2020

BELOWGROUND CHARACTERISTICS OF DOMINANT COASTAL DUNE GRASSES AND POTENTIAL COMMUNITY-LEVEL EFFECTS ON COASTAL EROSION

Shannon L. Walker
Virginia Commonwealth University

BELOWGROUND CHARACTERISTICS OF DOMINANT COASTAL DUNE GRASSES AND POTENTIAL COMMUNITY-LEVEL EFFECTS ON COASTAL EROSION

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science

in Biology at Virginia Commonwealth University

by

Shannon Louise Walker,

B.S. Biological Sciences The University of Southern Mississippi 2017

Director: Dr. Julie Zinnert,

Assistant Professor, Department of Biology

Virginia Commonwealth University

Richmond, VA

November 2020

Acknowledgements

I would like to thank my major advisor, Dr. Julie Zinnert, for her guidance and encouragement. I will carry the skills and knowledge I have gained under her direction with me in all my future pursuits. I would like to thank my committee members, Dr. Nicholas Cohn, Dr. Evan Goldstein, Dr. Catherine Hulshof, and Dr. Fernando Tenjo for providing their time, advice, and assistance. I would like to thank the Virginia Long-Term Ecological Research Reserve, Dr. Charles Cartin (VCU), U.S. Army Corp of Engineers (USACE), and the members of the USACE Field Research Facility at Duck, North Carolina for providing access to their facilities, resources, and research sites and opportunities in pursuit of this project. Thank you to all of my lab-mates in the Coastal Plant Ecology Lab. I am grateful to have spent these last two years with a group of such brilliant, hilarious, and supportive peers. Many thanks to those who assisted me in the field and in the lab—Dr. Nicholas Cohn, Emily Riffe, Edward Long, Austin Tuley, Joseph Brown, Andrew White, Megan Goeke, and Caitlin Bishop—whose help made this project possible. Thank you to all my friends and family who have been so supportive throughout this process over countless hours of phone and video calls. A special thank you to my parents Susan and David Walker for their life-long encouragement and love.

Table of Contents

List of Figures iv
List of Tables v
Abstract vi
Introduction 1
Methods 4
  Location 4
  Plant Community Transects 4
  Monocultural Plots 5
  Above- and Belowground Biomass and Characteristics 5
  Tensile Strength 5
  Statistical Analyses 6
Results 7
  Plant Community 7
    Overall Plant Community 7
    North – South Locations 7
    Pre- and Post-Dorian 8
  Focal Grass Species 8
    Leaf length and aboveground stem number 8
    Above- and belowground biomass 9
    Root traits and characteristics 10
Discussion 11
Figures 20
Tables 31
References 33
Vita 37

List of Figures

1. Illustration of plot locations along a given transect. Pink flags represent the location of the northwest corner for each plot 20

2. Bar graph (mean ± SE) of cover by functional group across the entire site (A), between north and south locations (B), and pre- and post-Hurricane Dorian (C). Letters denote post hoc differences across functional groups for the entire site (A) and of the significant interaction between location and functional group (B)........ 21

3. NMDS based on Bray-Curtis dissimilarity (k = 3, stress = 0.08) of species cover showing plots grouped by north and south locations as well as pre- and post-Hurricane Dorian. Species are denoted by their genus. 22

4. Leaf length (cm) (A) and aboveground stem number (B) differ significantly among focal species. 23

5. Above- (light grey) and belowground biomass (dark grey) for focal species (mean ± SE). Compact letter display (CLD) shows differences between species in above- and belowground biomass allocation........ 24

6. Belowground biomass (mean ± SE) for focal species divided into the three major components—belowground stems (A), rhizomes (B), and roots (C). 25

7. Rhizome number (A) and length (cm) (B) for each species. *Ammophila* possessed significantly longer rhizomes than the other species. 26

8. Root average diameter (A) and surface area per species (B). 27

9. The percent root surface area (mean ± SE) divided into five diameter size classifications for *Ammophila* (A), *Panicum* (B), *Spartina* (C), *and Uniola* (D)........ 28

10. Root tissue density (RTD; gcm-3) (A) and specific root length (SRL; mg-1) (B) for the four focal species. 29

11. Tensile strength (MPa) of roots by diameter (mm) for *Ammophila* (A), *Panicum* (B), *Spartina* (C), and *Uniola* (D). Roots follow a logarithmic trend from large to small diameter, with the greatest tensile strength values in roots less than 0.5 mm in diameter. *Ammophila* and *Spartina* exhibit the highest maximum tensile strength values of the four species. 30

