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Groundwater Thresholds for Root Decomposition and the Relation to Barrier Island Ecological State Changes

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GROUNDWATER THRESHOLDS FOR ROOT DECOMPOSITION AND THE RELATION TO BARRIER ISLAND ECOLOGICAL STATE CHANGES

by

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ABSTRACT

GROUNDWATER THRESHOLDS FOR ROOT DECOMPOSITION, AND THE RELATION TO BARRIER ISLAND ECOLOGICAL STATE CHANGES

Matthew L. Smith
Old Dominion University, 2015
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Barrier islands off the eastern shore of Virginia exhibit distinct habitats that abruptly transition between periodically brackish/freshwater marshes, wooded swales, and sparsely vegetated dunes. There is strong evidence that the plant communities and ecosystem processes occurring in each habitat are primarily influenced by nutrient availability and the distance between two of the three free surfaces: land and freshwater. At the Virginia Coast Reserve-Long Term Ecological Research Site in Virginia, USA, thresholds to belowground decomposition rates were identified by measuring decay of native roots and rhizomes at 32 elevations in relation to mean annual groundwater levels (-0.356 – 1.937 m). Negative exponential decay rates (k = 0.310 –0.915 yr^{-1}) varied according to average distance to the freshwater free surface, with lowest decay occurring in low elevation/anoxic conditions (marsh, and bottom soils of a wooded swale), and the highest decay occurring at mid to high elevations (upper soils in wooded swales and all dune sites). The majority of variance in decay rates can be explained by mean annual depth to the freshwater free surface ($r^2 = 0.78$). Locations with mean annual groundwater depths greater than 1 m appear substantially less affected by fluctuations in groundwater levels ($r^2 = 0.09$) than locations nearer to groundwater ($r^2 = 0.83$). Belowground decay was more rapid from 0-20 cm compared to 20-40 cm ($p < 0.05$) and was divided into 3 groups (low, moderate, and high decay) that correspond to the three interior barrier island ecological states. Results from this study indicate a strong relationship between decay rate dependence on groundwater levels and state changes on a barrier island.

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Throughout the course of my time as an ODU graduate student I have been tried and tested. I have been intellectually pushed more than I have ever been, and the adversity experienced in grad school has given me a sense of pride in what I have been able to accomplish. My successes as a Master's student are not mine alone, though, as there are many others who have helped me along the way. Of course nothing would have been possible without my major advisor, so I offer greatest thanks to Dr. Frank Day for his guidance, patience, wisdom, financial support, endless hours of editing, and for getting me to all the professional conferences I attended. My committee, Drs. Rich Whittecar and Kneeland Nesius have been a great source of wisdom and knowledge, too. My wife Jami Ivory, whom I followed to Virginia, helped out in almost every aspect of grad school. My biggest thanks I offer to her is for dealing with a full-time student/fiancée, then husband, all while achieving her own successes as a grad student elsewhere. The struggle has been real, but together we have made many things possible. My lab mates, Leah Gibala-Smith and Nathan Sedghi, helped me out in the field, as well as in the lab. They also offered a great amount of social support. Jeff Rollins, one of my first students who became a good friend, helped out with a ton of field work and always had a smile on his face. I think he may have enjoyed my fieldwork way more than I did! Ed Rietscha has definitely helped out by providing Jami and I with a comfortable home and rent cheap enough that it allowed us to survive in grad school and fund our own wedding. The VCR LTER staff helped out with field work logistics, and even though I lost two phones to Hog Island bay and almost died there, they got me to and from the island and kept me alive. This research was funded by subcontract GA11020-142301 on the University of Virginia's NSF grant DEB-1237733.

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INTRODUCTION

Atlantic Ocean barrier islands contribute 7.5% of the world’s barrier islands with 2,287 km of coastline (Stutz and Pilkey 2011). This number is constantly changing due to the mobile nature of barrier islands. Wave action, longshore and tidal currents, hurricanes, and northeasterly winds all act upon eastern US barrier islands, making them unique, mobile landscapes (Leatherman 1988). These islands are geologically dynamic landforms subjected to harsh environmental conditions and, as a result, are routinely reshaped and restructured. The rapid rate at which these islands change paired with extreme environmental conditions, severely limits the type of vegetation that can exist and makes them ideal candidates for ecological state change studies (Shao et al. 1996).

A shift from one ecological state to another, e.g. a grass dominated community to a shrub or tree dominated community, can occur due to internal or external processes (Walker and Meyers 2004). External processes include external changes in environmental or biotic conditions that affect internal processes. Wright and Chambers (2002), for example, identified fluctuations in water table depths as the primary mechanism for changes from grass dominated meadows to shrub dominated communities. Fire can also dramatically change, modify, and maintain ecosystems, and has been used as a tool to sustain ecological system states and prevent succession (Bond and Keeley 2005). Internal processes are generally attributed to biophysical interactions that change conditions within the system (Walker and Meyers 2004). Internal processes that lead to ecological changes have been widely observed. For example, Singh et al. (1990) indicated a relationship between leaf litter, soil properties, and decomposing microbes. Leaf chemistry affects soil properties and microbe populations. Microbe populations controlled by litter chemistry control the rate at which the litter is decomposed and can create a feedback loop that can affect entire ecological system processes. Ecological mechanisms driving resource availability and state changes may be subtle, and can vary over a gradient, but when system thresholds are exceeded abrupt changes may occur (Graziani and Day 2014; Scheffer et al. 2001).

Thresholds

It is well known that through evolution, plant species have developed characteristics that enable them to become superior competitors within a given area, and that there are conditions where these species exhibit optimal growth (no limiting resources in ideal growing conditions). According to R* theory, if a species' dependent resource is below a specific tolerance, reduced individual or population fitness will occur, especially in the presence of a more tolerant competitor species. If any dependent resource is reduced below a critical point for survival, or if any antagonistic variable exceeds a tolerance, fitness will also be drastically reduced.

Thresholds that limit plant growth and population fitness mainly exist through the abundance or availability of light, water, nutrients, CO_2, and temperature. The concept of thresholds that affect species' distributions, or even existence, has been around for quite some time (Holling 1973), and there have been many variations to the definition of an ecological threshold (Friedel 1991; Muradian 2001; Weins et al. 2002). Put simply and in terms of plant ecology, an ecological threshold is the discontinuity of a specific plant community through the exceedance of tolerances to a specific independent variable, resulting in a rapid change in species composition.

Rapid changes in plant species compositions are evident on barrier islands, especially those off the Delmarva Peninsula, VA. Here, they are spatially restricted by high winds, salt spray, high salinity, nutrient poor and mobile soils, and freshwater availability (Clark 1991; Hayden et al. 1991). On Hog Island, Virginia, where this study was conducted, rapid changes due to ecological thresholds produce distinct ecological states that are represented by specific plant associations.

System state changes

The interior ecological states on Hog Island change multiple times, transitioning non-linearly between dunes, shrub thickets, and marshes. From East to West, fore-dunes occur on the seaward side of the island and are dominated by beach grasses that stabilize the marine deposited sand and add organic matter to the soil, increasing nutrient retention and the facilitation of secondary species recruitment. Secondary dunes occur throughout the island and are dominated by shrubs, grasses, and less frequently, trees. As precipitation penetrates the soil surface and percolates through the dunes, it carries nutrients to lower elevations and discharge zones. Marshes, which can be either freshwater or brackish, are dominated by hydrophytic vegetation suited to growing in hypoxic, or often anoxic soils. Much of the marsh vegetation is salt tolerant as overwash events occur periodically and introduce chloride levels toxic to most other grasses. Thickets occur in areas behind the secondary dunes, which are partially protected from winds and salt spray, slightly elevated above the marshes and less affected by overwash events and salinity spikes, and are dominated almost exclusively by the actinorhizal shrub, *Morella cerifera*. *Morella cerifera* forms a symbiotic relationship with *Frankia spp*,. which provide nitrogen in exchange for carbon. Nitrogen is also introduced to the barrier island system through decay and leaching of litter. Furthest west on Hog Island is a bay/salt marsh dominated by *Spartina alternaflora* (Ehrenfeld 1990).

The transitions between system states occur rapidly and are one of the primary focuses of research at the VCR. During the 20th century, transitions from maritime forests to salt marshes and grasslands have been documented (Hayden et al. 1991). The shoreline of the northern end of Hog Island has been accreting seaward for quite some time, and in response to the gain in marine deposits, plants have colonized, stabilized, and enriched the soil, ultimately facilitating the establishment of later seral stages. The classic primary succession of dunes identified by Cowles (1899) is what allows the first of barrier island states to occur. Grasses continually stabilize blowing beach sands by diminishing wind velocities and reducing their capacity to carry sediments, as well as through their fine root networks. The stabilizing processes create dunes that are not eroded except during high energy storms. Without the specific dune building grasses, dunes would only develop as high as the highest storm surges. Areas behind where dunes form are protected and incur reduced storm related inundation, salt spray, and aeolian sands.

Without frequent disturbances from storms, secondary succession allows later seral grasses to become established. With enough time (sometimes only a matter of a few years) shrubs begin to gain dominance and create the second ecological state present in barrier island interiors. These late grass seres and shrub communities develop due to stabilized soils, but also due to the increasing width of the island, which allows fresh groundwater to accumulate. Locations where the groundwater elevation is high, or where the land surface elevation is low, develop into the third ecological state: inland freshwater/brackish marshes. These marshes typically occur at lower elevations, and during high energy storms when primary dunes are breached they become inundated with sea water, causing them to fluctuate between freshwater and brackish marshes. Because disturbance is so high within the VCR, the later stages of vegetation are often reset due to storms, elevation change, and groundwater changes.

Although succession and disturbances have led to the distinct patterns in the ecosystem states present on VCR barrier islands, these patterns are believed to be controlled by the relative positions of nonparallel free surfaces. The predominant driver being freshwater availability (an external process that affects many internal processes), which in turn is controlled by the land and sea free surfaces (Hayden et al. 1995).

Free surfaces

There are three free surfaces within a barrier island system: freshwater, seawater, and land. The seawater free surface exists due to the surrounding ocean, and is driven by mean sea levels. A freshwater lens rests above the seawater free surface as it is slightly lighter and receives its inputs from precipitation that percolates though the soils and does not mix with the saline sea water. Where the land free surface dips too low, the freshwater free surface creates ponds or freshwater marshes that may become brackish during storms that cause washover events. These saline intrusions above the freshwater lens can mix with the freshwater and cause the lens to temporarily partition. When this occurs, marshes become brackish with no freshwater lens, but the fresh groundwater is maintained beneath the shrub thickets and dune areas. The structure of barrier island freshwater lenses tend to be convex and accrete higher near island high points and/or in the middle of the island (Fetter 1972; Whittecar and Emry 1992). Groundwater levels vary across the barrier island landscape due to island width, elevation, and discharge locations. Because the freshwater/groundwater is not uniform across the island, vegetation patterns exist due to groundwater levels, and not necessarily the topography of the land free surface alone.

By definition, none of the free surfaces are static; the land, sea, and freshwater free surfaces present on barrier islands can modify the vegetation patterns if any one of them incurs a vertical change and increases or decreases the distance from land and freshwater free surfaces (Hayden et al. 1995). For example, if the freshwater free surface becomes closer to the land free surface due to any fluctuation of the three free surfaces, vegetation thresholds may be exceeded and a state change from one dominant plant community to another can occur.

Dunes are furthest from the freshwater lens, generally dry, and are the most exposed to salt spray and high winds. Swales are somewhat protected from high winds and salt spray, are closer to the freshwater lens, and have an organic matter build-up that assists in nutrient and moisture retention. The marshes are closest to the freshwater lens, often ponded via precipitation and overwash events, and they receive groundwater discharge from adjacent dunes. The relative positions of the free surfaces affects both beneficial or detrimental moisture levels, as well as many other factors that govern plant species distribution and abundances. Although plant assemblages on Hog Island are primarily controlled by these free surfaces, nutrients such as P, B, Cu, Fe, Mn, and Zn have also been associated with plant assemblages (McMillan and Day 2010); however, nitrogen and phosphorus are the most limiting.

