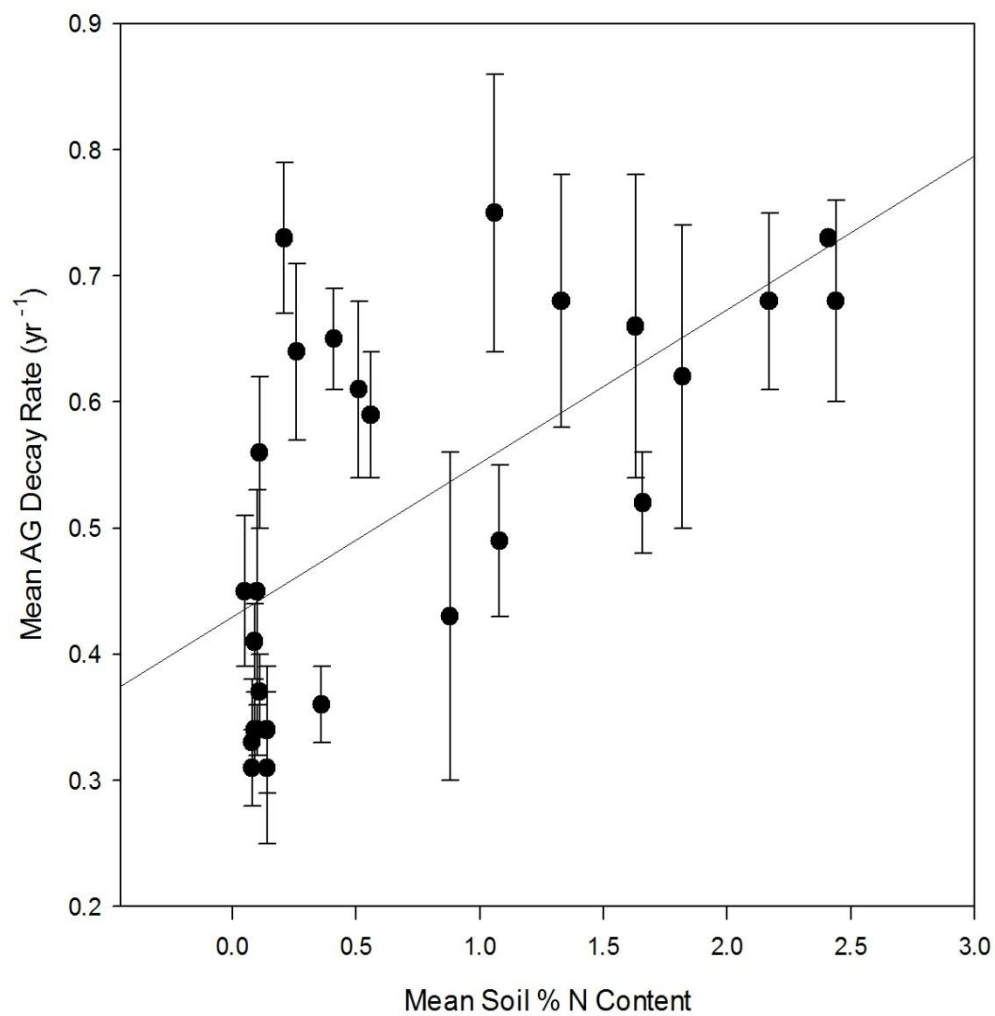


Figure 7. Mean aboveground decay rate (yr⁻¹) vs. mean soil % N content ($r^2 = 0.25$, $p < 0.001$).

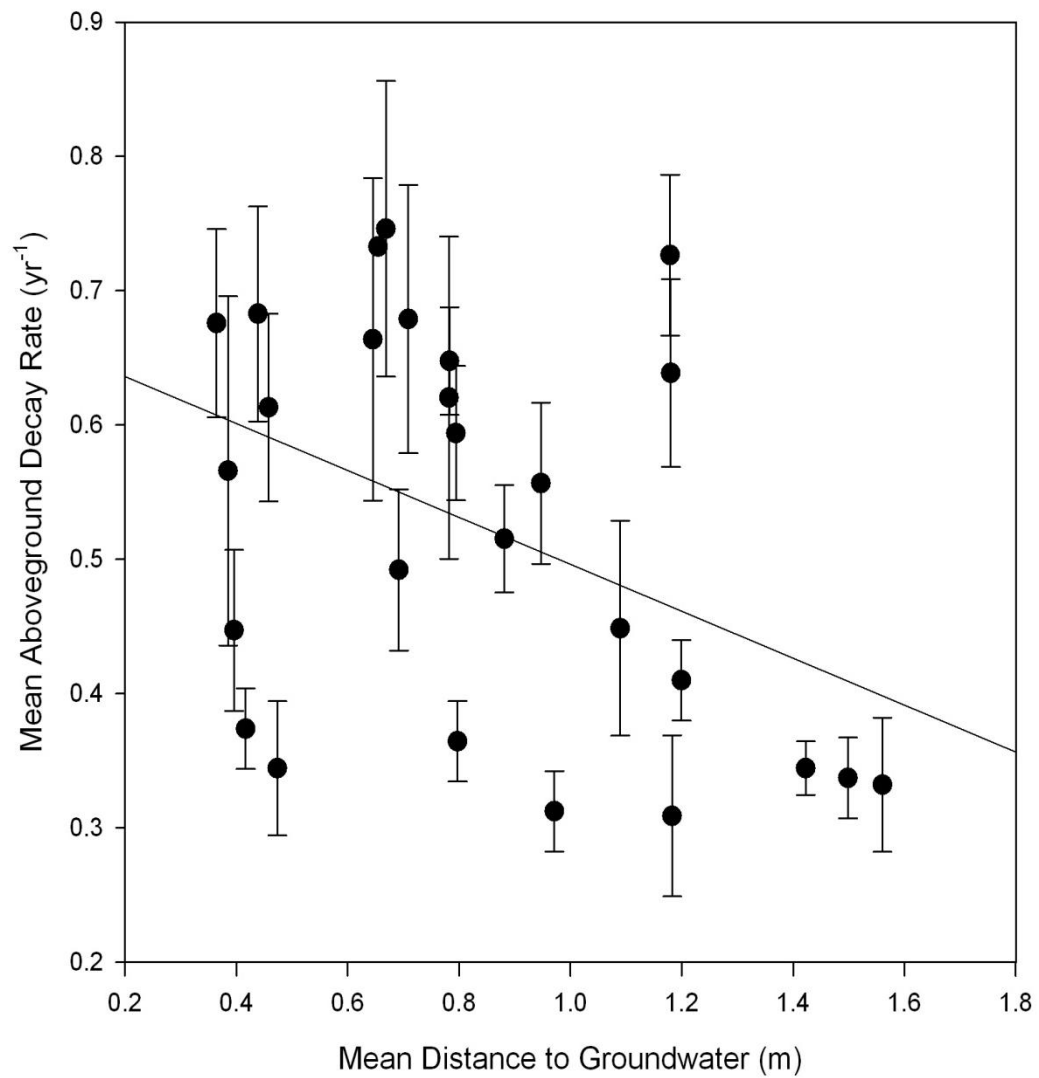


Figure 8. Mean aboveground decay rate (yr⁻¹) vs. annual mean distance to groundwater (m) ($r^2 = 0.14$, $p = 0.032$)