List of Tables

1. Overall species cover and functional group identity for all species and bare sand along transects. Species not present in a location are denoted with NA. 31

2. 3-way ANOVA results of log-transformed cover where Functional Group = functional groups (grasses, forbs, lianas, and shrubs), Location = north and south locations on the foredune, and Sampling = pre- and post-Dorian collection times. Significant p-values are given in bold. 32

3. 2-way ANOVA results of square-root-transformed percent root surface area. Significant p-values are given in bold. 32

4. Linear regression model components for log-transformed tensile strength data. Significant p-values are given in bold. CLD shows the results of ANCOVA interaction between species and root diameter with differences in slope between species evaluated using a Tukey's HSD post hoc.. 32

Abstract

BELOWGROUND TRAITS OF DOMINANT COASTAL DUNE GRASSES AND POTENTIAL COMMUNITY-LEVEL EFFECTS ON COASTAL EROSION

By Shannon Louise Walker, Bachelor of Science

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University

Virginia Commonwealth University, 2020.

Major Director: Dr. Julie Zinnert, Assistant Professor, Department of Biology

Natural dunes arise out of complex relationships between ecological, hydrological, and geological processes and are important for reducing erosion along coastlines. Aboveground structures of coastal dune grasses are known to impact erosional dynamics, and recent studies have shown that belowground structures—such as roots, rhizomes, and belowground stems—may be important in erosional resistance. My objectives were to 1) characterize above- and belowground characteristics of prominent dune grasses and 2) combine these data with functional group abundances and distribution to evaluate community effects on two adjacent locations of distinctive morphology and erosional characteristics and their response to storm disturbance. Whole plant samples of four dominant dune grasses—*Ammophila breviligulata, Spartina patens, Panicum amarum,* and *Uniola paniculata*—were collected from an unmanaged foredune and examined for above- and belowground characteristics. To assess the relationship among plant community, dune morphology, and storm effects, transects were also established in two locations of differing morphology along the same foredune and plant community data collected pre- and post-Hurricane Dorian. The four focal species differed in their suites of characteristics, indicating that these grasses may have species-specific impacts on dune erosional dynamics that arise from both above- and belowground factors. Plant community analyses further support that understanding species characteristics within a functional group at a given location may be critical in understanding the complex net effects of plant communities on erosional dynamics. This study demonstrates the necessity of considering belowground features of dominant vegetation as well as aboveground for understanding erosional dynamics in natural dune systems.

Introduction

Coastal dune systems have long been known to dramatically reduce wind and wave erosion along coastlines, as well as supply many ecosystem services (Hacker et al., 2019; Feagin et al., 2015; Charbonneau, 2015; Barbier et al., 2011). Many coastal communities incorporate the construction and maintenance of coastal dunes for the purpose of coastal defense against storm activity, and the practice has become widespread throughout the United States (*e.g.* Nordstrom et al., 2002). Coastal dunes are highly vulnerable to global climate change because of the tight coupling among island ecological processes, geomorphological processes, and oceanic/atmospheric drivers of disturbance (*e.g.* hurricanes, nor'easters, sea-level rise) (Brodie et al., 2019; Biel et al., 2017; Feagin et al., 2015; Durán & Moore, 2013; Feagin et al., 2005). With climate change, many coastlines and barrier islands are expected to experience increased erosion due to sea-level rise and changes in storm characteristics (*e.g.* Vousdoukas et al., 2020; Ranasinghe, 2016; Moore et al., 2014). As dunes serve a protective role for coastal communities, understanding factors which may increase their resistance and resilience to erosion is of vital importance (Feagin et al., 2015; Barbier et al., 2011).

Natural dune systems are highly dynamic and arise through complex interactions among local and regional hydrology, geology, and ecological processes (*e.g.* Brodie et al., 2019; Cohn et al., 2018; Biel et al., 2017; Feagin et al., 2015; Sigren et al., 2014). Interactions between aeolian and hydrologically transported sediments and dune vegetation are important in the dune building process (Brodie et al., 2019; Feagin et al., 2015). Aboveground features of dune grasses, such as stem height and density, have been shown to reduce wave energy and trap aeolian sediments (Hacker et al., 2019; Mullins et al., 2019; Maximiliano-Cordova et al., 2019; Charbonneau et al., 2016; Feagin et al., 2015; Silva et al., 2016). As sediments accumulate around the base of dune vegetation, some species respond positively to burial by increasing allocation of biomass to aboveground stems (Mullins et al., 2019; Brown & Zinnert, 2018). Dune-building species such as *Ammophila breviligulata*, *Spartina patens,* and *Uniola paniculata* dramatically increase the maximum height of coastal dunes through this process, especially over timescales of years (Hacker et al., 2019; Mullins, et al., 2019; Durán & Moore, 2013).