Nutrient availability and decay

Barrier islands are inherently nutrient poor ecosystems, as they are geologically young, composed of sandy soils that are well drained, easily leached of nutrients, and have low cation exchange capacities (CEC) (Tackett and Craft 2010; Shumway 2000; Ehrenfeld 1990; Kachi and Hirose 1983; Willis and Yemm 1961). They continually undergo primary and secondary succession, as well as system state changes, as bare sand is colonized, as frequent disturbance events denude or modify the landscape, or as environmental conditions exceed thresholds (Hayden et al. 1995). One of the primary macro nutrients found to be limited on barrier island soils is nitrogen, and it generally increases in availability with substrate age, although topographic position and plant communities also have some influence on its availability (Tackett and Craft 2010; Heyel and Day 2006; Shumway 2000). It is important for plants to efficiently utilize the scarce and limited resources in nutrient poor ecosystems, and there are multiple strategies by which this is accomplished.

Plants growing in resource limited soils but in areas with sufficient light, tend to allocate a substantial proportion of production to belowground perennial tissue compared to those growing with similar energy inputs and nutrient rich soil (Tilman 1988). This strategy is typical of Virginia Coast Reserve (VCR) barrier island marsh vegetation such as *Spartina patens, Distichlis spicata, Phragmites australis, Schoenoplectus americanus,* and other rhizomatous perennials. Other plants, like *Morella cerifera*, which commonly occurs on barrier islands, are actinorhizal and form symbiotic relationships with bacteria that enrich the soil with plant available nitrogen and stabilize the soil, increasing nutrient retention in the process (Bond 1967; Permar and Fisher1983). Plants incapable of symbioses with nitrogen fixing bacteria and growing on nutrient limited soils must rely on other processes to provide an adequate supply of nutrients. This is often accomplished by recycling nutrients through the process of decomposition.

The decomposition of leaf litter is primarily mediated by climate and to a lesser degree litter chemistry (Meentemeyer 1978; Aerts 1997; Singh and Gupta 1977). Through decay, immobilized nutrients stored in tissues are mineralized, stored in the soil and made available for future uptake. The nutrient concentration of litter, with the majority of analyses focused on nitrogen concentration, has been linked with soil quality (Perez et al. 2013; Berg 2008; Vitousek 1982; Chapin III 1980) and can also have significant effects on litter decay and nutrient recycling (Conn and Day1997; Hunt et al. 1988; Vitousek et al. 1994; McClaugherty et al. 1985). Plant litter decay also leads to the formation of humus and soil organic matter (SOM), which can have numerous benefits to the plant community, especially those growing on mineral soils. Humus can increase soil nutrient and water retention and CECs, and its organic acids are partially responsible for the weathering of mineral soils, thus increasing nutrient availability (Berg 2008).

Aboveground litter, although more heavily studied than the effects of belowground litter, may not always be the largest contributor to nutrient recycling. Belowground biomass and carbon allocation can constitute a substantial proportion of net primary production (NPP) (Janssens et al. 2001; Davidson et al. 2002; Niell 1992; Vogt 1991; Sims and Singh 1978). Thus, it is crucial to understand belowground decay, as it is also an important component to nutrient recycling (Silver and Miya 2001; Gordon and Jackson 2000; Aerts et al. 1992). Contrary to leaf litter, root decay is dependent on litter chemistry more so than climate (Silver and Miya 2001), although temperature and moisture are also important considerations (Gill and Jackson 2000; Davidson and Janssens 2006).

The macroclimate is somewhat uniform at all locations within a barrier island, the microclimate, however, varies drastically with fluctuations in each of the free surfaces. Other than plant litter chemistry, the primary factor that varies belowground and can affect belowground decomposition rates and nutrient recycling may be moisture, i.e. the distance between the freshwater and land free surfaces. Previous belowground decomposition studies have indicated reduced decay with depth and increased saturation (Tupacz and Day 1990; Hackney and De La Cruz 1980; Conn and Day 1997).

Previous research on the Virginia Coast Reserve/Long Term Ecological Research site (VCR/LTER) has focused on broad scale belowground decomposition (Conn and Day 1996; Conn and Day 1997). Graziani and Day (2015) recently investigated fine scale thresholds to aboveground decomposition. The purpose of this study was to expand the understanding of barrier island ecosystem process rates by analyzing belowground decay (a proxy for nutrient recycling), and by focusing on fine scale thresholds to belowground rates. Primarily, this study focused on the effect of the free surfaces on belowground decay, and on determining how well decay thresholds correlate to the current ecological system state.

METHODS

Study site

Hog Island, Virginia (37° 40’N, 75° 40’W), is located east of the Delmarva Peninsula’s eastern shore (Fig. 1). It is part of the Virginia Coast Reserve (VCR), owned and maintained by The Nature Conservancy, and has been a National Science Foundation funded Long Term Ecological Research site since 1987. It is approximately 11 km long, averages 0.8 km wide, and is oriented with the majority of its coast parallel to the Delmarva Peninsula. The VCR islands receive an average of 105 cm in precipitation each year and have average temperatures of 14.2 °C (Conn and Day 1997).

Hog Island soils originate from quartz-rich marine deposits, are geologically young, and as such they are limited in nutrients that restrict primary production. Primary succession by dune building grasses and forbs (*Ammophila brevigulata, Spartina patens, Panicum amarum, Cakile edentulata* as well as some less dominant species*)* initially stabilize and add organic matter to the sandy mineral soil, and assist the establishment of later successional species. The island interior maintains a pattern of swales and dunes with distinct boundaries between three distinct habitats/ecological states: marsh, shrub thicket, and dunes.

Marshes are dominated by a few hydrophytic species, namely *Spartina patens, Distichlis spicata, Schoenoplectus pungens, Typha spp.,* and *Phragmites australis.* Shrub thickets are almost exclusively dominated by *Morella cerifera*. Dune vegetation varies with age and the accumulation of organic matter and nutrients, but *S. patens, A. brevigulata, Aristida tuberculosa, P. amarum, and Schizachyrium scoparium* are common on both young and old secondary dunes. Differences in topography appear to cause the transition in states; however, it is the underlying hydrology that drives the vegetation patterns.

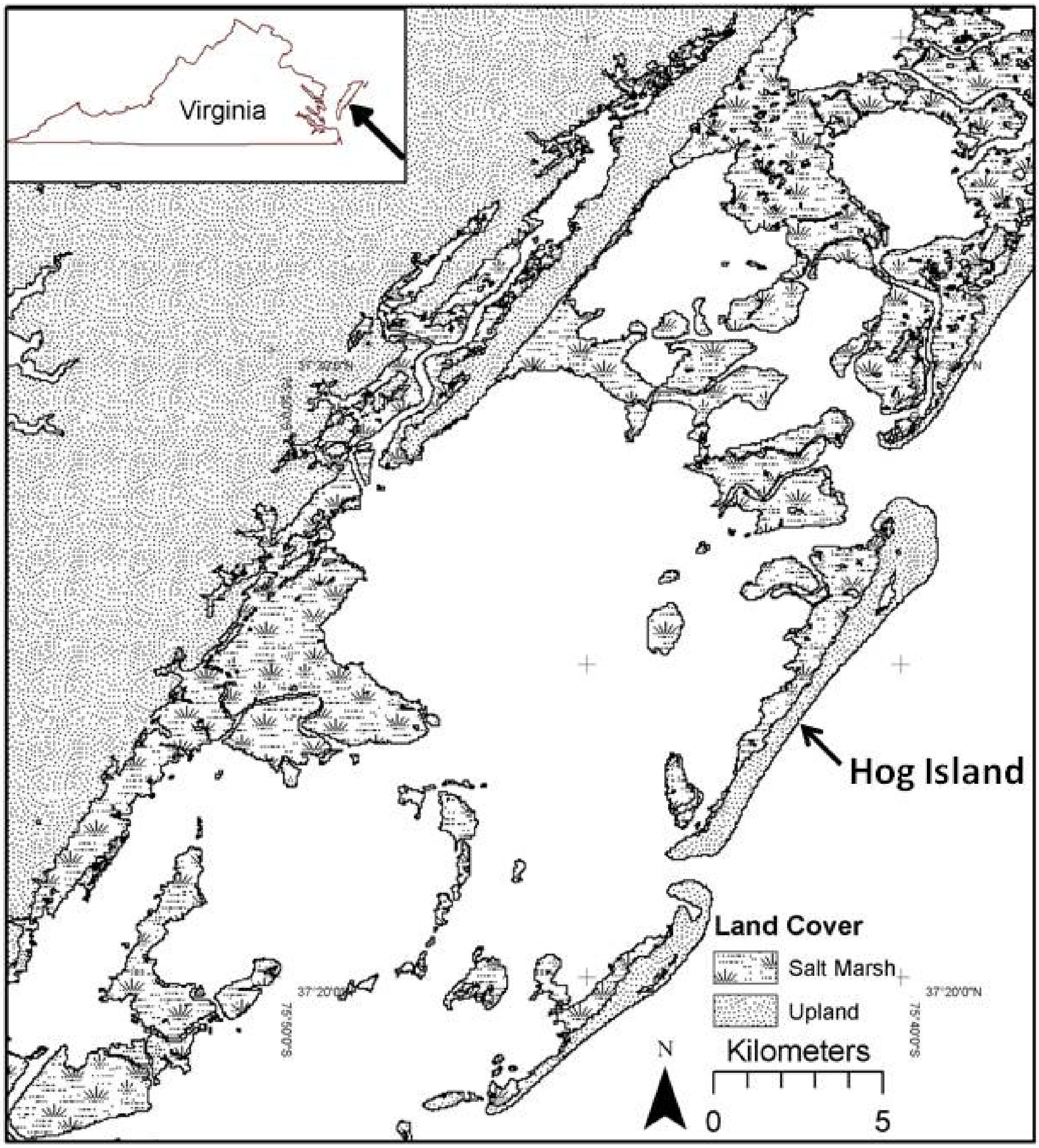

Fig. 1 Hog Island, Virginia

The interior of the northern part of Hog Island consists of several linear uneven aged dunes with swales and marshes occurring in between dune ridges at lower elevations. A dune system that formed in 1967 (Hayden et al. 1991) and its adjacent swale and marsh were selected for this study due to the proximity of two existing permanent wells equipped with Campbell Scientific CS 450-L pressure transducers that report groundwater elevation hourly. This dune was also selected because it contains some of the highest elevations on the island and provides the greatest breadth in a gradient-based analysis.

Decay measurements

A naturally occurring assortment of roots and rhizomes were collected from six marsh areas that were greater than 20 m from any *Phragmites* (Holm et al. 1977) to avoid the possible spread of the invasive plant through vegetative propagules, and also to minimize possible non native plant matter in the decomposition study. Root sizes ranged from 1 to 5 mm diameter. The majority of roots and rhizomes collected were from the dominant marsh vegetation, *S. patens* and *D spicata. Spartina patens* occurs at all elevations within the island, and marshes that contained the species were targeted. Marshes dominated by *Schoenoplectus americanus* were avoided due to instances of sprouting during a previous decomposition study (Sedghi and Day, *unpublished data*).

Roots were air dried, weighed (1.5 - 2.5 g) and placed in 1 mm nylon mesh litterbags. Using similar methods as Tupacz and Day (1990), litterbags were 40 cm long, 10 cm wide, divided into four 10 x 10 cm sections, and were inserted into the soil vertically to measure decay at four different depths. Subsamples of roots were oven dried at 70°C for 48 hours for air dry:oven dry mass ratios.