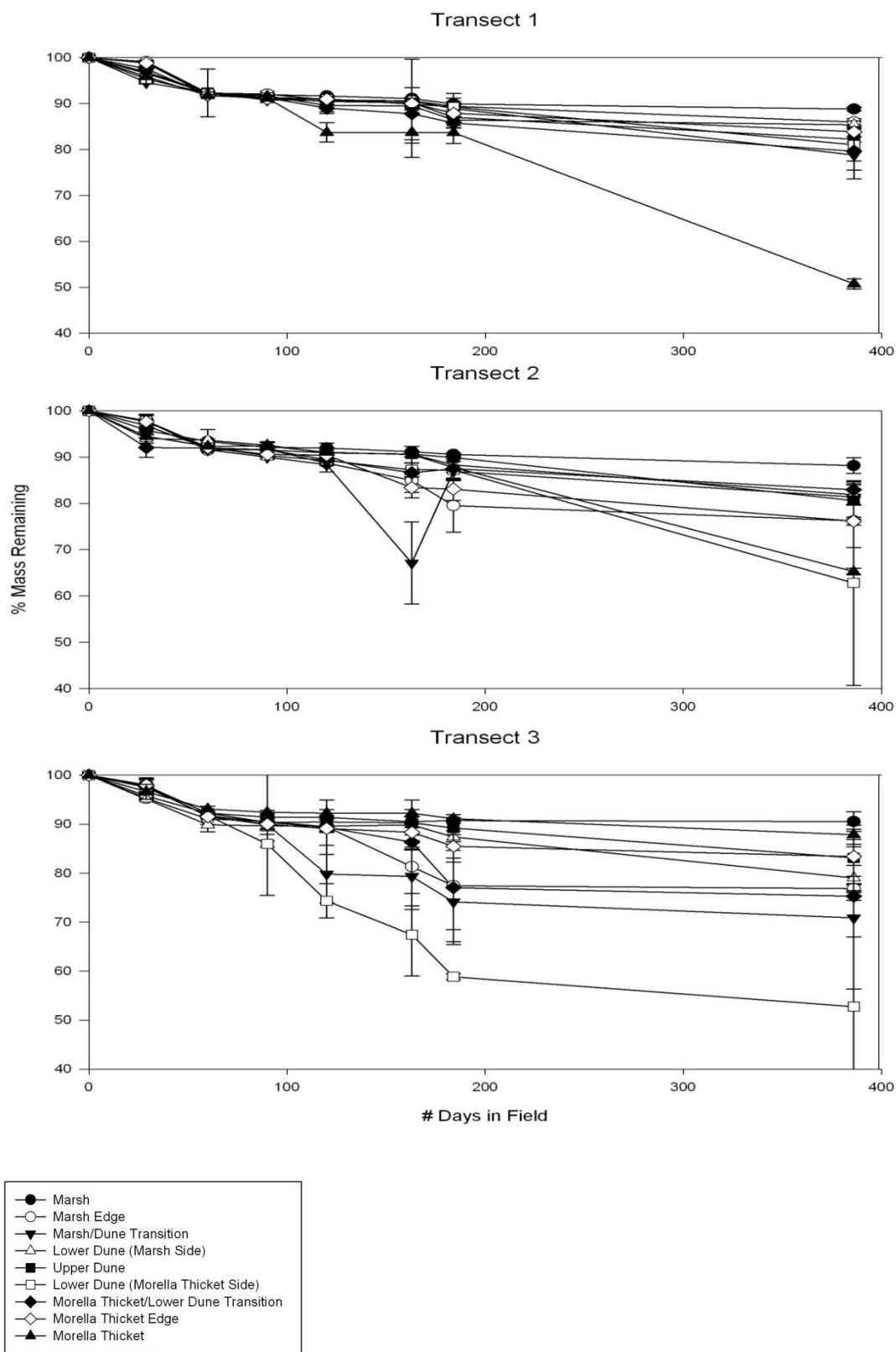


Figure 9. Belowground % mass remaining vs. # of days in the field. Transect 1 is the southernmost transect and Transect 3 is northernmost.

differed significantly from other stations (REGWF, $p = 0.05$) (Table 1). Regression of belowground decay rate (yr^{-1}) to elevation ($r^2 < 0.001$, $p = .898$) and annual mean distance to groundwater ($r^2 < 0.001$, $p = .963$) showed no significant relationship, unlike aboveground decay values (Figures 10 & 11). Belowground decay rate (yr^{-1}) showed no significant relationship with soil N values ($r^2 = 0.044$, $p = 0.60$) (Figure 12).

Surface Elevation and Groundwater

The Marsh (1.324 m) and Marsh Edge (1.346 m) had significantly lower elevations than other stations (REGWF, $p = 0.05$). The Upper Dune station had the highest annual mean distance to groundwater averaging 1.486 m (Table 1) (Figure 13). Annual mean distance to groundwater was lowest at the Marsh Edge station and Marsh station (0.416 m and 0.426 m) (Figure 13).

Soil N Content

Soil N content ($F = 11.884$, $p < 0.001$) varied significantly among litterbag/dowel sites (Table 1). Among litterbag/dowel stations, the Lower Dune (marsh side) and Marsh Edge stations had significantly higher mean soil N content than other stations (REGWF, $p = 0.05$). The Upper Dune and Marsh stations demonstrated significantly lower soil N content than other stations in the study area (REGWF, $p = 0.05$) (Table 1) (Figure 14). Regression analysis showed a significant inverse relationship between soil N and surface elevation ($r^2 = 0.108$, $p = 0.002$) (Figure 15).

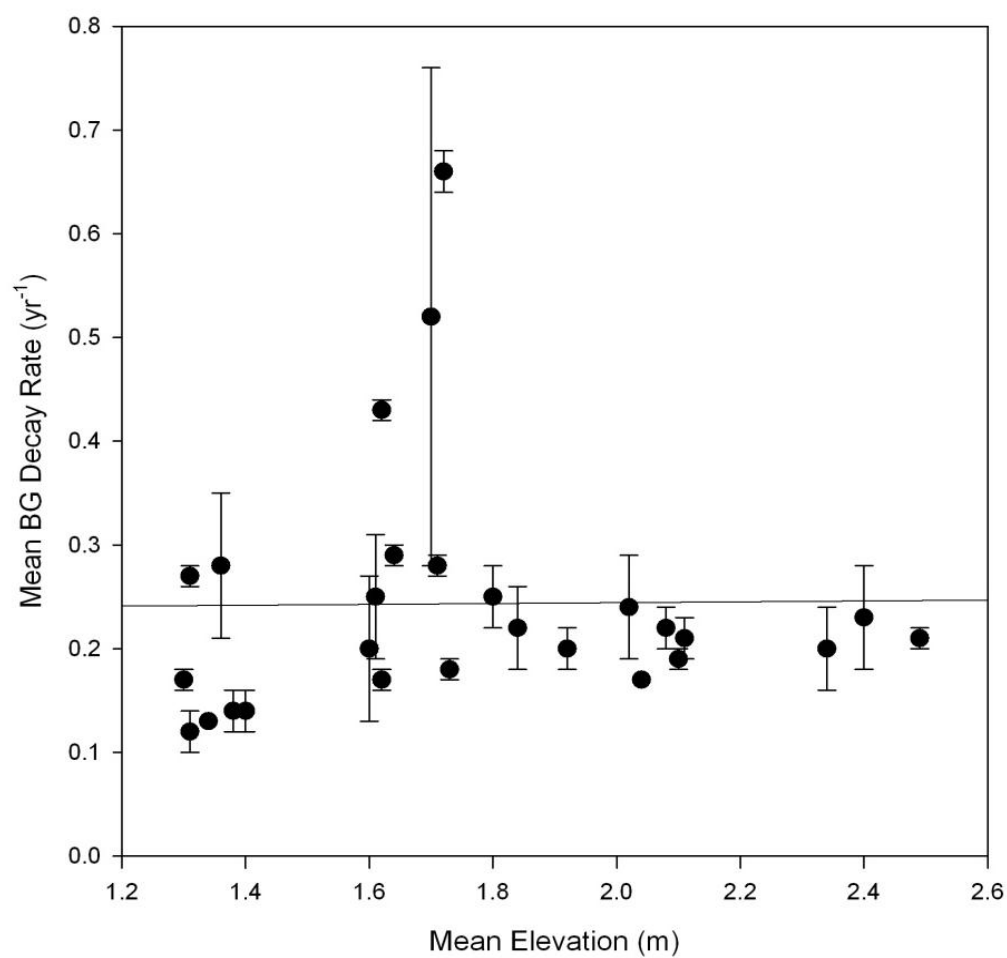


Figure 10. Mean belowground decay rate (yr⁻¹) vs. mean surface elevation (m) ($r^2 < 0.001$, $p = 0.898$).