Recent studies have demonstrated the importance of belowground features of dune grasses in stabilizing dune sediments and reducing erosion (De Battisti & Griffin, 2019; Bryant et al., 2019; Charbonneau et al., 2017). This was recently demonstrated in the dune building grass, *Ammophila breviligulata*—a dominant species along the northern part of the U.S. Atlantic coast (De Battisti & Griffin, 2019; Goldstein et al., 2018). These studies suggest that species with greater amounts of total belowground biomass dramatically reduce wave-induced erosion. Of plant belowground structures, roots in particular are known to stabilize sediments in diverse habitats through a variety of mechanisms (Feagin et al., 2015; Comino et al., 2010; De Baets et al., 2008; Moreno-Espíndola, et al., 2007; Reubens et al., 2007; Rillig & Mummey, 2006; Gregory, 2000). Roots provide physical reinforcement through entanglement of sediments, incorporation of sediment grains in tissues (rhizosheath), and physical resistance to sediment movement (reviewed in Feagin et al., 2015). Root tensile strength, the amount of pulling force a root can withstand before breaking, may also provide biomechanical reinforcement as has been shown in a variety of other soil types (Comino et al., 2010; De Baets et al., 2008). Additionally, roots exude a variety of substances into the area around the rooting zone (called the rhizosphere), which acts as a biological glue, adhering the surrounding sediment grains to the roots as well as to each other (Moreno-Espíndola, 2007; Rillig & Mummey, 2006; Gregory, 2000). This serves to stabilize sediments within the rhizosphere (Rillig & Mummey, 2006; Gregory, 2000).

Contributions of organic material from both above- and belowground structures also serves to increase the cohesiveness of sediment grains, reducing their erodibility (Feagin et al., 2015). A gap in the literature remains, however, of detailed knowledge about species-specific allocations to different plant structures (above and belowground), differences in root traits, and how these contribute to erosional resistance in coastal dunes.

Quantifying these species-specific structural characteristics in relation to the dune plant community is critical to understanding the emergent erosional resistance of these species *in situ*. Emergent erosive properties of dune systems may be related to the above- and belowground features of the entire community of species which compose that system. By examining the dune plant community at the plot-level and coupling this with quantification of the dominant species, preliminary investigation of how species-specific characteristics, dune morphology, and emergent dune erosional properties can be evaluated.

My objectives were to 1) evaluate species abundances and distribution at the community-level between two adjacent locations of distinctive morphology and erosional characteristics before and after storm disturbance and 2) characterize above- and belowground characteristics of specific species from the dominant functional group (*i.e.* dune grasses) that may inform erosion dynamics. Specifically, I characterized above- and belowground characteristics and biomass for four prominent graminoid species along the US Atlantic Coast: *Panicum amarum*, *Spartina patens*, *Uniola paniculata*, and *Ammophila breviligulata*. I also quantified plant community data from transects established along the leeward side of the foredune ridge pre- and post-storm as well as between two locations of different morphology and erosional responses.

Methods

Location

Samples were collected from the U.S. Army Corps of Engineers (USACE) Field Research Facility (FRF) in Duck, NC. The facility actively researches questions regarding sediment dynamics, oceanography, and morphology within a 1 km length of the Atlantic shoreline. Within the FRF, data on dune morphology have been actively recorded since 1981. Dunes were constructed on the property during the 1930s and 1940s and have since been unmanaged (Birkemeier et al., 1984). The Outer Banks is classified as a microtidal system and characterized by active beach erosion. As such, beach nourishment projects are frequent in the area, and the USACE FRF is actively researching sediment dynamics for erosion reduction applications. In order to represent the distribution of possible root diameters for tensile strength, additional root samples of each species were taken from Hog Island, VA— part of the Virginia Long-term Ecological Research Reserve.

Plant Community Transects

Plant community data were collected to quantify compositional differences between plots within each location north and south as well as between locations. Transects were established at each site on the leeward side of the dune stretching from the crest to the dune toe. Five, 0.25 m^2 plots were created along each transect (Figure 1). Measurements of species composition and functional cover were made within each plot. Plots were resampled following Hurricane Dorian, which impacted the FRF as a category 1 storm from September 6-7, 2019. In this location, maximum storm surge was an additional 1.06 m above mean sea level with 26.6 m/s top recorded windspeed.