Eight stratified random stations were established for decay measurements that varied along the transect by elevation and habitat (Fig. 2). The habitat and elevation of the eight decay

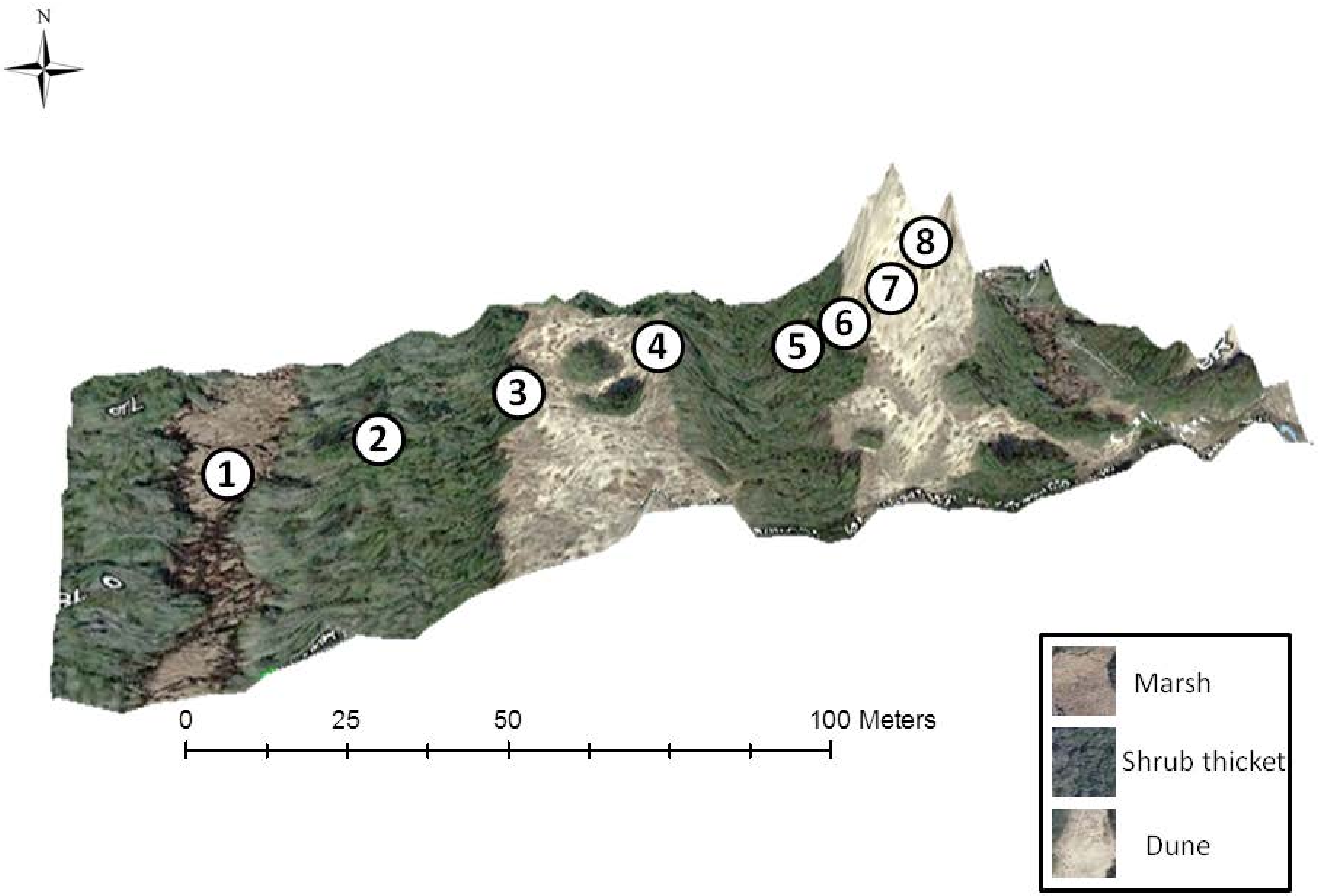

Fig. 2 The eight locations where litter bags were buried along an elevational gradient. Site name and land surface elevations corresponding to numbers in image are 1) Marsh 1.454 m 2) Low shrub 1.787 m 3) Low transition 2.316 m 4) Low dune2.652 m 5) High shrub 1.851 m 6) High transition 2.065 m 7) Mid dune 2.648 m 8) High dune 3.265 m. Note that the identifiers low, mid, and high refer to groundwater proximities to the land surface, and not the respective land surface elevations. Elevations in this image were exaggerated to help illustrate the topographic changes along the transect. This vertical exaggeration caused the appearance of a dune summit with an extreme slope and a sharp peak. The actual slope is much lower, and the dune summit is much more rounded.

stations used in this study were as follows: one marsh site (1.454 m), two shrub thicket sites (1.787 m and 1.851 m), two shrub thicket/dune transitional areas (2.065 m and 2.316 m), and three upper elevation dune sites (2.648 m, 2.652 m, and 3.265 m). Each litterbag was assigned a unique identification number used for random sampling. Forty-two litterbags were buried at each location, allowing seven sampling events with six replicates each. Litterbags were buried January 16th and 17th of 2014, and sampled after approximately 34, 62, 102, 132, 195, 256, and 371 days in the field. After collection, root ingrowths were removed and their occurrences per litterbag section were counted. The decay samples were gently cleaned, removed, oven dried at 70 degrees Celsius, and reweighed for mass loss.

Decay rates are reported using values obtained from a negative exponential model, although they appeared to be slightly linear in many cases; however, the linear model only produced slightly better values. Other decay studies on Hog Island have measured decay rates using a negative exponential model, thus it makes sense to report values here using the same model for comparison. Additionally, it is more common (with the exception of a few environmental conditions) for decay to follow a negative exponential trend rather than linear (Edwards 1977; Wieder and Lang 1982). Decay was estimated gravimetrically as percent mass loss from initial weights. Decay rates were fit to a negative exponential model via the following equation:

$$X = e^{-kt}$$

where X is the proportion of initial mass that remains after t years using average percent mass loss measurements (Wieder and Lang 1982).

Elevational measurements

The precise geospatial locations of the eight decay sites were obtained using a handheld Garmin 60 CSx GPS receiver. Points were taken each removal date (seven points for each site), and converted to one point per site by averaging the coordinates in ArcMap 10.2.2. The elevation of each of these averaged points was obtained by averaging the elevation from all surrounding cells of a 1 meter resolution bare earth digital elevation model (DEM). The DEM was created from LiDAR data obtained in 2013 (USACE-TEC and JALBTCX 2013).

Groundwater elevation was calculated using two existing permanent wells equipped with Campbell Scientific CS-450 pressure sensors with atmospheric equilibration. Measurements from these wells are taken every 15 minutes, averaged, and reported hourly. One well (S2) is located in a swale 43 m NW of the western most litterbag site, and the second well (R2) is located on a dune ridge 15 m north of the midpoint of the transect (Fig. 3). Groundwater depths were

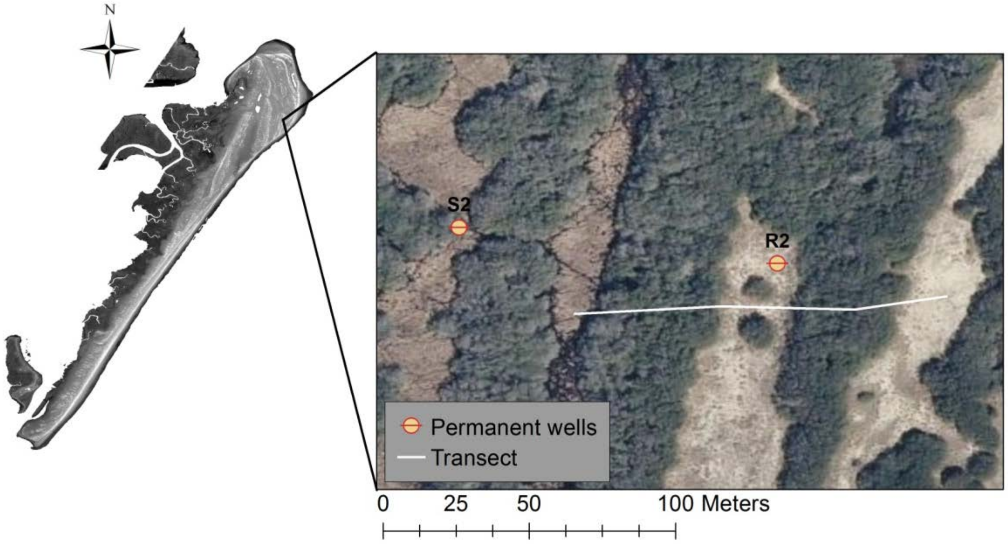

Fig. 3 Permanent wells in proximity to transect. The transect began in the marsh (West), then passed through two shrub thickets, a dune where the R2 well is located, and ended at the islands highest dune (East).

calculated at each well by subtracting groundwater elevation from the land surface elevation. Due to a faulty data logger on the well (R2) located on the dune, groundwater depths had to be extrapolated from measurements obtained from the one functioning well (S2).

In order to extrapolate data from the S2 well, a relationship between groundwater at the S2 and R2 well locations was obtained from a Pearson product-moment correlation analysis in R. Island soils are sandy, thus, topography should not affect groundwater levels over the short distance between wells; a linear relationship was expected. Multiple correlations were conducted using data paired by day and hour from years 2009-2012 to verify consistency in the relationship between the two wells. All yearly data indicated R2 groundwater levels were lower than S2 values. Data from the year 2012 had the least abnormal data and the strongest relationship, and therefore was used in this study. The slope from the 2012 analysis was applied to data recorded during the study period and used to determine groundwater depths at each of the eight decay sites. All groundwater depth measurements for the duration of the study were averaged to determine the average depth to groundwater (yr^{-1}) at each of the eight sites.

In addition to the extrapolated groundwater levels, mean annual groundwater levels were estimated using two separate groundwater models. In the first model, groundwater was assumed to slope linearly from the marsh, where the functioning permanent well was located, eastward to the beach (roughly 220 – 400 m depending on location) where land surface elevations were even with mean sea level (MSL); this location was assumed to be the interface between groundwater and the sea. The mean annual groundwater elevation for the entire marsh where the S2 well was located was assumed to be uniform. Groundwater elevations for 333 random point locations within the dune system and along 53 transects that ran from marsh to beach (to obtain groundwater slope values) were calculated based on their distance from the marsh (Fig. 4). These locations, as well as 53 marsh and 1000+ beach locations, were used to

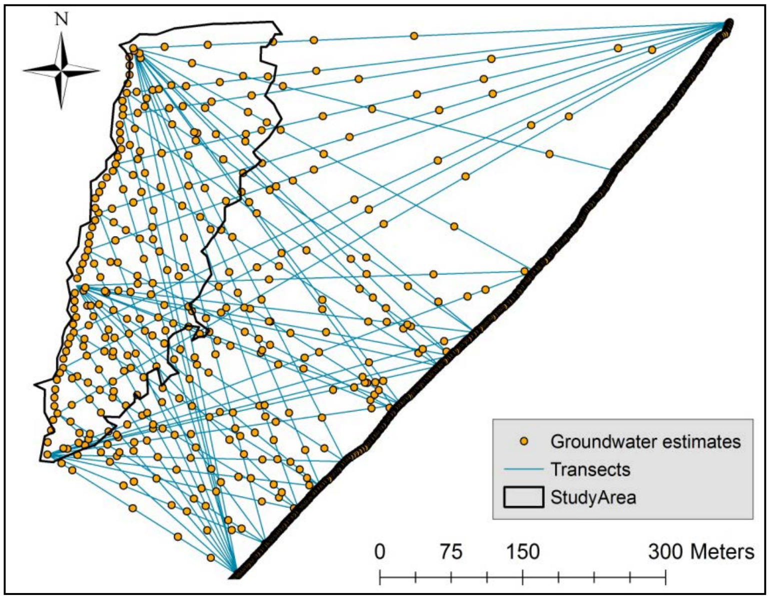

Fig. 4 Transects and point locations where groundwater levels were calculated for interpolation. Transects ran from the marsh (West) to the beach (East).

interpolate mean annual groundwater elevations for the surrounding area using the regularized spline interpolation method (Frank 1982) in ArcMap 10.2.2. This technique was used for its ability to model smooth surfaces such as groundwater. Average annual groundwater elevations for the eight decay sites were obtained by averaging all adjacent cell values from the spline interpolation model. Subtracting the groundwater elevation from the land surface elevation created a mean depth to groundwater model that covered the entire study location at a 1 m resolution.

The second groundwater model was also created using a regularized spline interpolator similar to the aforementioned. The assumptions remained the same except groundwater was not assumed to slope linearly to the beach. Here, groundwater was assumed to discharge at the beach locations with elevations the same as MSL; however, groundwater slopes were assumed to increase with proximity to discharge zone according to the following modified Dupuit equation:

$$h = \sqrt{h_1^2 - \frac{(h_1^2 - h_2^2)x}{L}} \qquad \text{(Fetter 2001)}$$

where:

h is the head at x
x is the distance from the marsh
L is the distance the marsh to the beach at the point h_2
h_1 is the head at the marsh
h_2 is the head at L (the beach, or 0 m)

Groundwater elevations calculated for each of the 333 locations along 53 transects, were used with the spline interpolator to obtain groundwater elevations for the eight study sites and entire dune system. Both models' depth to groundwater values obtained for the dune system were used later in the analysis to identify geographic locations/plant communities which correspond to specific groundwater depths.

Soil properties

Soil pits were dug at each site to the depth of 40 cm (the max depth of decay measurements) and characterized. Three soil samples were taken for each of the four depths at all eight sites using a soil corer with a 10 cm long head. Soil was oven dried at 70°C for 48 hours, then sieved and homogenized with a 2 mm sieve to remove litter, course detritus, and course roots. Dry sieved soil was ground with mortar and pestle, and analyzed for %C and %N using a Thermo Scientific™ FLASH 2000 Elemental Analyzer. Organic matter content was measured gravimetrically by heating the soil to 500 °C and calculated via the loss on ignition (LOI) method.