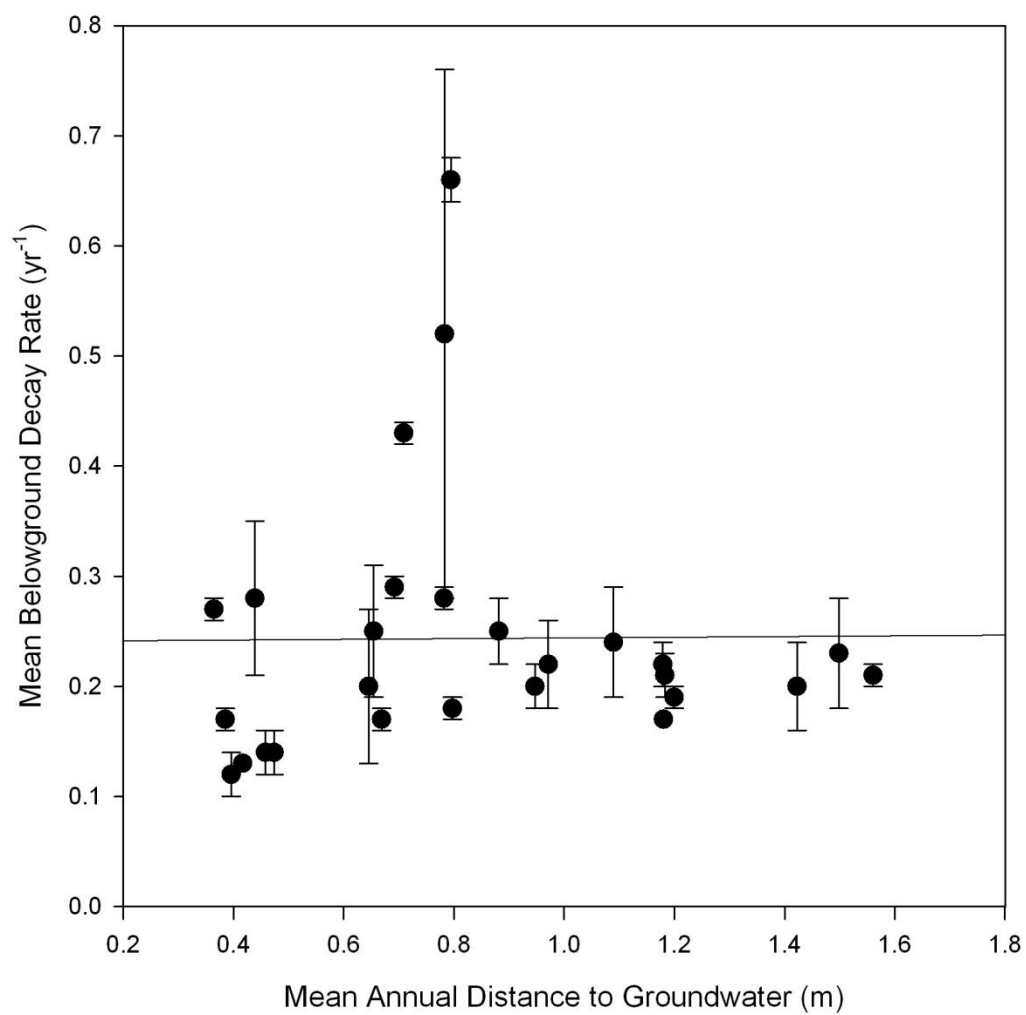


Figure 11. Mean belowground decay rate (yr⁻¹) vs. annual mean distance to groundwater (m) ($r^2 < 0.001$, $p = .963$).

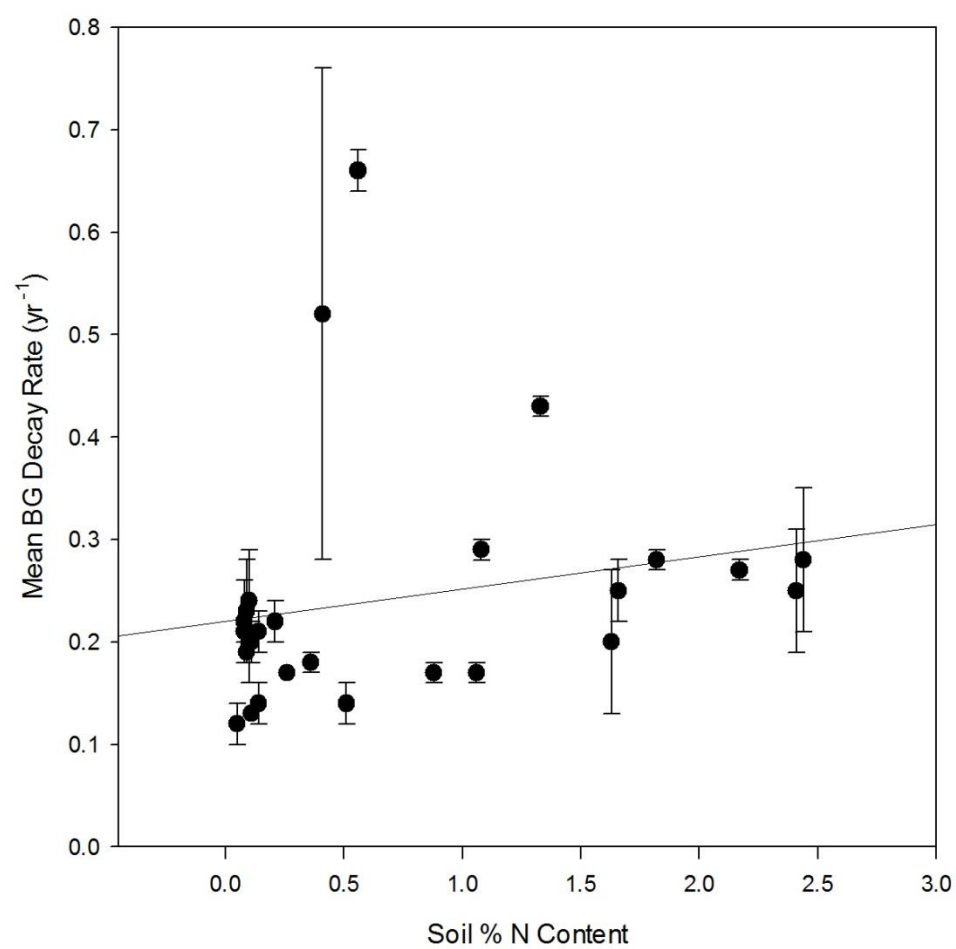


Figure 12. Mean belowground decay rate (yr⁻¹) vs. mean soil N content (% N) ($r^2 = 0.044$, $p = 0.60$).