Monocultural Plots

Monocultural stands of *Ammophila breviligulata*, *Spartina patens*, *Panicum amarum*, and *Uniola paniculata* were identified at each site. A monocultural plot was a 0.25 m^2 area in which only the focal species was present. Any edge of a monocultural plot was located at least 0.5 m from the canopy of any other species. Whole plants were removed from each plot by hand-digging ($n_{Ammophila}$ = 10, n_{Uniola} = 11, $n_{Spartina}$ = 15, $n_{Panicum}$ = 18). Plants were separated into above- and belowground components in the field and put on ice. Upon returning from the field, root samples for tensile strength measurements were separated from each plant and placed in 15% EtOH. Roots were selected from representative diameter classes and different locations along the root matrix. Following the procedures of Böhm, 1979, these were refrigerated until analyses can be completed. Remaining above- and belowground components were placed in labeled bags, covered with distilled water, and frozen until further analyses can be made.

Above- and Belowground Biomass and Characteristics

Aboveground components were assessed for stem number and maximum leaf length per stem. Belowground components were separated into belowground stems, rhizomes, and roots and roots scanned using WinRHIZO. All above- and belowground components were then dried in an oven at 60º C for 48 hours and weighed for dry biomass.

From the WinRHIZO scans and biomass, root tissue density (RTD), specific root length (SRL), average root diameter, root surface area and root diameter distribution were assessed by species. RTD is the ratio of total root biomass to total volume for a given sample. SRL is the ratio of total root length to total biomass.

Tensile Strength

Subsampled tensile strength roots were rehydrated in distilled water for a minimum of 30 minutes following the procedures of Böhm, 1979. Roots were tested with an MTS Insight 30

Universal Testing Machine (UTM) using a 50 N load cell. MTS Advantage Wedge Action Grips were modified with 5 mm thick packaging foam and 220 grit sandpaper to prevent damage to the root sample while providing enough grip to pull the sample. The Testworks 4 software was then used to assess the resulting tensile strength data.

Statistical Analyses

Data were analyzed in R version 4.0.1. A three-way ANOVA was used to assess cover by functional group, north and south location, and pre- and post-Hurricane Dorian sampling period. There was no significant interaction among the three factors. Significant two-way interactions and main effects were analyzed using a Tukey's HSD post hoc. PerMANOVA analyses were used to assess groups based on Bray-Curtis dissimilarity of species cover with 999 permutations, followed by pairwise comparisons with a false discovery rate (FDR) p-value adjustment. The dissimilarity matrix was visualized using Non-metric Multidimensional Scaling (NMDS). A one-way ANOVA or Kruskal-Wallis test was used for biomass, above- and belowground measurements, and root trait metrics of focal species followed by a Tukey's HSD or Nemenyi post hoc, respectively. Percent root surface area distributed by diameter class per focal species was assessed using a two-way ANOVA. ANCOVA and pairwise t-tests were conducted to compare slopes of root tensile strength and diameter for each species. In all tests, focal species data were logarithmic or square root transformed when possible to meet parametric assumptions.

Results

Plant Community

Overall Plant Community

Total plant species richness across all transects was 18. Living cover differed significantly among the four major functional groups—graminoids, lianas, shrubs, and forbs (F = 183.47, p < 0.0001; Figure 2). Graminoids represented the greatest amount of living cover at Duck, FRF (7.7 ± 1.5 %). These graminoids were *Ammophila breviligulata, Uniola paniculata*, *Spartina patens*, and *Panicum amarum*. *Spartina patens* had the greatest cover of all species (4.5 ± 1.0%; Table 1). Shrubs (4.2 ± 1.1%), forbs (3.7 ± 0.8%), and lianas (2.2 ± 0.6%) all had similar cover. The shrub *Iva imbricata* had the second highest cover of all species (3.6 ± 1.0%). Functional groups also demonstrated distinctive distributions along the dune profile. Graminoids, lianas, and shrubs were distributed only along the dune crest and dune face, while forbs could be found across the entire profile. Most forb species occurred along the dune crest and face except for the annual forb *Cakile edentula* which could only be found along the beach. This is consistent with its normal distribution in coastal ecosystems. Though functional groups differed significantly in cover, it is important to note that most of the dune surface was not covered by vegetation (Figure 2). Bare sand was the most dominant cover type (74.8 ± 3.2%).