Vegetation

Three plant communities (marsh, shrub thicket, and dune) were identified remotely utilizing 2013 satellite imagery obtained from Virginia Information Technology Agency (VITA 2013). All three communities were visually identified, and traced to create polygon shapefiles that represented each respective community. These polygons are referred to as “observed” throughout the study. The observed shrub thicket polygon overestimated actual shrub habitat due to the large canopy from which the polygon was created. To compensate for this, multiple direct measurements were taken from the border of the shrub community (measured from the actual stem) to the end of the canopy that overlaid the dune and marsh communities. From these measurements, the average distance the shrub canopy overlaid the other habitats was calculated and corrected for.

Some dune and marsh areas were completely concealed by the shrub canopy, and these areas had to be corrected for differently. The elevations of the marshes east and west of the study site were averaged to determine elevations where marshes would occur. Incorporating the marsh elevations from the eastern and western marsh was assumed to compensate for the change in groundwater levels from the west marsh to the east. Elevations within 1 standard deviation were considered to be marsh habitat. Dune areas that were completely concealed were identified using this same process, except to calculate the average elevation where dunes occur; the highest of dune ridges were not included.

Because depth to groundwater and freshwater availability exerts a strong influence on vegetation patterns (through physiological processes), not necessarily elevation, the average depth to groundwater was calculated for both the marsh and dune polygons from both the linear and Dupuit interpolated models, and used to identify the habitats concealed beneath the shrub canopy. The marsh and dune polygons created from elevation and both interpolated depth to groundwater models were overlaid and where the three models overlapped was considered to be “observed” dune and marsh habitat. Observed shrub habitat was the area between observed marshes and dunes. Isolated marsh and dune polygons that were visually concealed by the shrub community were field checked to determine the accuracy of habitat corrections.

Soil characteristics were used to validate the accuracy of the observed habitats. Vegetation specific to dune or marsh areas were also used, but reduced light availability beneath the shrub canopy likely prevented dune or marsh plants (which have low shade tolerances) from growing in these areas. Hydric soil field indicators as outlined in the United States Department of Agriculture, Natural Resources Conservation Service (NRCS) (2010) were the primary indicators used to verify marsh habitat. Secondary indicators were used from observations within marsh areas. Secondary indicators included a distinct black/darkened litter layer, topographic location (depressions), hydrophytic vegetation or absence of vegetation and few roots occupying the soil, exposed *Morella cerifera* roots with a pedestalled appearance that likely occurs from a combination of saturated/loose soil, windthrow, and erosion, and a water table in the upper 15 cm. In order for observed marsh areas to be validated as actual marsh areas, any one of the NRCS’s hydric soil indicators, or three of the five secondary indicators had to be present.

In order for observed dune polygons to be verified as dune habitat, soil within 40 cm had to have a layer with 2.5Y hue and a chroma/value of 5/3. These color specifications were chosen due to actual dune and transition areas (locations where shrub branches overlaid actual dune habitat) containing the said characteristics. The soil also had to contain few/sparse roots, a shallow organic horizon, be located on an apparent mound or ridge, have arching shrubs growing over the dune, but be void of vegetation or contain vegetation specific to the dunes. If three or more of these characteristics were met, it was accurately considered a dune area.

To determine whether or not decay thresholds correspond to the observed habitats, polygons were created for the statistically demarcated decay groups and were overlaid on the observed habitat polygons to determine the percent overlap. From the amount of correct overlap, the efficacy of using decay thresholds to identify ecological state changes was interpreted.

Data analysis

Belowground decay rates were determined from seven sampling events where percent mass loss measurements were obtained over the course of 377 days. The 32 decay rates (eight sites and four depths per site) were compared to groundwater levels using regression analyses. An asymptotic regression was performed for decay rates and mean annual groundwater levels using the law of diminishing returns (Hartley 1961). Additional linear regressions were conducted for decay rates in relation to groundwater levels less than and greater than one m. A 2-way ANOVA was used to identify thresholds in decay rates among the eight sites and four depths. Two outliers, identified as studentized residuals greater or less than ±2.5, were identified for the low transition location but no cause for the extreme rates of decay were identified and they were not removed from the 2-way ANOVA. Additionally, 40 cm decay rates for the high shrub location were not normally distributed but due to the marginal violation of this assumption the data were not transformed. A one-way ANOVA was used with OM measurements from the top 10 cm. The lower 30 cm could not be transformed to meet the assumption of homogeneity of variances and was not statistically analyzed. Data for the top 10 cm were square root transformed to meet the assumption of equal variances. An additional regression was conducted on the OM from the top 10 cm and groundwater depths. Variability in root ingrowth counts were too extreme and could not be transformed to meet the assumption of equal variances. Root ingrowths were not statistically analyzed, although averages per site and depth are reported. All analyses were conducted using SigmaPlot version 11 and SPSS version 18.

Thresholds to belowground decay were used to create decay polygons for comparison with observed habitat polygons. These were used to identify the relationship among decay thresholds and habitat type/ecological state.

RESULTS

Groundwater free surface

The swale (S2) and dune ridge (R2) groundwater elevations were strongly correlated (*t*=210, *p*<0.001). Swale groundwater elevations from 2012 are higher than those from the dune (r^2=0.86) (Fig. 5), indicating that although the land surface elevation increases in this direction, the groundwater elevation decreases.

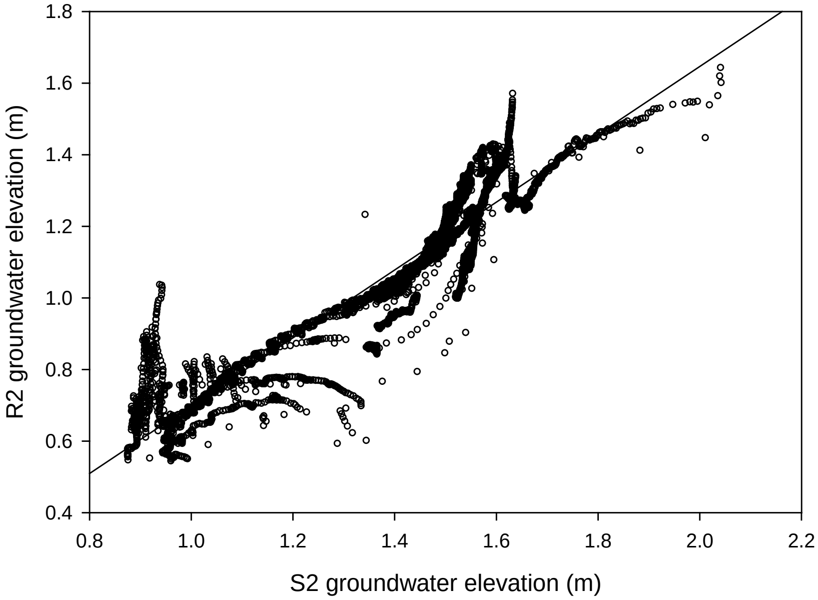

Fig. 5 Pearson correlation coefficient analysis results (r^2 = 0.85) for the S2 (marsh) and R2 (dune) wells.

Land surface elevations generally increased as the study site transitioned from marsh→shrub thicket→dune habitats (Table 1). For groundwater depths interpolated from the S2-R2 correlation (S2R2), and the Dupuit groundwater model, mean annual groundwater levels exceeded the land surface elevation for the marsh location only. Mean annual depth to groundwater was 0.02 m in the marsh location for the linear groundwater model. All other locations had mean annual depth to groundwater levels that increased with habitat (Fig. 6). The three methods used to obtain groundwater levels produced similar values for the eight decay site locations, although the Dupuit interpolation method generally produced the shallowest groundwater depths, followed by the S2R2 method, then the linear interpolation method (Table 1).

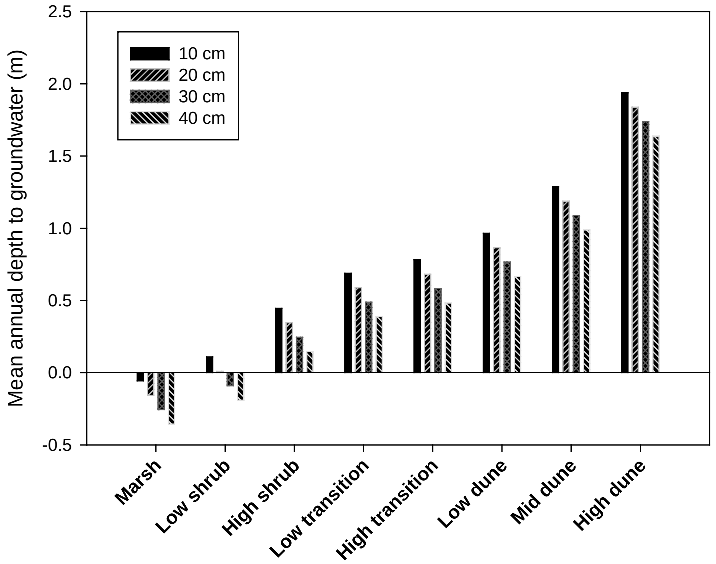

Fig. 6 Average groundwater depths (yr^{-1}) from the Dupuit groundwater model, by site and depth.

Table 1 Mean annual groundwater depths from the land surface for each of the eight decay sites.

Site	Dupuit (m)	S2R2 (m)	Linear (m)
Marsh	-0.007	-0.013	0.021
Low shrub	0.312	0.406	0.412
High shrub	0.648	0.674	0.916
Low transition	0.891	0.999	1.015
High transition	0.984	0.933	1.323
Low dune	1.168	1.404	1.314
Mid dune	1.490	1.542	1.823
High dune	2.140	2.182	2.460

Soil properties

Percent soil organic matter (SOM) was extremely different between the top 10 cm and the lower depths, as well as by location (Fig 7). Percent SOM for the top 10 cm was significantly different among stations (*F*=157.903, *p*<0.001). Depth to groundwater may explain much of the differences in SOM (r^2= 0.41); however, regression results were not significant (*p* = 0.09) (Fig. 8). Soils beneath the *Morella cerifera* canopy had substantially more SOM than all other locations.

Marsh soils contained a substantial percent of muck, produced hydrogen sulfide odors, and the mineral horizon was entirely gray (5Y 5/1). The only other location with soil this color was the bottom soil (19-40 cm) from the low shrub location (lower elevation and shallower groundwater depths than the other shrub location) where the soil was stratified with

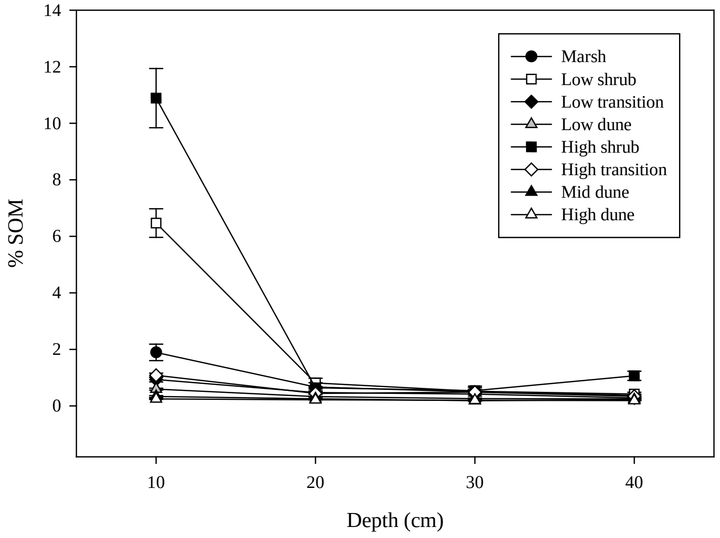

Fig. 7 Percent soil organic matter results via LOI method.