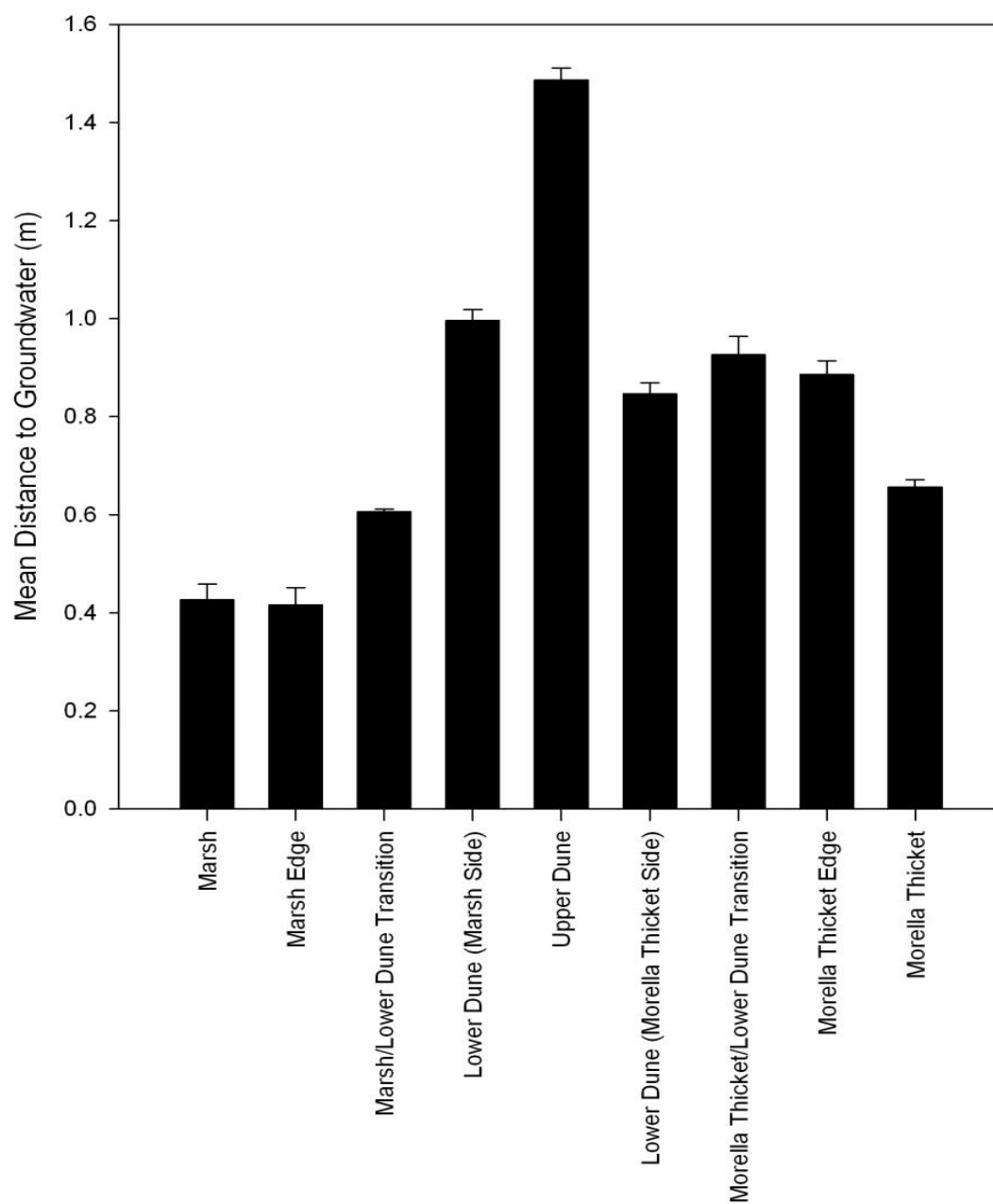


Figure 13. Annual mean distance to groundwater for all litterbag/dowel placement stations throughout the study period. Stations are in order from East (Marsh) to West (*Morella* Thicket).

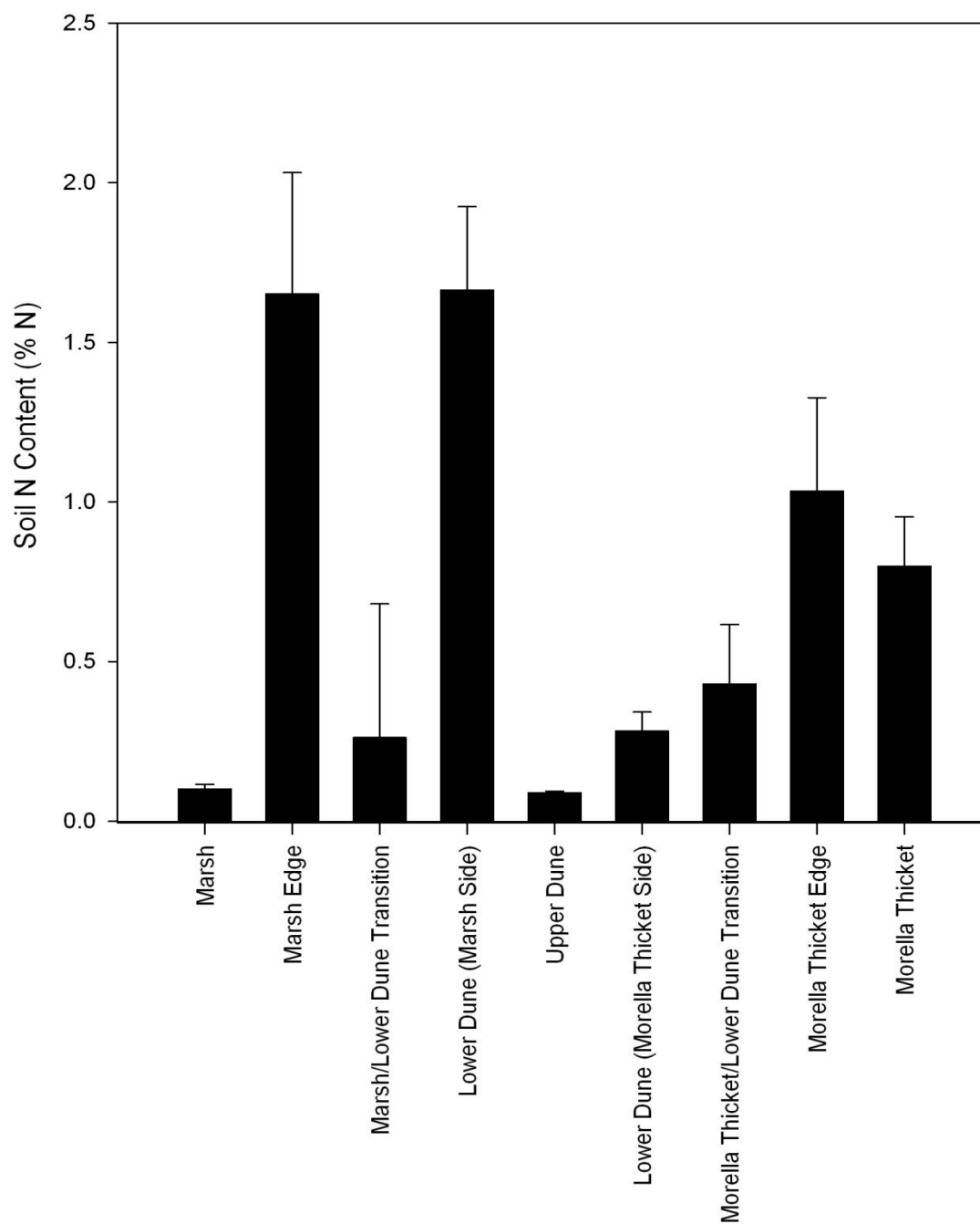


Figure 14. Mean soil N content for all litterbag/dowel placement stations. Stations are in order from East (Marsh) to West (*Morella* Thicket).

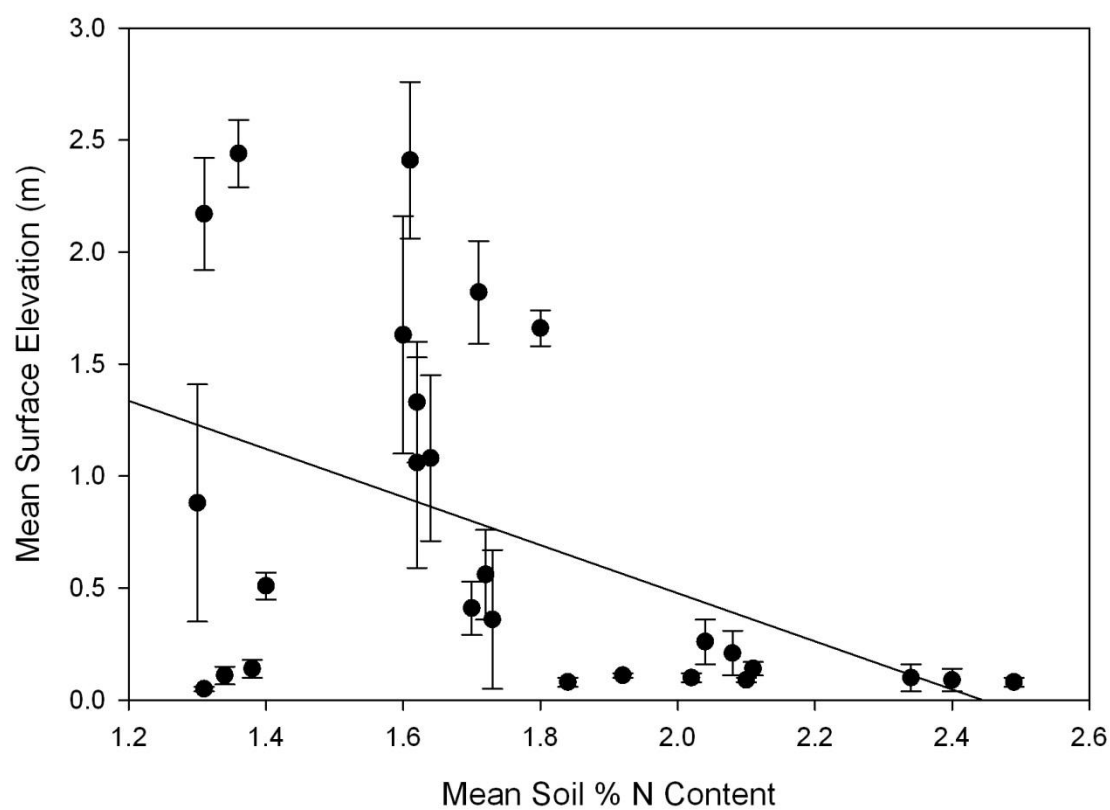


Figure 15. Mean surface elevation (m) vs. mean soil N content (%) ($r^2 = 0.108$, $p = 0.002$).