North – South Locations

There was a significant interaction between the north and south locations and functional cover ($F_{4,480}$ = 5.88, p = 0.0001; Figure 2; Table 2). In the south, graminoids, shrubs, and forbs had similar cover while graminoids, forbs, and lianas had similar cover in the north. Bare cover was identical between locations, but within graminoid, shrub, and forb groups, cover was higher in the south than the north (Figure 2; Table 2). The two locations differed in species composition, and higher shrub cover in the south was likely due to high cover of *I. imbricata*, which was not present in the north (F = 4.19, p = 0.001; Figure 2; Table 1). The south also had higher forb cover which can be attributed due to the greater cover of both *C. edentula* (2.2 ± 0.9%) and *Solidago sempervirens* (2.7 ± 1.1) as well as the cover of additional forb species not present in the north (Figure 2; Table 1).

Pre- and Post-Dorian

Following Hurricane Dorian, community composition changed significantly (F = 2.56, p = 0.01; Figure 3). This is attributed to the loss of one species, *C. edentula*. When *C. edentula* was removed from community analyses, Hurricane Dorian no longer had any significant impact on community composition (F = 0.85, p = 0.53). This loss of *C. edentula* is likely a combination of both the influence of Hurricane Dorian and seasonal senescence of this annual species. Hurricane Dorian did not have any significant impact upon functional cover (Figure 2; Table 2).

Focal Grass Species

Leaf length and aboveground stem number

Individuals of *Ammophila breviligulata*, *Uniola paniculata*, *Spartina patens*, and *Panicum amarum* (hereafter referred to by genus) were assessed for above- and belowground characteristics. These species differed significantly in both aboveground leaf length ($X^2 = 76.30$, $p < 0.0001$) and stem number ($X^2 = 11.45$, $p = 0.01$; Figure 4). *Ammophila* (58.3 ± 1.8 cm) and *Uniola* (48.5 ± 2.6 cm) had the longest leaves with *Uniola* exhibiting considerable variation in leaf length (2.5 – 103.0 cm). *Spartina* (34.5 ± 1.5 cm) and *Panicum* (34.6 ± 2.1 cm) had similar distributions and had leaves that were ~40% shorter than *Ammophila* and ~30% shorter than *Uniola*. *Uniola* and *Ammophila* had high variability in stem number (1 - 33 and 2 - 27 stems, respectively) compared with *Spartina* and *Panicum*. All species except *Spartina* exhibited at least one individual with an extremely high stem number.

Above- and belowground biomass

Consistent with high aboveground stem measurements, both *Ammophila* and *Uniola* also had the greatest aboveground biomass ($F = 5.98$, $p = 0.002$; Figure 5). Patterns in belowground biomass were similarly distributed, with *Ammophila* and *Uniola* having significantly more mass than *Spartina* and *Panicum* ($F = 11.19$, $p <0.0001$). Belowground to aboveground biomass ratios were ~1:1 in *Ammophila* (0.8 ± 0.2), *Panicum* (1.2 ± 0.3), and *Spartina* (1.0 ± 0.2), but was higher and more variable in *Uniola* (1.9 ± 0.6). When belowground biomass was partitioned among the three major structures (*i.e.* stems, rhizomes, and roots) distinctive patterns in species belowground allocation emerged (Figure 6). *Ammophila* and *Uniola* had the greatest biomass in belowground stems compared with *Spartina* and *Panicum* ($F = 13.56$, $p < 0.0001$; Figure 6). Nearly 50% of total belowground biomass in *Ammophila* was devoted to rhizomes (although highly variable, 4.7 ± 3.3 g; Figure 6), compared to 7% in *Uniola* and 24% in *Spartina*. *Panicum* allocated a similar proportion of belowground biomass to rhizomes (46%) as *Ammophila*, but significantly less total biomass (1.0 ± 0.6 g; $F = 3.30$, $p = 0.03$). Although rhizome number did not differ among species ($X^2 = 4.48$, $p = 0.21$), *Ammophila* had significantly longer rhizomes (68.7 ± 12.6 cm; $X^2 = 30.11$, $p < 0.0001$; Figure 7), with the longest rhizome greater than 200 cm. Root biomass differed among species ($F = 4.21$, $p = 0.01$; Figure 6). *Uniola* and *Ammophila* had high root biomass with *Uniola* possessing 45% more root biomass than the other species combined, though it did not differ significantly from *Ammophila*.