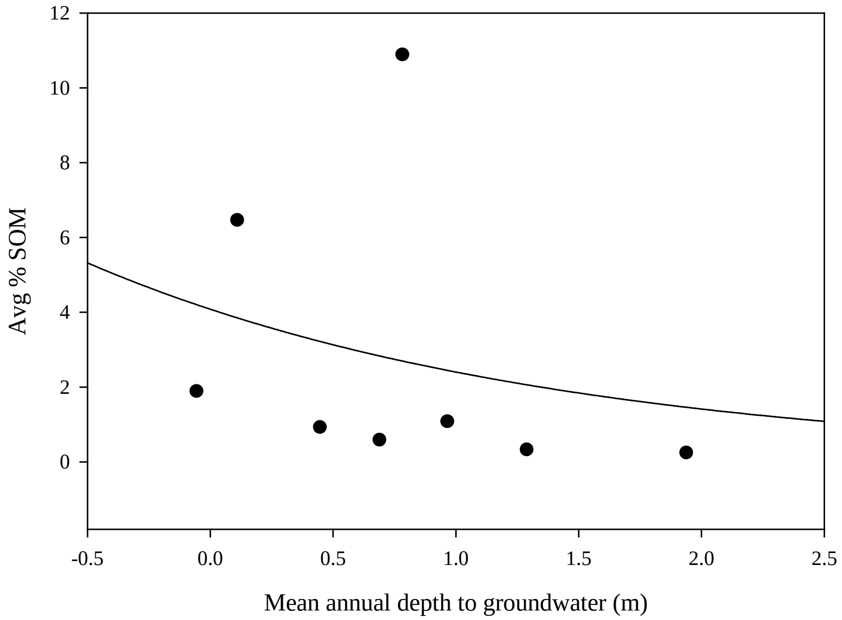

Fig. 8 Average %SOM for top 10 cm of soil for the eight study locations vs average depth to groundwater (yr^{-1}).

gray and dark gray (5Y 5/1 and 4/1)(Table 2). The shrub locations had thick organic layers, but the low shrub differed from the high shrub location in organic layer thickness, the presence or absence of an Oa layer, and soil color. Both the low and high transitional areas had small organic layers due to *Morella cerifera* litter and deep loamy sand layers, but the lower transitional area had slightly more complex soils. All dune soils were loamy sand with no organic layer. The groundwater depths at the time soil was being characterized were slightly lower than the average annual depths to groundwater for the marsh, low shrub, and high shrub locations. All transitional and dune locations had groundwater depths greater than 100 cm, but could not be measured.

Table 2 Soil characteristics for each of the eight study locations.

Location	Avg. depth to groundwater yr^{-1} (cm)	Groundwater depth (cm)	Depth	Texture	Color
Marsh	-0.651	9 cm	0-8 cm	Mucky peat	7.5YR 2.5/2
	-	-	8-12 cm	Mucky mineral	10YR 3/2
	-	-	12-30 cm	Loamy sand	5Y 5/1
Low shrub	31.168	40 cm	0-3 cm	Oi	2.5YR 2.5/4
	-	-	3-5 cm	Oe	5YR 2.5/2
	-	-	5-6 cm	Oa	5YR 2.5/1
	-	-	6-9 cm	Sandy loam	2.5Y 3/3
	-	-	9-19 cm	Loamy sand	2.5Y 4/4
	-	-	19-40 cm	Loamy sand	5Y 5/1
	-	-	19-40 cm	Loamy sand	5Y 4/1
High shrub	64.796	76 cm	0-3 cm	Oi	2.5YR 2.5/4
	-	-	3-10 cm	Oe	5YR 2.5/2
	-	-	10-40 cm	Loamy sand	2.5Y 4/3
Low trans	89.052	>100 cm	0-0.5 cm	Oi	2.5YR 2.5/4
	-	-	0.5-4 cm	Oe	2.5YR 2.5/3
	-	-	4-8 cm	Loamy sand	2.5Y 3/3
	-	-	8-24 cm	Loamy sand	2.5Y 4/3
	-	-	24-40 cm	Loamy sand	2.5Y 5/3
High trans	98.415	>100 cm	0-0.5 cm	Oi	2.5YR 2.5/4
	-	-	0.5-1 cm	Oe	5YR 2.5/2
	-	-	1-40 cm	Loamy sand	2.5Y 5/3
Low dune	148.994	>100 cm	0-40 cm	Loamy sand	2.5Y 5/3
Mid dune	116.764	>100 cm	0-40 cm	Loamy sand	2.5Y 5/3
High dune	213.987	>100 cm	0-40 cm	Loamy sand	2.5Y5/3

Decomposition rates

Trends in mass loss were consistent for all 4 depths at the marsh location (Fig. 9). Mass loss for both shrub locations exhibited similar trends with greater mass loss in the upper depths, but the low shrub exhibited a distinct difference between the top 10 cm and all lower depths (Fig. 9). The transition zones also revealed this trend of decreased decay with depth, but mass remaining at the end of the study was less for all depths compared to marsh and shrub locations (Fig. 9). At the end of the study, the mid and high dune locations had reduced mass loss in the top 10 cm but this trend was not consistent throughout the study period; mass loss per depth at these two locations were inconsistent throughout the study (Fig. 9). The four depths at the low dune location did not reflect similar mass loss trends per depth as the mid and high dunes, but overall mass loss did show consistency with the other dune sites (Fig. 9).

Average decay rates (yr^{-1}) ranged from 0.31 to 0.91 and generally increased by site with depth from groundwater (Table 3). Decay were most rapid in the top 10 cm for all sites except the mid and high dune sites where the 20 cm section exhibited the most rapid decay (Fig. 10).

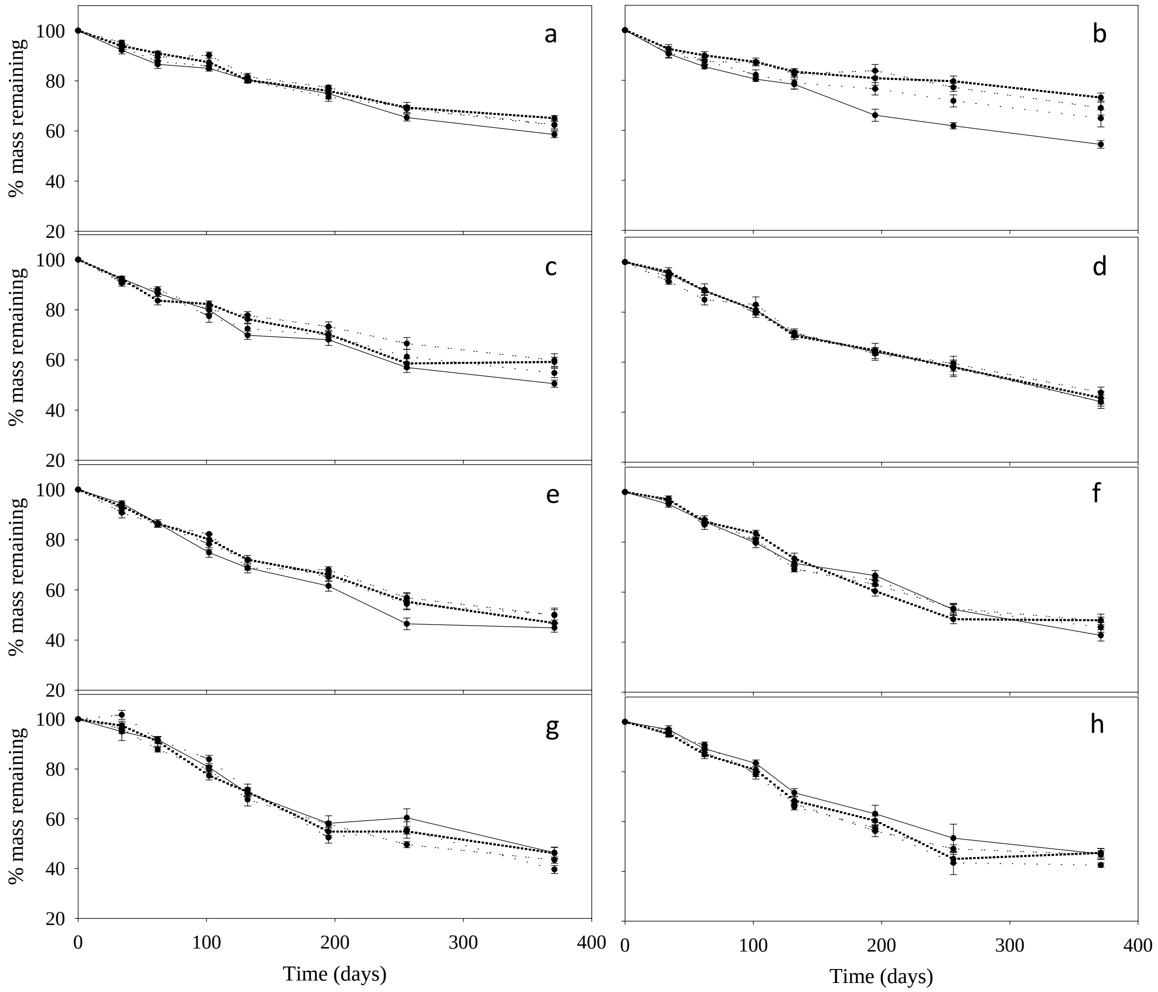

Fig. 9 Percent mass remaining for all sites and depths. Depths: 0-10 cm (solid line), 10-20 cm (dashed line), 20-30 cm (dotted line), and 30-40 cm (dash-dot line). Sites: marsh (a), low shrub (b), high shrub (c), low transition (d), high transition (e), low dune (f), mid dune (g), and high dune (h).

Table 3 Decay rates and soil characteristics in relation to land surface elevation, habitat, soil depth, and depth to groundwater.

Elevation (m)	Habitat	Depth	Avg annual depth to groundwater (m)	k (yr^{-1})	% Soil N	% Soil C	%SOM
1.454	Marsh	10 cm	-0.0565	0.527	0.06	0.88	1.89
		20 cm	-0.1565	0.466	0.00	0.22	0.67
		30 cm	-0.2565	0.423	0.00	0.28	0.49
		40 cm	-0.3565	0.466	0.00	0.21	0.37
1.787	Low shrub	10 cm	0.1093	0.602	0.18	3.08	6.47
		20 cm	0.0093	0.434	0.02	0.48	0.81
		30 cm	-0.0907	0.310	0.00	0.25	0.52
		40 cm	-0.1907	0.370	0.00	0.21	0.42
2.316	Low transition	10 cm	0.6881	0.814	0.19	3.30	0.93
		20 cm	0.5881	0.810	0.05	1.74	0.47
		30 cm	0.4881	0.778	0.00	0.30	0.42
		40 cm	0.3881	0.731	0.03	0.59	0.28
2.652	Low dune	10 cm	0.9652	0.844	0.00	0.01	0.59
		20 cm	0.8652	0.771	0.00	0.00	0.33
		30 cm	0.7652	0.713	0.00	0.00	0.25
		40 cm	0.6652	0.714	0.00	0.00	0.25
1.851	High shrub	10 cm	0.4456	0.674	0.13	0.46	10.89
		20 cm	0.3456	0.595	0.00	0.20	0.64
		30 cm	0.2456	0.518	0.32	0.19	0.54
		40 cm	0.1456	0.511	0.00	0.11	1.06
2.065	High transition	10 cm	0.7818	0.791	0.00	0.30	1.08
		20 cm	0.6818	0.684	0.00	0.14	0.44
		30 cm	0.5818	0.749	0.00	0.10	0.48
		40 cm	0.4818	0.691	0.00	0.11	0.34
2.648	Mid dune	10 cm	1.2875	0.762	0.00	0.00	0.33
		20 cm	1.1875	0.915	0.00	0.00	0.25
		30 cm	1.0875	0.767	0.00	0.00	0.18
		40 cm	0.9875	0.824	0.00	0.00	0.22
3.265	High dune	10 cm	1.9375	0.750	0.00	0.00	0.25
		20 cm	1.8375	0.843	0.00	0.00	0.22
		30 cm	1.7375	0.738	0.00	0.00	0.20
		40 cm	1.6375	0.755	0.00	0.00	0.19

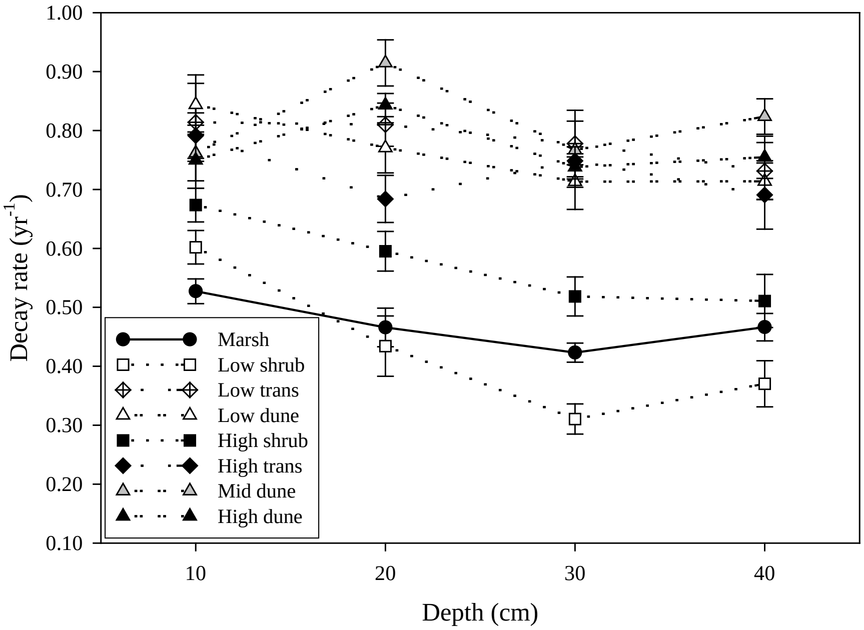

Fig. 10 Results from the 2-way ANOVA. R-E-G-W-F *post hoc* analysis identified 3 distinct groups of decay rates (yr^{-1}) that were significantly different ($p<0.05$). Three decay groups are as follows: low (marsh & low shrub), moderate (high shrub), and high (all transition and dune locations).