State Change Thresholds

The Marsh and Marsh Edge litterbag/dowel stations were dominated by swordgrass (*Schoenoplectus pungens* (Vahl) Palla). Wax myrtle (*Morella cerifera* L.) dominated the Marsh/Lower Dune transition, *Morella* Thicket edge and *Morella* Thicket stations. All other stations were dominated by little blue stem (*Schizachyrium scoparium* (Michx.) Nash) (Table 1) (Figure 16).

Elevation and distance to groundwater appeared to be important determining factors to vegetation composition. Stations dominated by *S. pungens* had the lowest mean elevation and were closest to fresh groundwater. Stations dominated by *S. scoparium* had the highest mean elevation and were farthest from groundwater (Figures 16 & 18).

Dominant vegetation and elevation (groundwater) levels seem to be indicators of areas where high rates of decay may occur. Aboveground and belowground decomposition rates were highest at stations dominated by or in very close proximity to (Marsh Edge station) *M. cerifera*. The lowest aboveground and belowground decomposition rates were found in the *S. pungens* dominated Marsh station (Figures 16, 17 & 18). The maximum elevation where *M. cerifera* was found to be dominant was 1.81 m above sea level (ASL) and the lowest elevation was 1.53 m ASL. *S. scoparium* dominated areas with elevations greater than 1.81 m ASL and *S. pungens* dominated areas with elevation lower than 1.53 m ASL (Figure 16).

Soil N content was highest in the eastern (marsh side) stations dominated by *S. pungens* and *S. scoparium*. Soil N content was lowest at the *S. scoparium* dominated Upper Dune station (Figure 20). Elevation was the only variable found to contribute to

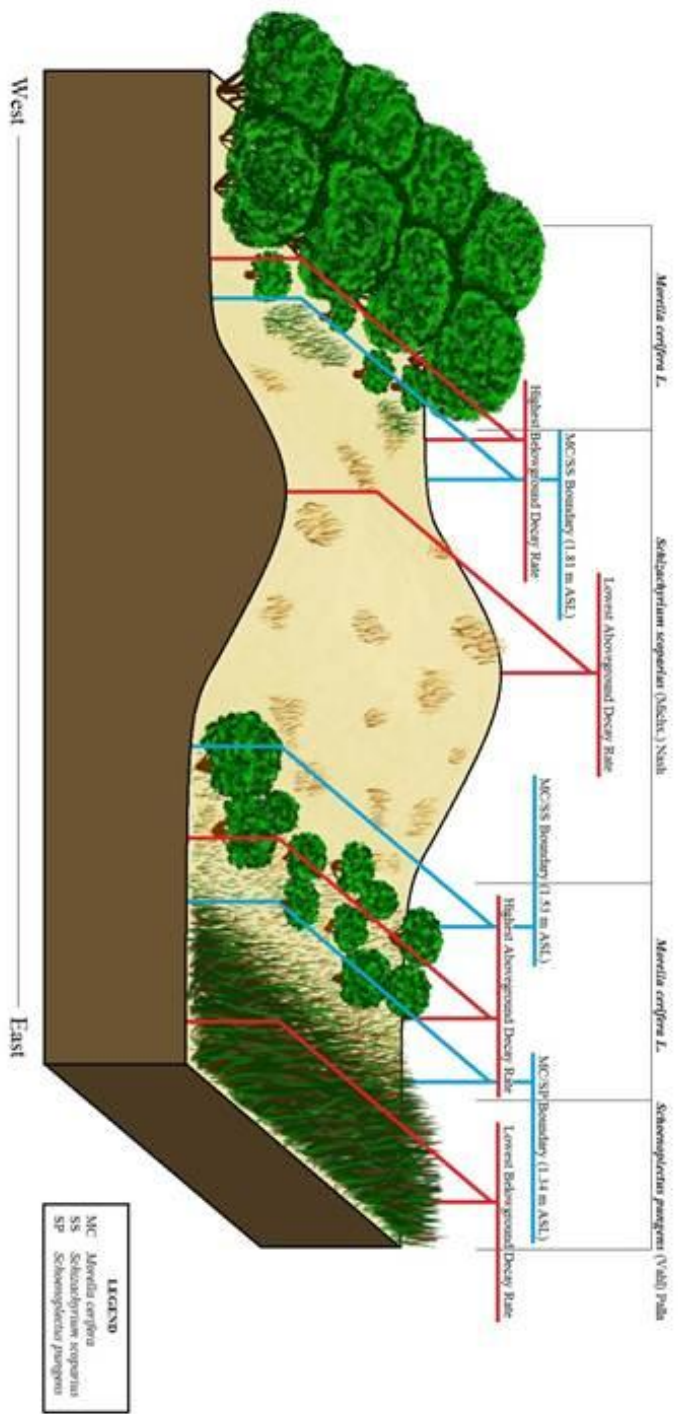


Figure 16: Example of a transect highlighting possible thresholds for changes in system state.

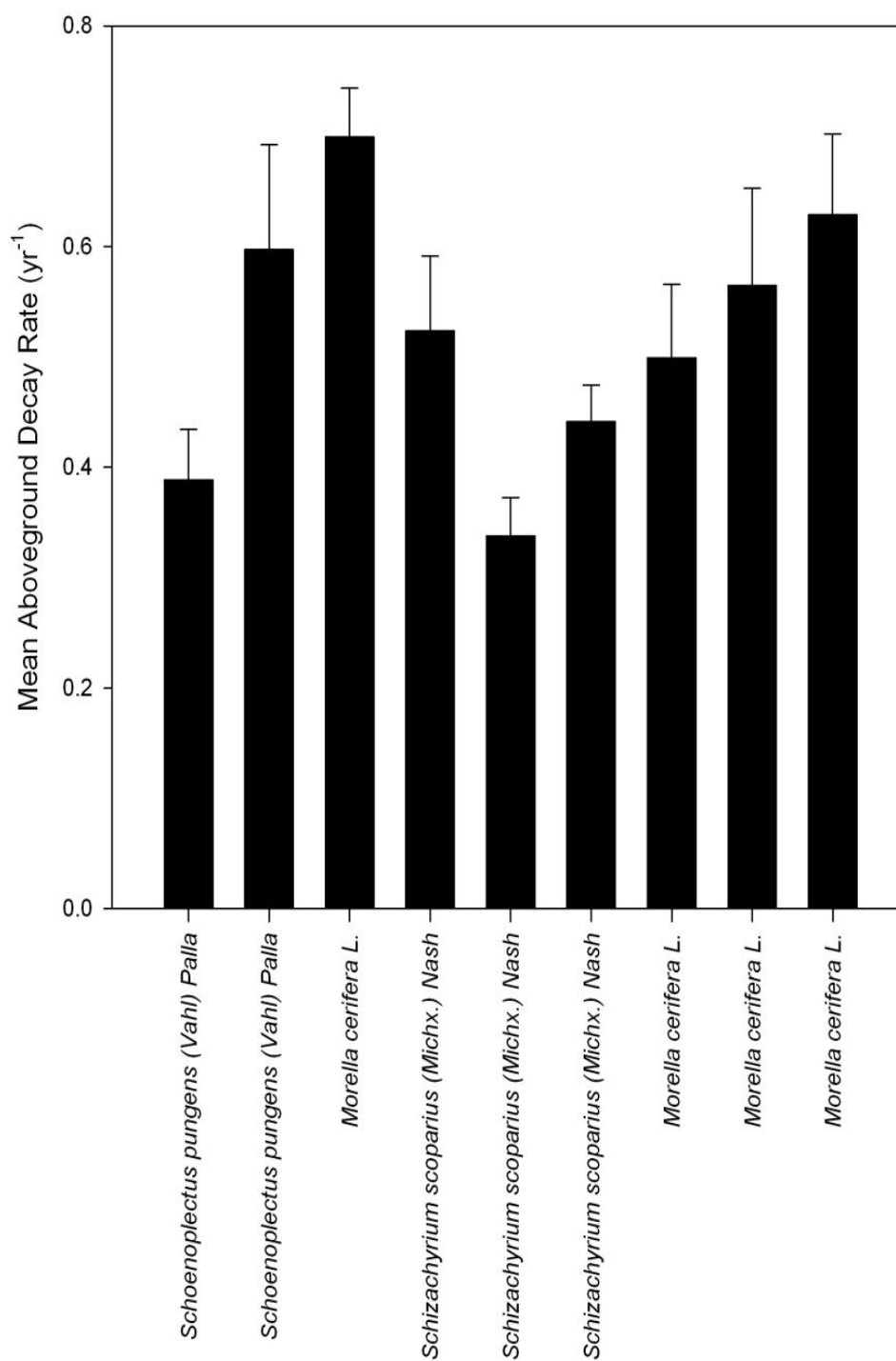


Figure 16. Mean aboveground decay rate (yr⁻¹) vs. litterbag/dowel station dominant species. From left to right stations on X-axis are in order from East (Marsh station) to West (*Morella* thicket station).