Root traits and characteristics

When assessed for root characteristics and traits, species diverged from patterns seen in biomass allocation. *Uniola* had the highest average diameter roots, while *Ammophila* and *Spartina* had the smallest (F = 34.22, p < 0.0001; Figure 8). Species differed in total root surface area, but due to high variability in total root surface area within species no post-hoc differences were seen (F = 3.11, p = 0.04; Figure 8). To account for this high variability, surface area distribution was assessed as the percentage of the root system surface area that fell within a given diameter class. There was a significant interaction between diameter class and species ($F_{12,\ 215} = 25.03$, p < 0.0001; Table 3). Species had roots that fell within all diameter classes but allocated greater root surface area to diameter classes similar to the average root system diameter (Figure 9). *Ammophila* and *Spartina* allocated more surface area to smaller root diameter classes. *Panicum* devoted the greatest proportion of its biomass to roots 1.0-1.5 mm in diameter—the middle of the root diameter distribution. *Uniola* devoted most of its root surface area to the largest diameter classes. Root tissue density (RTD) (F = 13.04, p < 0.0001) and specific root length (SRL) (F = 26.97, p < 0.0001) differed by species, with *Ammophila* and *Spartina* both having the highest values for these two traits (Figure 10). Log-transformed tensile strength analysis revealed unequal slopes among species ($F_{3,92}$ = 6.64, p = 0.0004; Table 4). Slopes were significantly different among all species except for *Ammophila* and *Spartina*. These two species exhibited the highest maximum tensile strength values (4314 MPa and 2878 MPa, respectively) and had the steepest slopes (Figure 11; Table 4). *Panicum* and *Uniola* exhibited much lower maximum tensile strength values (1373.5 and 1281.1 MPa; Figure 11).

Discussion

The results of this study are some of the first to concurrently collect data on both plant community and dominant functional group above- and belowground characteristics to understand erosional dynamics on dune systems. Both types of data can be used to understand how vegetation may play a role in erosional dynamics. My objectives were to **1) evaluate species abundances and distribution at the community-level between two adjacent locations of distinctive morphology and erosional characteristics before and after storm disturbance and 2) characterize above- and belowground characteristics of specific species from the dominant functional group (*i.e.* dune grasses) that may inform erosional dynamics.** My study revealed that the characteristics of the plant community, dune morphology, and effects of storm disturbance are highly complex, as dune characteristics arise from complex interactions among physical aspects of the dune, local forces and conditions, and the suite of characteristics exhibited by the plant community. The data collected on above- and belowground characteristics of dominant dune grass species further demonstrate the complex nature of plant communities, as no two species converged on identical suites of characteristics despite their shared functional identity.

The dune plant community at Duck, FRF was similar to those of other Outer Banks, NC. Species richness (18 species) fell within the typical range for Outer Banks islands (10-32 species; Hacker et al., 2019). Due to both frequent disturbance and island ecology, low overall species richness is common in dune systems. Similar to other islands in the Outer Banks, graminoids were the dominant functional type on the foredunes at Duck, FRF (Hacker et al., 2019). The graminoid species at Duck, FRF are also four of the most dominant dune grass species of the Atlantic and Gulf Coasts of the United States—*Ammophila breviligulata*, *Uniola paniculata*, *Spartina patens*, and *Panicum amarum*. Of these species, *S. patens*—a moderate dune-building grass—was the most dominant. This differs from patterns seen on other Outer Banks islands where *U. paniculata* or *A. breviligulata* dominate foredunes, though was similar to other locations along the northern Atlantic coast, such as Hog Island, Virginia (Hacker et al., 2019; Day et al., 2001).

Spartina patens inhabits a wider range of habitat types than the other focal species including foredunes, swales, and coastal marshes and is adapted to high disturbance (Brantley et al., 2014). High cover of all functional types at the crest of the FRF foredune, including saplings of maritime shrub species *Morella pennsylvanica* and *Prunus serotina*, indicate that the foredune has been eroding (Brodie et al., 2019), with the crest representing an ecotone between swale and foredune plant communities. *Spartina patens* may be better able to exploit the FRF foredune than the more typically dominant dune grasses due to its capacity to tolerate high disturbance and multiple habitats.

The differences in plant community and functional cover between the north and south locations may indicate ecomorphodynamic relationships between dominant vegetation type and foredune characteristics (Goldstein et al., 2017; Durán & Moore, 2013). A recent study examined the morphological change between the north and south locations along the foredune at Duck, FRF over two and a half years (Brodie et al., 2019). The south was characterized by broad, low dunes significantly lower in elevation than the north. Although both locations showed high seasonal variation, the south location was net accretive over the 2.5-year study period. Conversely, the north had significantly greater elevation and the foredune was narrower. Over the study period, the north also decreased in volume and retreated inland (Brodie et al., 2019).