Groundwater values obtained from the Dupuit groundwater model explained the majority of the variation in decay rates with an asymptotic regression ($r^2=0.78$, $p<0.001$). Decay values became asymptotic where groundwater depths reached approximately 1 m (Fig.11). Groundwater values obtained from the other methods explained slightly less of the decay rate variances, and were not used for further analyses. Linear regressions indicate groundwater at depths shallower than 1 m explain 83% of variation in observed decay rates ($r^2=0.83$, $p<0.001$) (Fig. 12), whereas groundwater depths greater than 1 m may have little to no direct effect ($r^2=0.09$, $p=0.51$) on belowground decay (Fig. 12).

The 2-way ANOVA results indicate that decay rates varied by depth ($F=10.679$, $p<0.001$), with the top 20 cm decaying differently than the bottom 20 cm ($p<0.05$). Pairwise comparisons by depth, though, indicate the only specific locations with significant differences occurred in

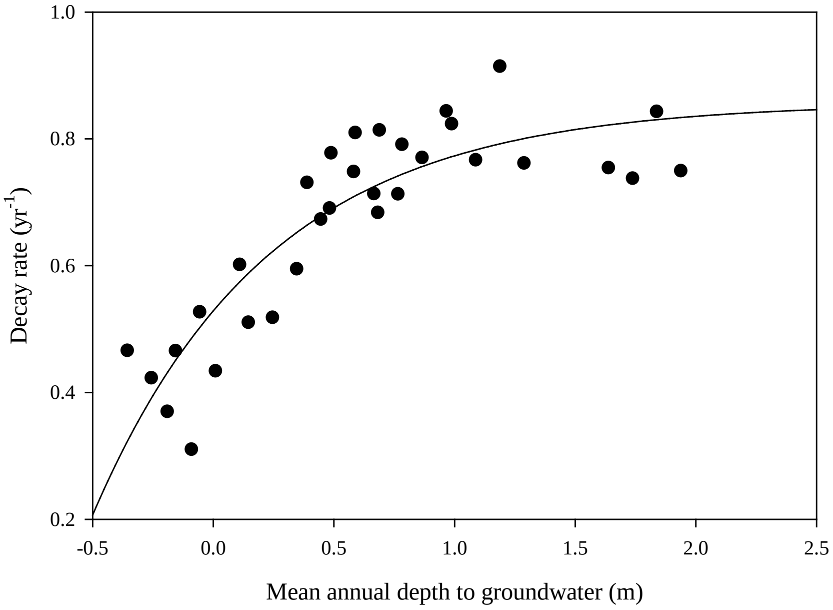

Fig. 11 Asymptotic regression for mean decay rates (yr^{-1}) vs mean annual depth to groundwater ($r^2=0.78$ $p<0.001$). Groundwater values are from the Dupuit method.

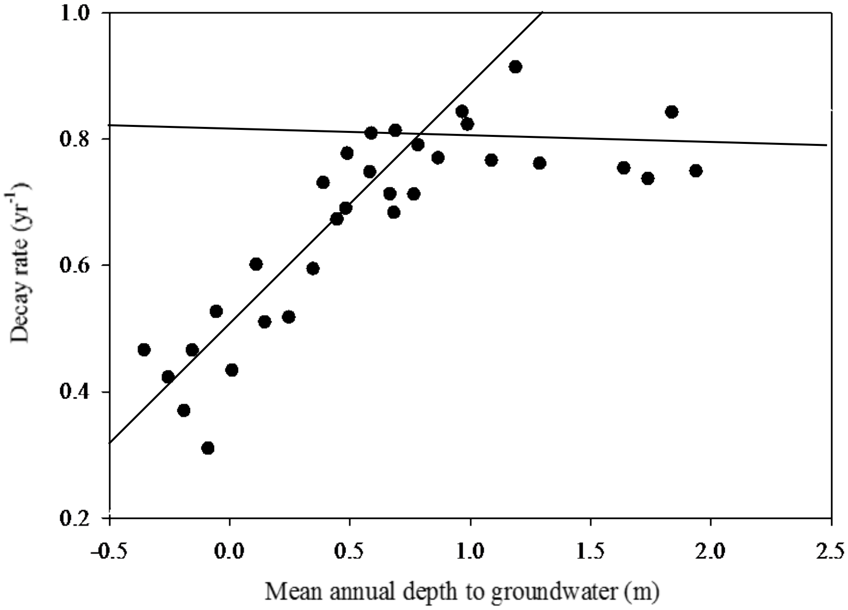

Fig. 12 Linear regressions for mean decay rates (yr^{-1}) vs mean annual depth to groundwater ≤ 1 m ($r^2=0.83$ $p<0.001$) and ≥ 1 m ($r^2=0.09$ $p=0.51$).

shrub thickets and the mid dune. In the shrub thickets, the 10 cm location decayed significantly more rapidly than the bottom 30 and 40 cm locations. The mid dune did not follow this trend. The mid dune's 20 cm location decayed significantly more rapidly than the top 10 cm (Table 4).

Table 4 2-way ANOVA pairwise comparison results for site decay rates by site. The only sites with significant differences among depths were in the shrub thickets and at the mid dune location. Values are differences in estimated marginal means. Highlighted values represents significant differences ($p<0.05$)

Depth	10 cm	20 cm	30 cm	40 cm
10 cm	**Low Shrub**	0.168	0.291	0.232
20 cm			0.124	0.064
30 cm				-0.06
10 cm	**High Shrub**	0.078	0.155	0.163
20 cm			0.077	0.084
30 cm				0.008
10 cm	**Mid Dune**	-0.153	-0.005	-0.062
20 cm			0.148	0.091
30 cm				-0.017

Decay rates also varied by location (F=59.64, p<0.001), and two thresholds were identified ($p<0.05$), separating decay rates into three groups: high (all transitional and dune areas), moderate (high shrub), and low (marsh and low shrub) (Fig. 10). Pairwise comparisons identified many differences in decay rates by location for each of the four depths; however, few significant differences occurred among transition and dune sites for all depths (Table 5).

Root ingrowths

The ingrowth occurrences may give insight to decay processes and are therefore reported here. The number of roots grown into each litterbag section varied by site and depth, and although a statistical quantitative analysis could not be performed, patterns were

Table 5 2-way ANOVA pairwise comparison results for site decay rates by depth. The depth to groundwater at each site is listed on the bottom and right axes. Values are differences in estimated marginal means. Highlighted values indicate significant differences (*p*<0.05).

HABITAT	**Marsh**	**Low shrub**	**High shrub**	**Low trans**	**High trans**	**Low dune**	**Mid dune**	**High dune**	
Marsh		-0.075	-0.146	-0.287	-0.264	-0.317	-0.235	-0.222	**-0.057**
Low shrub			-0.072	-0.212	-0.189	-0.242	-0.160	-0.148	**0.109**
High shrub				-0.140	-0.118	-0.170	-0.088	-0.076	**0.446**
Low trans					0.023	-0.030	0.052	0.064	**0.688**
High trans		**10 cm**				-0.053	0.029	0.042	**0.782**
Low dune							0.082	0.094	**0.965**
Mid dune								0.012	**1.288**
	-0.057	**0.109**	**0.446**	**0.688**	**0.782**	**0.965**	**1.288**	**1.937**	**DEPTH TO GROUNDWATER (m)**

HABITAT	**Marsh**	**Low shrub**	**High shrub**	**Low trans**	**High trans**	**Low dune**	**Mid dune**	**High dune**	
Marsh		0.032	-0.129	-0.344	-0.218	-0.305	-0.449	-0.377	**-0.157**
Low shrub			-0.161	-0.376	-0.250	-0.336	-0.481	-0.409	**0.009**
High shrub				-0.215	-0.089	-0.175	-0.320	-0.248	**0.346**
Low trans					0.126	0.039	-0.105	-0.033	**0.588**
High trans		**20 cm**				-0.087	-0.231	-0.159	**0.682**
Low dune							-0.144	-0.073	**0.865**
Mid dune								0.071	**1.188**
	-0.157	**0.009**	**0.346**	**0.588**	**0.682**	**0.865**	**1.188**	**1.837**	**DEPTH TO GROUNDWATER (m)**

HABITAT	**Marsh**	**Low shrub**	**High shrub**	**Low trans**	**High trans**	**Low dune**	**Mid dune**	**High dune**	
Marsh		0.113	-0.095	-0.355	-0.325	-0.290	-0.344	-0.315	**-0.257**
Low shrub			-0.208	-0.467	-0.438	-0.403	-0.456	-0.428	**-0.091**
High shrub				-0.259	-0.230	-0.195	-0.248	-0.220	**0.246**
Low trans					0.029	0.065	0.011	0.040	**0.488**
High trans		**30 cm**				0.035	-0.018	0.010	**0.582**
Low dune							-0.054	-0.025	**0.765**
Mid dune								0.029	**1.088**
	-0.257	**-0.091**	**0.246**	**0.488**	**0.582**	**0.765**	**1.088**	**1.737**	**DEPTH TO GROUNDWATER (m)**

HABITAT	**Marsh**	**Low shrub**	**High shrub**	**Low trans**	**High trans**	**Low dune**	**Mid dune**	**High dune**	
Marsh		0.096	-0.044	**-0.265**	**-0.224**	**-0.247**	**-0.357**	**-0.288**	**-0.357**
Low shrub			-0.141	**-0.361**	**-0.321**	**-0.344**	**-0.454**	**-0.384**	**-0.191**
High shrub				**-0.221**	-0.180	**-0.203**	**-0.313**	**-0.244**	**0.146**
Low trans					0.041	0.018	-0.092	-0.023	**0.388**
High trans		**40 cm**				0.180	-0.133	-0.064	**0.482**
Low dune							-0.110	-0.041	**0.665**
Mid dune								0.069	**0.988**
	-0.357	**-0.191**	**0.146**	**0.388**	**0.482**	**0.665**	**0.988**	**1.637**	**DEPTH TO GROUNDWATER (m)**

identifiable. Standard errors for the high shrub, and low and high transition sites had the largest variability in data. The marsh, and low shrub sites had consistent counts of ingrowths at all depths. These two sites also showed a large decrease in ingrowths with depth, especially in the 40 cm section. The low and high shrub locations did not appear similar except for the 10 cm section, which was similar for all locations except dune areas. The dune sites had substantially fewer root ingrowths in the 10, 20, and 30 cm sections compared to all other sites; however, deeper roots seemed relatively equal to, or more abundant than, the marsh and low shrub 40 cm sections (Fig 13).