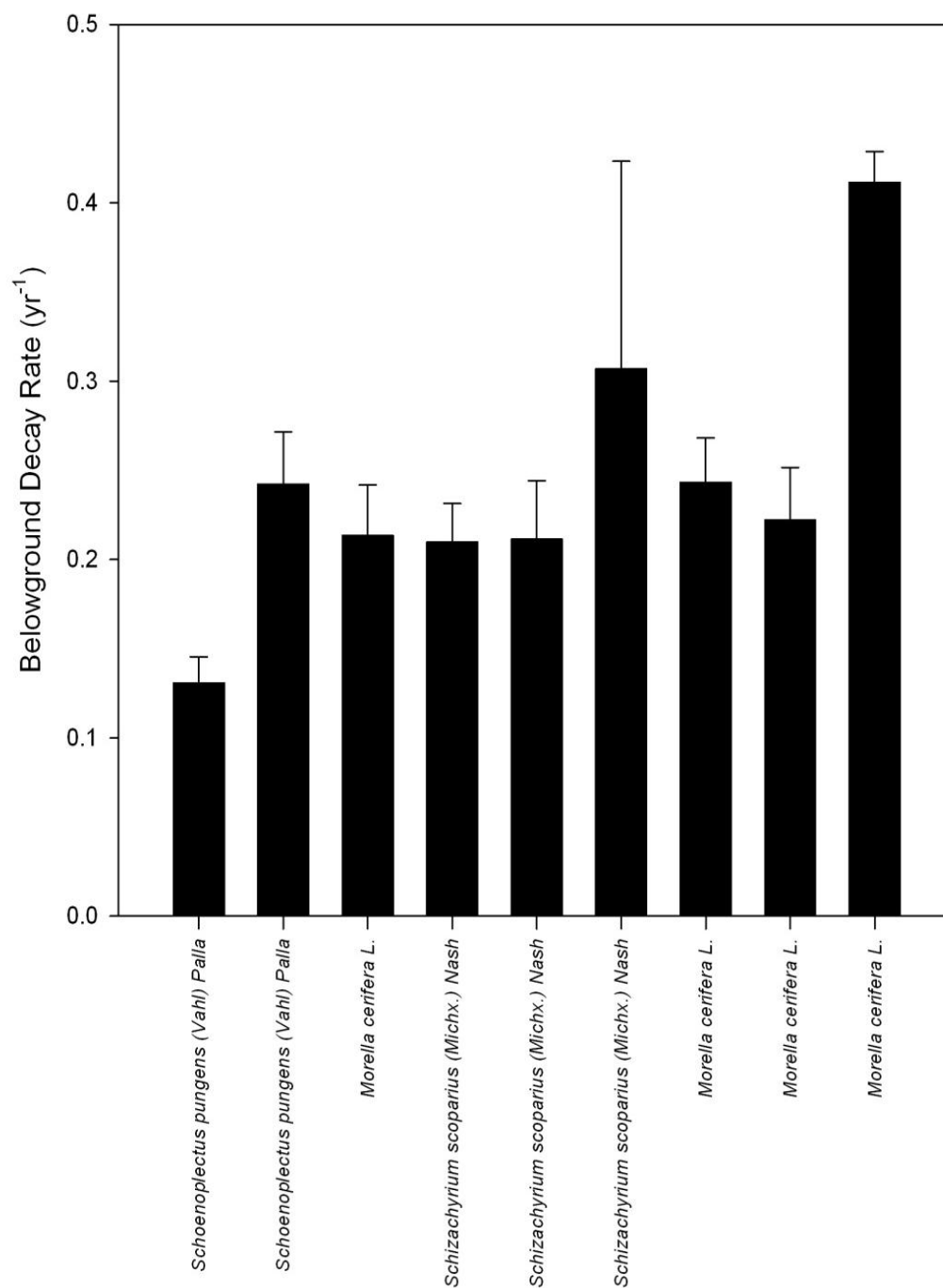


Figure 17. Mean belowground decay rate (yr⁻¹) vs. litterbag/dowel station dominant species. From left to right stations on X-axis are in order from East (Marsh station) to West (*Morella* thicket station).

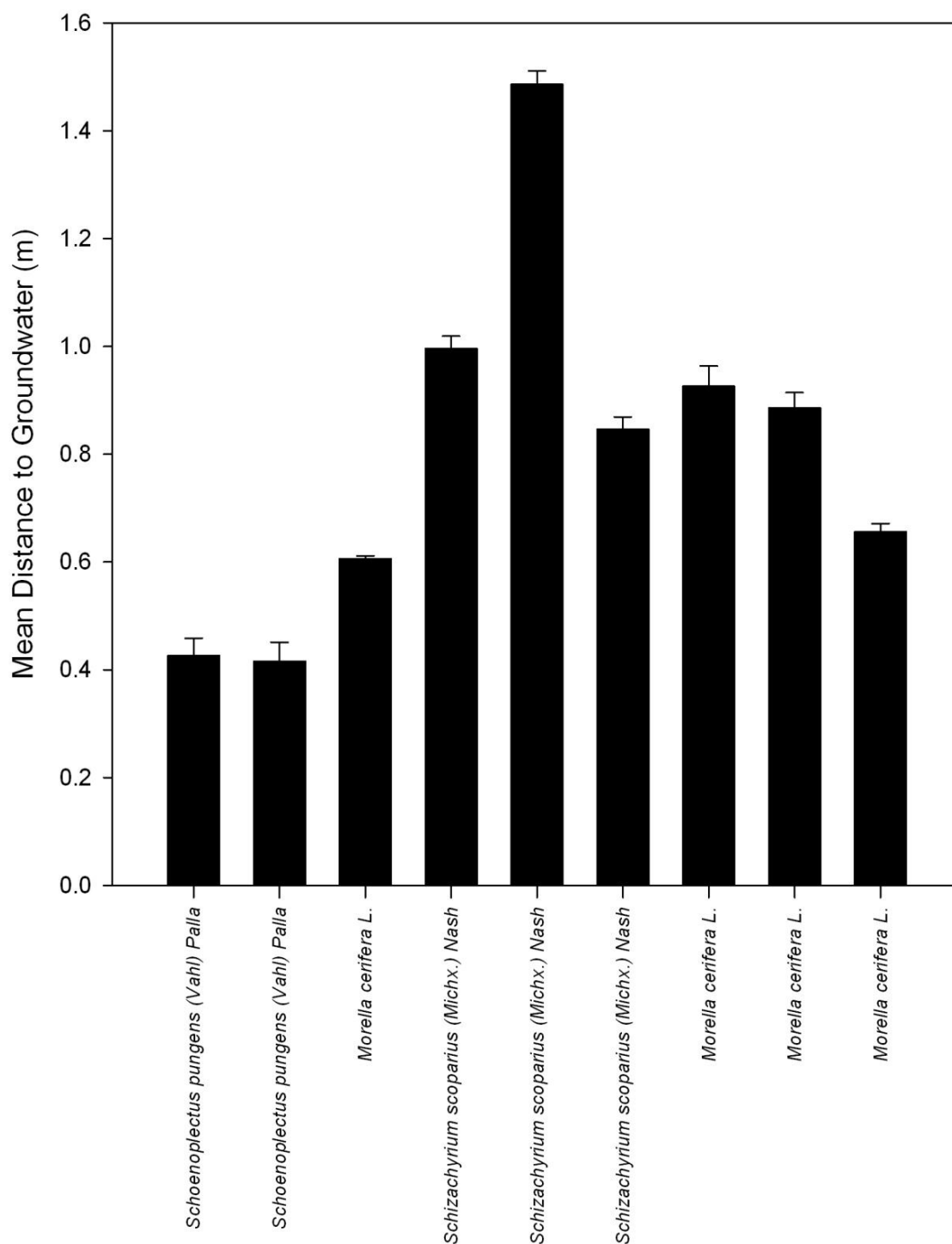


Figure 18. Mean distance to groundwater (m) vs. litterbag/dowel station dominant species. From left to right stations on X-axis are in order from East (Marsh station) to West (Morella thicket station).

variation in soil N content. A negative relationship with elevation was observed, but consistent variation in soil N between system states was not identified (Figure 20).