My study shows that the north and south locations also differ in plant community and functional cover. The south was characterized by higher cover of shrubs, graminoids, and forbs (consistent with net accretion) compared to the north. The presence of the shrub species *I. imbricata* may also demonstrate secondary succession in the south foredune plant community, indicating differences in plant community interactions between the two locations. The steep, narrow foredune in the north may limit plant establishment on the dune face due to sediment instability and less-habitable microclimate. Brodie et al. (2019) demonstrated that the north was net erosive and only sparely distributed clumps of vegetation on the dune face experienced sediment accretion during the study period. With lower vegetative cover overall and lower functional cover of dune-building grasses in the north, sediment may be less likely to become trapped and stabilized. In areas that lack vegetation the steep angle of the dune face may also limit sediment deposition (Brodie et al., 2019). Interactions between vegetative cover and dune morphology may reinforce the net retrogradation of this location. Despite these differences in cover and morphology, Hurricane Dorian, which struck Duck as a category 1 storm in September 2019, did not significantly affect dune functional cover. There was a non-significant trend of decreased cover following the storm and a change in plant community due to the loss of the annual species, *Cakile edentula*. This is likely a combination of the storm effects and seasonal plant senescence (*i.e.* end of growing season).

Although most of the total dune surface in this study was not covered by vegetation (75 ± 3% bare sand), aboveground structures may still play a key role in sediment accumulation and erosional dynamics at Duck, FRF. Aboveground vegetation has been shown in wave flume experiments reduce erosion in simulated dunes by interacting with wave forces under both collisional and overwash regimes (Bryant et al., 2019; Maximiliano-Cordova et al., 2019; Silva et al., 2016). Aboveground vegetation is also important for intercepting and accumulating sediments, which can promote dune formation and recovery (Hacker et al., 2019; Mullins et al., 2019; Maximiliano-Cordova et al., 2019; Charbonneau et al., 2016; Feagin et al., 2015; Silva et al., 2016). Kuriyama et al. (2005) demonstrated that even at low densities aboveground vegetation may significantly reduce the movement of aeolian transported sediments. Further, even in net erosive locations, sparse clumps of vegetation may still accrete sediments as has been observed at Duck, FRF (Brodie et al., 2019).

Belowground vegetative structures may also play an important role in erosional processes by stabilizing sediments that have been trapped by aboveground parts (De Battisti & Griffin, 2019; Bryant et al., 2019; Charbonneau et al., 2017; Zarnetske et al., 2015). Recent experimentation has shown that belowground structures may reduce sediment loss under certain wave erosional regimes, however quantification of their effects has been limited to assessments of raw belowground biomass (De Battisti & Griffin, 2019; Bryant et al., 2019). These studies have demonstrated the importance of total raw biomass in potentially reducing erosion, but these data alone may not provide sufficient information about species-specific belowground interactions (Klimešová et al, 2018). Roots, rhizomes, and belowground stems all serve different roles in plant physiology and thus interact differently belowground (Klimešová et al., 2018).

Although high in surface area, roots are a very small proportion of total belowground biomass (Figure 6). More massive structures such as belowground stems and rhizomes may be important for physical resistance to erosional forces and may contribute organic material to the sediment over time (De Battisti & Griffin, 2019; Feagin et al., 2015). However, these structures differ from roots, which have evolved features for exploring and directly manipulating the sediment environment to obtain nutrients and water and for anchorage (Klimešová et al., 2018).

These adaptations have led to features that may contribute to sediment stabilization through the cohesive action of rhizosphere-associated exudates, sediment enmeshment in rhizosheath tissues, and physical reinforcement of slopes via root system tensile strength (Feagin et al., 2015; Comino et al., 2010; De Baets et al., 2008; Moreno-Espíndola, et al., 2007; Reubens et al., 2007; Rillig & Mummey, 2006; Gregory, 2000). As such, quantifying only total belowground biomass may underestimate the contribution of roots in reducing sediment erosion which may be disproportionate to their raw biomass.

Just as different dune species vary in their aboveground features which can have significant impacts on erosional forces, belowground structures also demonstrate a high degree of variation among species (Klimešová et al., 2018). These differences may reflect adaptations to the dune environment and differential niche exploitation. Because these differences likely affect the way specific species directly interact with sediment, especially through the actions of root systems, understanding the spectrum of both above- and belowground adaptations may provide greater insights into species-specific erosional patterns.

In the species examined here, above- and belowground biomass allocation was approximately 1:1, with some variation among species possibly due to both species-specific differences and differences in *in-situ* sand burial. Both *Ammophila* and *Uniola* generally had the greatest raw biomass though allocation patterns had a high degree of variability across all biomass measurements especially for these two species. When belowground features—especially roots–were examined for characteristics other than raw biomass, however, these species diverged.