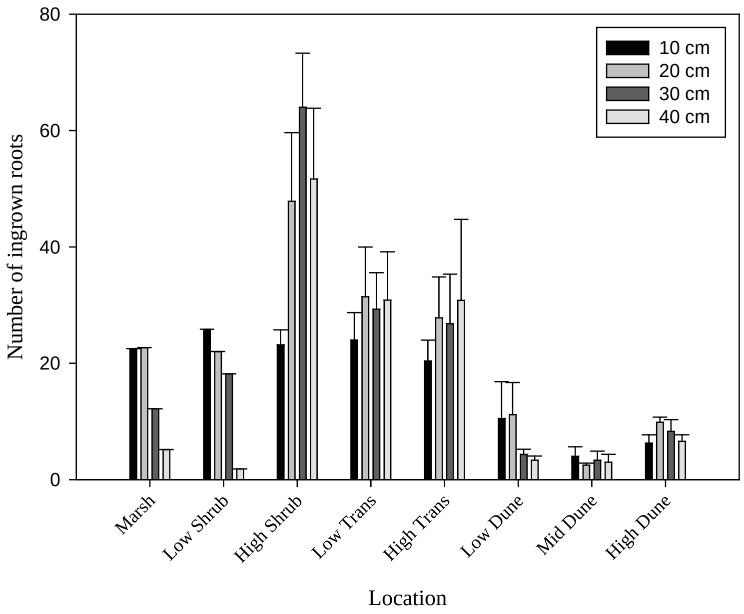

Fig. 13 Root ingrowths for each litterbag section and site. Error bars are 1 standard error.

Vegetation states

Of the observed marsh and dune habitat areas concealed by the shrub canopy, 93% (14/15) of field checked locations were identified as a wetland (Appencix A) or a dune habitat (Appendix B). The observed plant communities occupied 9,828 m^2, 17,347 m^2, and 19,810 m^2 for the marsh, shrub, and dune habitats respectively (Fig. 14). The decay threshold polygons underestimated observed dune area, and severely over estimated observed marsh area. The low decay threshold polygon occupied 98% of the observed marsh, but also occupied 68% of the observed shrub habitat (Fig. 15a). Only 1% of the low threshold polygon occurred in the observed dune habitat. The moderate decay threshold polygon occupied 2% of the observed marsh habitat, and 31% of both the observed shrub and dune habitats; however, 69% of the observed shrub polygon did not overlap with the moderate decay threshold polygon (Fig. 15b).The high decay threshold polygon occupied 68% of the observed dune, 1% of the observed shrub, and none of the observed marsh habitats (Fig. 15c). Overall, the low, moderate, and high decay polygons overlapped correctly with the corresponding marsh, shrub, and dune observed polygons 65% of the time.

Fig. 14 The three observed communities created from the combination of elevation and two mean annual depth to groundwater models

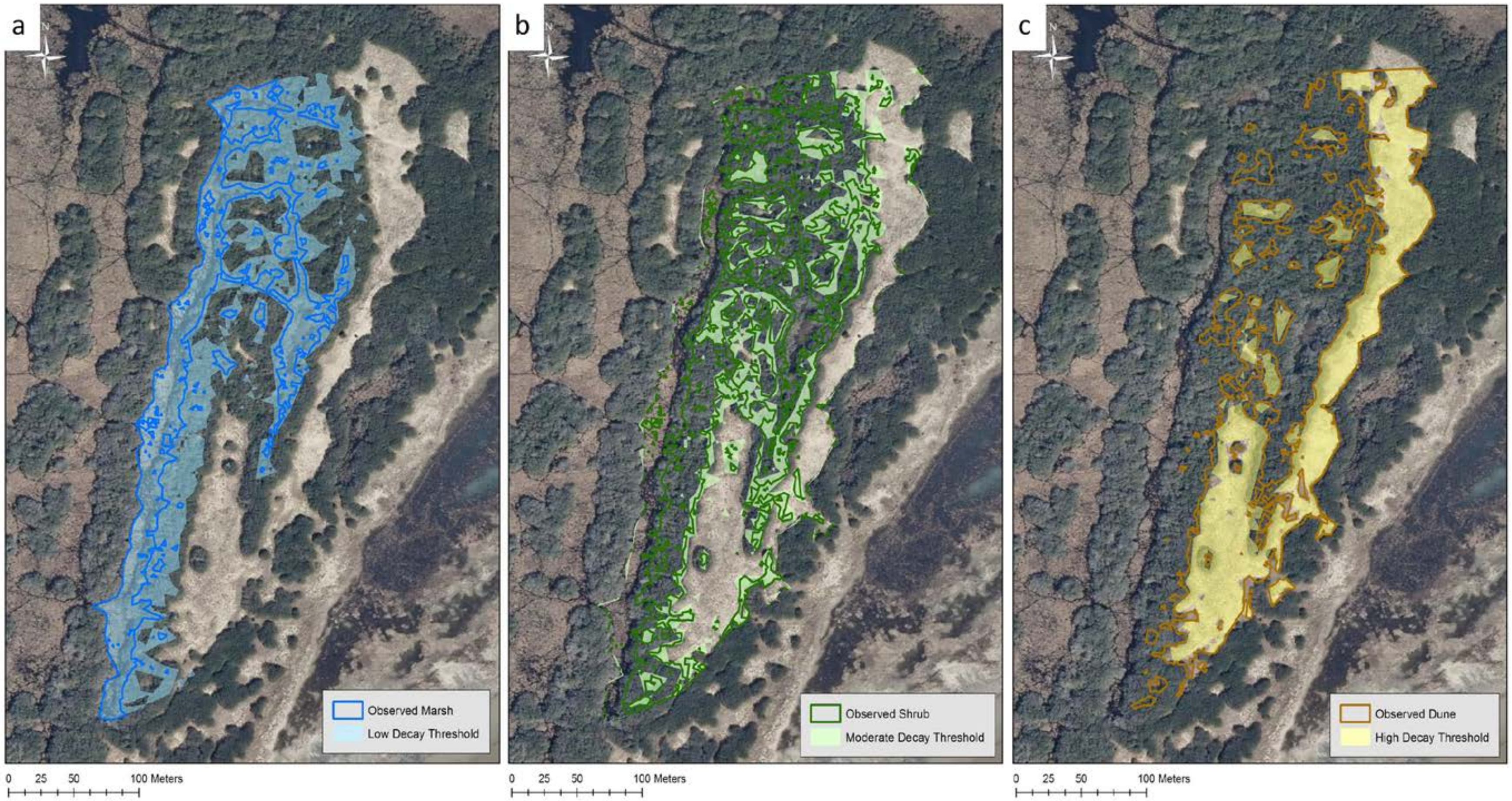

Fig. 15 Observed habitats with the corresponding decay threshold polygon. Observed marsh and low decay threshold polygon (a), observed shrub thicket with moderate decay threshold polygon (b), and observed dune habitat and high decay threshold polygon (c).

DISCUSSION

Groundwater levels provided a strong metric that can be used to predict belowground decay rates on the Virginia barrier islands. In general, areas nearer the groundwater surface experienced reduced decay compared to the sites where there was likely little or no interaction between decomposing substrate and groundwater. These reduced decay rates are likely attributed to periods of hypoxic or anoxic soil conditions, which can affect decay in a variety of ways.

Decomposition

Areas that are inundated with stagnant waters for extended periods of time become anoxic as decomposing microbes utilize the remaining dissolved oxygen (O_2) for respiration. Following the depletion of O_2, microbes use the next most efficient elements and compounds in a predictable sequence according to reduction potentials. Oxygen has the highest reduction potential, followed by nitrates, iron and manganese, sulfates, then other less reducing compounds (Craft 2001). Seawater is relatively rich in sulfates (SO_4^{2-}), and as such, locations that receive seawater inputs contain SO_4^{2-} that can be used as a final electron acceptor during anaerobic decay. When SO_4^{2-} is used as a final electron acceptor, hydrogen sulfide (H_2S) is produced (Craft 2001). The presence of H_2S in soil, as noted by its intense odor, is a primary wetland indicator by the Natural Resource Conservation Service (NRCS 2010). Hydrogen sulfide in the marsh location indicates that 1) the marsh is periodically inundated by seawater and occurs in an anoxic state, and 2) that marsh soils are low enough in oxygen, iron, manganese, and nitrates to necessitate the use of SO_4^{2-} in anaerobic microbial respiration.

Although areas below mean annual groundwater levels experienced the lowest decay rates, these rates are higher than values from a previous Hog Island study. Marsh belowground decomposition rates obtained by similar methods reported were from 0.21 to 0.33 yr^{-1} in anoxic marsh soils using pure *S. patens* roots and from 0.21 to 0.51 yr^{-1} using a site specific native mixture (Conn and Day 1997). My values were similar to the native mixture decay rates they reported. Adams et al. (*unpublished)* reported belowground decay rates from Hog Island marshes that were much higher (0.48 to 1.13 yr^{-1}) than the marsh values I observed. Fluctuating water tables can reduce decay when levels rise and soils become anoxic, but they can also lead to increased decay rates. The periodic rewetting of soil and litter from groundwater fluctuations causes pulses of optimal decay conditions, and can result in overall increased decay (Sorensen 1974; Brinson et al. 1981; Neckles and Neill 1994). Conn and Day (1997) reported some Hog Island swale locations to have fluctuating oxic/anoxic soils due to water table drawdown. Decay in locations that were below the mean annual groundwater level may have experienced groundwater drawdown periods. This would have created oxic conditions where aerobic respiration would lead to the higher decay rates that were observed. Other chemical differences in substrates or soil chemistries, as well as the possibility of soil perturbation and oxygenation, may have also led to the differences in decay rates among studies.

Aerobic respiration is far more efficient than anaerobic, and anaerobic conditions in the marsh likely explain the reduced decay rates that were observed. The marsh location, however, did not exhibit the lowest decay rates. These were observed in the 20-30 and 30-40 cm sections of the low shrub site where conditions were likely anoxic as well. Conn and Day (1997) reported belowground decay rates from *Morella cerifera* sites that showed a similar trend. Their shrub location decay rates at the 20-40 cm depths (from 0.13 to 0.34 yr^{-1}) were significantly lower than the upper depths, and were also substantially lower than marsh decay rates at the same depths. The bottom two litterbag sections of the low shrub location were below mean annual groundwater levels, but there was no indication of hydrogen sulfide production here. It is possible that since there is mainly atmospheric deposited sulfates in this location (which are scant in comparison to marine deposited), decay was limited by less efficient final electron acceptors. Because the mean annual groundwater level for this site was between the 20 and 30 cm depths, and because of the large gap in mass remaining between the 10 cm section and lower depths, anoxia and anaerobic decay appear to be a plausible explanation for reduced decay in the lower sections of the low shrub location.

Soil characteristics provide additional evidence supporting anaerobic decay in the low shrub location. Increased time in saturated soil creates anoxic conditions that reduces decay, and if system inputs are greater than outputs (eg. herbivory and decay) organic matter begins to accumulate. Mucky peat, which is a wetland indicator, was observed in the marsh location. In the low shrub location, a one cm thick Oa soil layer was present. Soils with Oa layers one to two cm thick may also be used in the field to indicate hydric soils (Hurt and Carlisle 2001). The presence of this Oa layer is evidence that the groundwater in this location is much higher than in the high shrub location and may help explain why the high shrub location exhibited higher decay rates.

The proximity of groundwater explained the majority of decay, but in addition to its direct effect (anaerobic vs aerobic), it may indirectly affect rates by controlling the distribution and abundance of the microbial populations responsible for decay (Mentzer et al. 2006). Both bacteria and fungi can completely degrade cellulose and lignin; however, fungi cannot completely degrade lignin anaerobically (Berg 2008). Seo and DeLaune (2010) found fungi denitrification rates far exceeded bacterial denitrification in moderate redox conditions (Eh > +250 mV), whereas bacterial denitrification was clearly dominant under more redoximorphic conditions. Due to deeper groundwater levels, the high shrub location likely had conditions that favored greater fungal decomposition, which could lead to greater lignin breakdown. The 0-10 cm depth in both shrub locations were above the mean annual groundwater levels, and had similar decay rates (a difference of only 0.072). Below this depth the two sites differed, especially at the 20-30 cm depth where significant differences were observed (a difference of 0.208). Regardless of differences between shrub sites, shrub decay rates observed in this study were substantially higher than those reported by Conn and Day (1997) at all depths. Because groundwater is the primary driver to belowground decomposition, it is likely that moderate differences in groundwater levels between studies are responsible for the differences in reported values. Additionally, groundwater can affect rooting depths and belowground biomass (Lieffers and Rothwell 1987; Megonigal and Day 1992; Weltzin et al. 2000; Murphy et al. 2009), which can indirectly affect decay rates.

Although not statistically analyzed, the low shrub location had ostensibly fewer root ingrowths than the high shrub location; it also showed substantially less variance at all depths. Low shrub root ingrowths were the lowest of all sites at 30-40 cm in depth. High shrub ingrowths at this same depth were remarkably greater, indicating more allocation of biomass to acquire a limiting resource. In this case, water would likely be the limiting resource as *Morella cerifera* forms a symbiotic relationship with nitrogen fixing actinomycetes and must grow in close proximity to groundwater (Young et al. 1995). Groundwater levels were lower in the high shrub location, and likely caused the fine roots to grow deeper. Greater annual depths to groundwater may explain the higher number of root ingrowths for the bottom three litter bag sections. This greater rooting depth may have implications on decomposition rates and the distinct differences observed in decay between shrub sites.