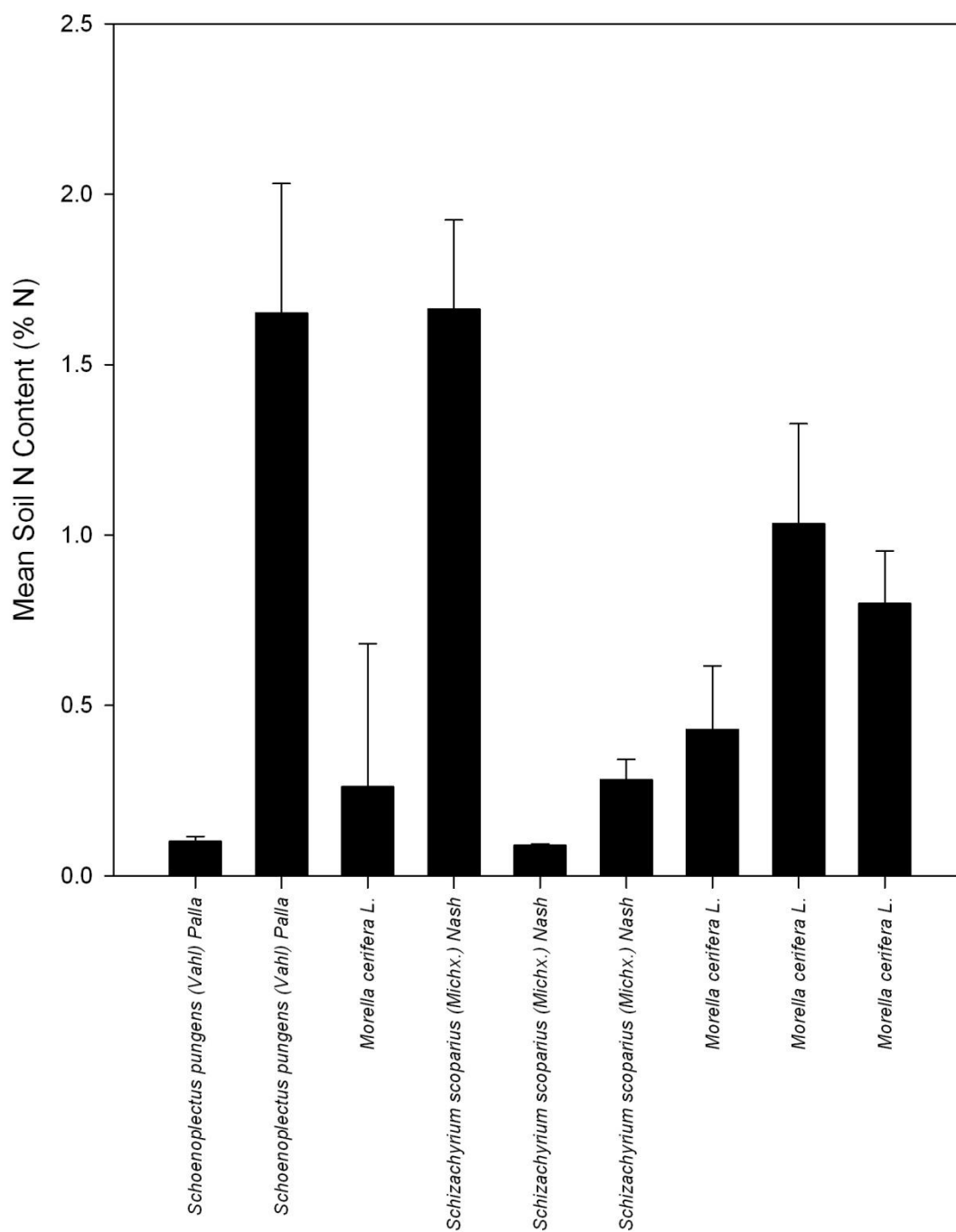


Figure 19. Mean soil N content (%) vs. litterbag/dowel station dominant species. From left to right stations on X-axis are in order from East (Marsh station) to West (*Morella* thicket station).

DISCUSSION

Aboveground Decomposition

Litter decomposition rate has been shown to be controlled by environmental factors, litter quality, and soil organisms (Murphy *et al.*, 1998). It has been shown that litter decay is controlled by a wide variety of chemical properties of the litter, including N concentration (Austin, 2002; Ostertag and Hobbie, 1999), P concentration (Coulson and Butterfield, 1978), and lignin concentration or the lignin to nutrient ratio (Aerts, 1997). Furthermore, nutrient and lignin based control of decay rates may be absent or weak in litter of certain species due to relatively low concentrations found in these types of litter (Taylor *et al.*, 1989; Aerts, 1997). Therefore, it can be assumed that factors other than nutrients or lignin may exert a strong influence on litter decay rates. The failure of litter quality variables to predict decay rates in extreme environments exemplifies the importance of environmental factors. Swift *et al.* (1979) hypothesized that litter quality controls the potential rate of decomposition only as long as environmental and soil related factors are held constant.

In this study, the Marsh station had the second lowest annual aboveground decomposition rate. Aboveground decomposition studies conducted by researchers in areas with varying hydroperiod similar to the study area (Poie de Neiff *et al.*; Pegman and Ogden, 2010) found comparable ($k = 0.080\text{--}0.667 \text{ yr}^{-1}$) aboveground decomposition rates to those observed in the marsh swale. It is suggested that hydroperiod can have a positive effect on decay rates in frequently moist areas by affecting soil pH and nutrient concentrations (Day 1982). Poi de Neiff *et al.* (2006) found that sites where leaf litter was subjected to alternate periods of standing water decomposed faster than completely

dry or submerged sites. This could be an explanation for the higher aboveground decay rates observed at the Marsh Edge and Marsh/Lower Dune Transition stations. Conn and Day (1997) found that soil saturation and anoxic conditions created conditions of minimal decay in swale environments. The aforementioned conditions might have contributed to the minimal aboveground decay in the Marsh station.

Decomposition has been found to be slower than expected in areas exposed to higher solar radiation levels at or near the soil surface. Studies (Bell *et al.*, 1978; Gholz *et al.*, 2000; Murphy, *et al.*, 1989) have shown that decomposition rate is higher in lower areas that experience water inundation as compared to adjacent upland areas. The aboveground decomposition rates documented during this study were much lower at the Upper Dune station than at other stations. It is suggested that higher temperature, lower moisture and higher UV radiation might create a stressful environment for litter decomposers in these areas (Gholz *et al.*, 2000). This would have a negative effect on decay rate in the dune areas.

Annual aboveground decomposition rates observed in the shrub dominated swale were higher than the rate of $0.06\text{--}0.29\text{ yr}^{-1}$ observed in a study conducted by MacLachlan and Van der Merwe (1991) in coastal dune slacks. The rates observed during this study are similar to the rate of $0.28\text{--}0.72\text{ yr}^{-1}$ observed during a study in a semi-arid grassland conducted by Throop and Archer (2007). Throop and Archer suggested that areas vegetated by woody shrubs can have a positive effect on decomposition rate compared to adjacent barren areas. During this study the highest decay rates were observed in areas that were dominated by or shaded by foliage of the woody shrub *Morella cerifera* L.

Belowground Decomposition

Slow decay is frequently attributed to water logged litter due to anaerobic conditions (Pegman and Ogden. 2010; Conn and Day, 1997). Poi de Neiff et al. (2006) found that decomposition at sites subjected to alternate periods of standing water decomposed faster than completely dry or submerged sites. This could be an explanation for the higher aboveground and belowground decay rates observed at the Marsh Edge and Marsh/Lower Dune Transition stations.