One of the primary functions of roots is to support growth by accessing belowground resources. Water may be the primary resource *Morella cerifera* roots seek as they require sufficient soil moisture to support their high transpiration demands (Guofan et al. 1995). The greater abundance of roots could produce more exudates, which are typically rich in sugars and organic acids, and may facilitate higher microbial populations. Root ingrowths were frequently growing in and around the decay substrate within each litterbag, putting it in direct contact with the rhizosphere where exudates are most concentrated. Root exudates have been implicated with affecting microbial communities (Bardgett 2014; Hamilton III and Frank 2001), which are the predominant source of decay when using one mm mesh litterbags. Kuzyakov et al. (2007) added root exudates to soil, which increased the mineralization of plant litter. Increased root ingrowths would increase the presence of root exudates, which could be partially responsible for the increased rates of decay observed in the high shrub location. Additionally, the organic acids in root exudates can weather mineral soils (Berg, 2008), increasing nutrient availability, microbial populations, and overall decay.

Although interactions between groundwater and decay substrates likely caused reduced decay in the marsh and shrub locations, the lack of interaction led to high variability and decay for transition and dune locations. Decay rates were most rapid at the transition and dune sites, but these sites were also most variable in percent mass loss by depth. Figure 9 (d-h) shows that the order of highest to lowest mass loss by depth changes multiple times throughout the study period, while lower sites remained fairly stable. Silver and Miya (2001) suggested root decay is most dependent on litter chemistry, while other studies point out that moisture and temperature are also important considerations (Gill and Jackson 2000; Davidson and Janssens 2006).

The transition and dune sites likely have little to no moisture or temperature moderation from groundwater, as they are furthest from mean annual groundwater levels. At these locations where soil insolation should be the highest and temperature effects from groundwater the lowest, soil temperature fluctuations should be most dramatic between day/night, as well as seasonally. Soil moisture at these locations is also predominantly dependent on unpredictable and periodic precipitation patterns. Large storms may wet all soil depths, but light storms may only wet the upper depths. Additionally, the upper depths may lose soil moisture more rapidly due to evaporative processes. Large fluctuations in temperature and moisture may help explain the large variability in mass loss at the four depths for transition and dune sites. Regardless of the variability in mass loss, dune and transition decay rates were most rapid among sites and had values similar to those reported by Conn and Day (1997) for similar dunes (from 0.46 to 0.97 yr^{-1}).

The values reported here are similar to other belowground decomposition values reported from Hog Island dunes, shrub thickets, and marshes; however, a separate Hog Island study focusing on aboveground decay reported different trends. Graziani and Day (2015) found greatest rates of aboveground decay within shrub thickets, at marsh edges and marsh/dune transition locations. Lowest rates of aboveground decay were observed where water extremes were most prevalent (dune and marsh locations). As seen by the contrasting above and belowground litter decomposition results it is important to study decomposition both above and belowground to obtain a more holistic understanding of ecosystem processes.

Decay thresholds and vegetation states

Thresholds to decay produced three decay polygons (low, moderate, and high) that appear to correspond with the three vegetation states that occur on Hog Island. Access to a freshwater resource may be responsible for plant distributions, but thresholds to decay and nutrient recycling in response to groundwater levels may also play a critical role. Specific plant characteristics and processes are important to plant succession, and belowground processes may be equal or more important to aboveground processes in influencing changes to species dominance or community structure, especially in nutrient poor systems (Gleeson and Tilman 1990). Decay rates and nutrient cycles specific to plant communities have been widely observed

(Facelli and Pickett 1991; Wardle et al. 1997; Aerts et al. 1999; Cortez et al. 2007). Hog Island soils are extremely nutrient limited, and increases in nitrogen can change species distributions and biomass patterns (Day et al. 2004). Water has a strong impact on nutrient cycling and availability (RodrÍguez-Iturbe and Porporato 2004) and was strongly linked to decay rates corresponding to the specific habitats observed in this study.

The highest rates of decay were located in dune and transition areas that are furthest from groundwater levels. These locations also had the least soil development and ability to retain nutrients. Soils that are not within close proximity to groundwater, have high permeability, low production, and high rates of decay exhibit slow development (Sevink 1991). Net primary production is severely retarded on Hog Island dunes by limited nutrients, specifically nitrogen (Heyel and Day 2006), which also affects species structure and composition (Day et al. 2004). It is likely that the combination of low dune NPP, proximity to groundwater, and rapid decay in this location coupled with high soil permeability and leaching prevents soil development and the ability for succession to advance to later seral stages. Inputs to the system are rapidly lost and the dunes are maintained in a state that is sparsely vegetated by grasses and forbs tolerant of the inhospitable growing conditions. This state should maintain until some mechanism allows litter to accumulate aboveground where decay rates are the slowest and reduced mineralization can slowly provide nutrients that are not immediately leached from the system. The development of an organic layer would also aid with nutrient and moisture retention. Because the dunes occur at the highest island elevations, they are also exposed to the highest winds that constantly blow litter and immobilized nutrients to lower elevations. This high rate of belowground decay and abiotic variables such as wind and soil permeability are likely maintaining this system state.

The marsh state, which corresponded to the lowest rates of decay, is maintained by high groundwater, periodic salinity spikes (due to overwash events), and is limited to hydrophytic vegetation. The reduced decay that occurs here is directly in response to anoxic and/or hypoxic conditions. Because the decomposers in this system are often without oxygen, they rely heavily on iron, manganese, and nitrogen. This prevents the system from accumulating inorganic nutrients, and any nutrient inputs are rapidly assimilated by either plants or microbes. In response to hydrodynamics, the marsh, like many other estuarine and fresh/brackish wetlands, likely exists in a nutrient limited state (Craft 2001) with the majority of nutrients immobilized via reduced decay.

Beneath the low shrub canopy, reduced decay was also observed. Although a substantial portion of the low decay threshold polygon overlapped the observed shrub polygon, it still corresponded strongly with actual marsh/wetland habitat. The soils in the low shrub location could possibly indicate wetland type hydrology that could have skewed the results. Due to all the microtopographic variability within the island, determining at high resolution where marsh/wetland soils and upland soils occurred would be extremely difficult and was beyond the scope of this study.

Moderate decay rates were observed in the high shrub location only, and corresponded to a specific habitat polygon the least. *Morella cerifera* grows in a narrow range, and cannot exist without sufficient supply of moisture for its high rates of transpiration. Predicting where this species can occur, or where it does occur based on its canopy, inherently leads to a high amount of error. The restricted locations in which it can occur due to freshwater availability and the extensive area that it appears to occur based on canopy cover alone can cause difficulties predicting its range. The decay rate polygon occupied observed shrub and observed dune habitat equally, but it only occupied the lower dune areas near the transitions. More replication in the shrub thickets may have yielded more accurate results, but these results still provide compelling evidence of distinctly different decay rates in the high shrub thicket.

Many reasons for the moderate decay rates observed in the high shrub location were proposed earlier. These include root exudates, nitrogen inputs, fluctuating groundwater levels and periods of anoxia and hypoxia. Additional explanations may be due to a positive feedback where *Morella cerifera* modifies its habitat, creating optimal decay rates that support further growth. Brantley and Young (2007) observed less than one percent light beneath *Morella cerifera* canopies compared to above. Crawford and Young (1998) identified large air and soil temperature differences and microclimate effects due to *Morella cerifera* canopies. The shrubs roots may also cause hydraulic lifting, and increase soil moisture and decay. Reduced insolation, temperature differences, and other microclimate effects caused by the shrub may have contributed to the moderate observed decay rates.

Conclusions

External processes such as precipitation and groundwater fluctuations have large effects on plant dominance, structure, overall biomass, and clearly have a large impact on internal ecosystem processes such as decay and nutrient availability. The nutrient cycling of belowground litter through decomposition may play an important role in driving vegetation patterns through the mineralization of organic nutrients. The specific decay rate thresholds identified here correspond with the distinct plant communities that occur on Hog Island. It is not clear the overall impact the freshwater lens has on thresholds to plant distributions, but results from this study suggest it plays in important role in nutrient immobilization and mineralization, which may assist in driving state changes or in maintaining each respective system state.

Identifying the effects barrier island free surfaces have on ecosystem processes is important to understanding barrier islands as a whole. For example, more shrub thickets lead to greater meso-predators such as raccoons and foxes (Gehrt 2003), which lead to reduced numbers of nesting shore birds (Erwin 2001). Conversely, less shrub habitat may be beneficial to nesting shore birds. Identifying drivers to changes in plant communities is directly related to species conservation, and as the effects of climate change become more pronounced and as sea levels rise, it is critical to understand how system processes will react in order to predict the ecological consequences. The high rates of sea level rise predicted for Mid-Atlantic coastal regions will alter barrier island landscapes through changes in the land and freshwater free surfaces. Sea levels and sediment supplies will control island accretion, elevation, and the relative locations of the free surfaces of which system processes are dependent upon. These changes will modify the abundances and distributions of plant communities, which maintain and further modify island geomorphology, and affect all higher trophic levels.

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WETLAND CRITERIA

	SITE														
Primary indicators	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
A4 Hydrogen sulfide															X
A7 Mucky mineral	X	X			X	X	X	X	X		X	X	X	X	X
A9 Muck	X	X	X	X	X	X	X	X	X		X	X	X	X	X
S1 Sandy mucky mineral	X	X			X	X	X	X					X	X	X
S4 Sandy gleyed matrix															
S5 Sandy redox									X						
S6 Striped matrix															
Secondary indicators															
Darkened litter layer	X	X	X		X	X	X						X	X	X
Topography (depression)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Vegetation (hydrophytic/absence)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Pedestalled roots		X	X	X	X		X								
High watertable	X	X	X										X	X	X
Species code		PEPU, PADI, MISC	PEPU, PADI	PEPU, BOCY			PEPU, BOCY	PEPU	PEPU		PEPU, BOCY	PEPU			
Wetland (Y/N)	Y	Y	Y	Y	Y	Y	Y	Y	Y	N	Y	Y	Y	Y	Y

UPLAND CRITERIA

	SITE														
Indicators	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Vegetation	X	X	X	X	X		X	X	X	X	X	X		X	X
Shallow O horizon	X					X	X	X					X		X
Few/sparse roots			X	X	X	X	X	X	X	X	X	X	X	X	X
Color	X		X	X	X	X	X	X	X	X	X	X	X	X	X
Topography	X	X	X	X		X	X					X	X	X	X
Arching shrubs	X		X	X		X									
Species code	FERU, PHAM, RUAR, EUCA, SPPA, AMBR														
Dune (Y/N)	Y	N	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y

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EDUCATION:

M.S. in Biology, Old Dominion University, Norfolk, VA, December 2015
B.S. in Environmental Science, Humboldt State University, Arcata, CA, May 2013
B.S.O.E. in Business Management, Wayland Baptist University, Plainview, TX, February 2009

SCIENTIFIC PRESENTATIONS:

Smith ML, Day FP (2015) Belowground Decomposition Rate Thresholds and Their Relationship to Plant Community State Change Along a Virginia Barrier Island Dune/Swale Transect. Society of Wetland Scientists Annual Meeting, Providence, RI.

Smith ML, Day FP (2015) Belowground Decomposition Rate Thresholds and Their Relationship to Plant Community State Change Along a Virginia Barrier Island Dune/Swale Transect. Ecological Society of America Annual Meeting, Baltimore, MD.

Smith ML, Day FP (2015) Belowground Decomposition Rate Thresholds and Their Relationship to Plant Community State Change Along a Virginia Barrier Island Dune/Swale Transect. Long Term Ecological Research All Scientists Meeting, Estes Park, CO.

Makely L, Del Valle-Martinez I, Kimbrell C, Long Z, Smith C, Smith ML (2015) Northwestern United States agriculture: evaluating habitat suitability of *Cydia pomonella* in Washington State from 2003 to 2065. American Society for Photogrammetry and Remote Sensing Annual Meeting, Tampa, FL.

ODU ASSISTANTSHIPS

Graduate Teaching Assistant (General Biology) August 2013 – December 2015
Graduate Research Assistant (Dr. Frank Day) Summers of 2014 and 2015