Belowground on the upper dunes decay rate was found to be very slow. This could be attributed to litter quality factors due to the fact that slow decomposing pine dowels were utilized in this study. Litter with high initial lignin content, like wood, has been found to decay more slowly than other litter types (Murphy, *et al.*, 1998). In addition, higher temperature, lower moisture and higher UV radiation found in open dune areas have been thought to create poor conditions for decomposition (Gholz *et al.*, 2000). This would have a negative effect on belowground decay rate in the dune areas.

Shrub dominated swale belowground decomposition rates were the highest of all areas investigated. Faster belowground decay rates found in the *Morella* Thicket Edge and *Morella* Thicket stations could possibly be attributed to microclimate. Because the western swale is dominated by a woody shrub, micro- and macro-decomposers in this area could be more adept at decomposition of woody material than in other locations in the study area.

Decay rate patterns similar to those observed during this study were seen in a study conducted by Gholz *et al.*, (2000). They found that the decay constant (k) was much greater aboveground (k = 0.303) than belowground (k = 0.051). Differences in

above vs. belowground decay rates may be attributed to differences in tissue chemistry between the two types of litter and environmental differences found aboveground vs. belowground. Woody tissues have higher lignin content than leaf tissues (Melillo, Aber, and Muratore, 1982). The higher amounts of lignin found in woody tissues can lead to decreased decay rates versus tissues with lower percentages of lignin.

Environmental Landscape

M. cerifera has nitrogen fixing symbionts associated with its roots (Tiffany and Eveleigh, 1983). It was expected that soil N content would be higher in areas dominated by this species, which was the case in all areas except for the Lower Dune (marsh side) and Marsh Edge stations. Plant patches have been shown to concentrate soil resources such as N and organic C under plant canopies, while relatively infertile soils occur in the inter-canopy spaces (Carrera and Bertiller, 2010). The aforementioned sites may not have been dominated by *M. cerifera* but most were shaded by or were in close proximity to, the canopy of surrounding *M. cerifera* thickets. It has been shown that bare soil patches, in comparison with vegetative patches exhibited lower soil nutrients due to exposure to higher precipitation, greater erosion and increased temperature (Carrera and Bertiller, 2010). This could account for the differences in soil N content observed during this study.

A positive trend between soil N content and aboveground/belowground decay rate was observed during this study. This parallels research conducted by Conn and Day (1996) where decay rates increased in areas that had been fertilized with nitrogen, demonstrating that soils with high N content can influence decay rates on barrier islands.

A varying body of work exists concerning soil nutrients and their effect on decomposition rate. Indications of enhanced decay, neutral effect and negative effect have all been reported concerning soil nutrient concentrations and decay rates (Fog 1988). Some researchers have shown that soil N content has a negative or negligible impact on decomposition rate (McClaugherty *et al.*, 1985; Hunt *et al.*, 1988). It has been shown that in terrestrial systems, nitrogen amendment of soils increased decomposition rate (Hunt, 1988). Other research suggests that soil N content and other fertility factors could influence decay rate through their effects on litter chemistry (Ostertag and Hobbie, 1999; Conn and Day, 1997).

High soil N content has been shown to increase litter N content, creating a positive feedback loop that supports higher decay rate (Conn and Day, 1997). The increased litter and soil N content could explain the higher decay rate observed in areas that are dominated by the canopy and stems of *M. cerifera*. But, soil N content is not the only environmental factor that varies between sites; other factors, such as soil macrofauna and microbes, moisture and temperature could also contribute.

Elevation of litterbag/dowel stations affected distance from groundwater as expected. Stations with higher surface elevation were located farther from groundwater. The Marsh and Marsh Edge stations were the closest to groundwater and were frequently inundated, as evidenced by the dominant vegetation type sword grass (*Schoenoplectus pungens* (Vahl) Palla)). Many studies have found that aboveground and belowground decomposition rates are affected by elevational gradients (Vitousek *et al.*, 1994; Murphy *et al.*, 1989). The resulting differences in decomposition rate have been attributed to changes in temperature and moisture regimes that influence these areas. The differences

in decomposition rates observed over the rather small change in elevation could affect microclimate, in turn affecting the makeup of micro- and macro-decomposers found. The microclimates located at the Marsh Edge and *Morella* Thicket Edge stations are protected from direct sunlight by an overhead canopy. This factor combined with the closeness to groundwater at these sites could possibly support conditions that contribute to the decomposition process. The sandy soils that make up barrier islands have demonstrated 30-60 cm of upward groundwater capillary movement (Shafer, 2003) and could contribute to enhancing moisture conditions for decomposition in areas closer to the groundwater table. A study by Van Cleve and Sprague (1971) found increases in decay caused by changes in moisture were minimal until temperature was changed as well. Higher study area temperatures ($> 30^{\circ}\text{C}$) elicited a lower decomposition rate response than did lower temperatures ($20\text{-}30^{\circ}\text{C}$). The dominant vegetation in lower areas consists of thicker vegetation that forms a canopy over litter. On barrier islands, increasing elevation brings the soil surface farther from fresh groundwater, reducing fresh water availability by dampening the effect of natural hydroperiods caused by precipitation and tide fluctuations. The restriction on available groundwater at higher elevations would explain the trend of decreasing mean aboveground and belowground decay rate observed on all three transects as elevation increased. The creation of favorable temperature and moisture conditions here could also contribute to differences in decay rates.

State Change Thresholds

Both aboveground and belowground decomposition rates showed a significant positive relationship with increasing soil N content. Specific levels of soil N could define thresholds for predicting decomposition rate, but further work needs to be conducted to

determine if a relationship between soil N and litter chemistry is demonstrated. These data did not suggest that soil N content was a good indicator of state change at the site. Further investigation is required to determine the cause of variation in soil N levels among sites.

Surface elevation did demonstrate a significant relationship with changes in aboveground decay rate, but not belowground. It is hypothesized that temperature, hydrology and nitrogen availability are the primary environmental factors regulating decomposition on barrier islands (Day, 1995). This research has produced evidence that suggests that decay rate may be directly influenced by surface elevation, but evidence also suggests indirect effects of surface elevation on decomposition rates. Elevation on Hog Island not only affected groundwater availability and dominant vegetation at the study area, but also demonstrated a negative relationship with soil N content. This combined with the fact that soil N influenced decay rate, both aboveground and belowground, suggest that elevation may be an important environmental driver, both directly and indirectly, to decomposition rate.

Elevation and surface distance to groundwater also impacted the abundance and makeup of plant communities found at this research site. Ecosystem states observed in the swales shifted from sword grass dominated freshwater marsh to wax myrtle dominated shrub thickets with approximately 0.5 m of elevation increase. Elevation increases of another 0.25 m again shifted the ecosystem state from wax myrtle thickets to graminoid dominated dunes. These data suggest that elevation is an important driver of ecosystem states found on barrier islands. Continuing research into the interaction between environmental variables, like elevation and groundwater levels, and state

changes could be used to predict community changes resulting from sea level rise and climate change.

Data from this research also suggests that there is a relationship between site species composition and aboveground decay rates. Aboveground decay rates were highest at stations dominated by or adjacent to populations of *M. cerifera*. The increased decay rates associated with these areas could be the result of increased N from the symbiotic N-fixing bacteria associated with the roots of this shrub. Elevation directly affects the dominant vegetative species through its effect on the quality and quantity of fresh groundwater. This leads to the conclusion that elevation indirectly affects decay rates through its control on ecosystem states. It would be intriguing to see if the resulting indirect effects of elevation on decay rates increased or decreased over longer study periods.

Conclusions

Ecological systems can harbor multiple states that differ in ecological services, ecological process rates and species makeup and abundance (Bestelmeyer et al., 2011). Interactions between environmental variables and decomposition rate were observed during this study. The fact that one observed environmental variable did not completely explain the observed variation in decay rates demonstrates that there is a web of interacting factors in the environment that affect rates of decay. Aboveground decay rates varied greatly among stations, but less variation was observed belowground. A longer study period using dowels as a standard material might show some variation in rates of decay.

Small scale decomposition studies are important to determine the thresholds at which environmental factors are having an effect on decomposition rate. This would allow researchers to extrapolate any significant interactions up to a larger scale and possibly apply results to the ecosystem as a whole. It is necessary to conduct more studies on litter decay on barrier islands examining changes in litter chemistry through time. The effects of environmental factors explain some of the variation observed during this study, but a look into the interaction of initial litter chemistry with environmental variables would be important as well.

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