When evaluating traits indicative of interaction with sediment, *Ammophila* and *Spartina* had much smaller average diameter roots with the majority of their root surface area distributed in the smallest diameter root classes (0.0 – 1.5 mm), higher SRL, higher RTD, and higher tensile strength relative to *Uniola* and *Panicum*. These traits can be used to better understand how the root systems of species interact with the sediment matrix. Distribution into finer roots with higher tensile strength may create networks that reinforce sediment when subject to erosive forces (*i.e.* wave action) and may provide stronger anchorage in the dune making the plants less likely to be uprooted during storm events (Comino et al., 2010; De Baets et al., 2008).

Panicum was different overall compared to the other species, and generally fell into the middle along a continuum of root characteristics (with *Ammophila* and *Spartina* on one end and *Uniola* on the other). The root system surface area was normally distributed with tight clustering around the average root diameter, indicating low variability in root diameter. In general, *Panicum* has been relatively understudied despite the fact that it is often equally abundant as other dominant graminoids such as *Ammophila* and *Uniola* (Hacker et al., 2019, Riffe & Zinnert, unpublished data). *Panicum* may serve an important role in the dune environment both in erosional and ecological dynamics due to both its ubiquity and unique set of belowground features. Further investigation may provide greater insights into how the combination of characteristics in *Panicum* may drive its behavior in the dune environment.

Lastly, *Uniola* was similar to *Ammophila* in biomass and many aboveground characteristics. In root characteristics, however, it was generally quite different from the other species. It had large diameter roots, low RTD and SRL, and the weakest root tensile strength of the species studied. Given that the majority of its surface area was distributed in larger diameter roots and it had the lowest tensile strength values, it is possible that *Uniola* may be more susceptible to being uprooted during storm events. However, its generally high root biomass may compensate for the low tensile strength of its root system and assist in anchorage; the effects of total root biomass and factors such as rooting density on tensile strength in dune grasses should be directly studied (Comino et al., 2010; De Baets et al., 2008).

Belowground characteristics may be of further importance for understanding observations of dominant species behavior and effects on the dune environment. For example, despite similarities in vertical growth response to burial, *Ammophila* and *Uniola* are known to facilitate different dune morphologies through differences in lateral growth patterns (Goldstein et al., 2017, Stallins & Parker, 2003). *Ammophila*—known to exhibit rapid lateral growth—can drive the formation of continuous dune ridges under the right conditions. Rapid lateral growth is common in clonal grasses as a foraging strategy—especially in low-nutrient environments such as dune systems—and clonal growth via rhizomes is often utilized as a way to exploit nutrient pockets (*reviewed in* Klimešová et al., 2018). The significantly greater rhizome length and biomass of *Ammophila* demonstrated in this study supports the possibility that rapid clonal growth in *Ammophila* may be a nutrient foraging strategy. High SRL indicates a greater allocation to root length per unit biomass—a characteristic typically attributed to enhanced root exploration of the soil—providing greater evidence that *Ammophila* may be strongly adapted for locating and exploiting nutrient pockets in the low-nutrient dune environment (Reijers et al., 2020; Roumet et al., 2016). Indeed, rapid exploitation of nutrient pockets has even been observed in *Ammophila* through its occasional predation of diamondback terrapin nests (Lazell & Auger, 1981).

This example illustrates how understanding ecological behaviors of these species through measurable physiological adaptations can provide context and drivers for how species interact with the dune environment. Measuring these adaptations by quantifying both above- and belowground characteristics may be important for understanding species-specific effects. Rather than demonstrating convergence, the four dominant dune grass species examined in this study displayed dissimilar suites of characteristics. The fact that no two species were identical in above- and belowground characteristics may illustrate that these species have adapted to exploit different niches in the dune environment. The adaptations that arise from differential niche exploitation are the vary features that ultimately result in species-specific interactions with the dune environment. Quantifying these characteristics are therefore critical to a more thorough understanding of these complex dynamics.

The belowground species differences found in my study demonstrate the potential importance of considering characteristics and traits in addition to raw biomass for understanding complex interactions between dominant plants and dune dynamics. The four species specifically examined for these characteristics are often considered jointly as the graminoid functional group in community assessments. However, these data demonstrate that the intrinsic differences in the suite of characteristics among these dominant graminoids may be ecologically significant. A more detailed understanding of characteristics and traits exhibited by dominant functional groups and knowledge of species differences may be necessary for interpreting overall plant community effects in coastal dunes. The suite of characteristics, ecological behavior, and emergent effects on erosional dynamics exhibited by graminoids are highly complex and frequently species-specific. Further, mycorrhizae are known to have their own significant effects on erosional and ecological dynamics, and differences in mycorrhizal associations among these four species may also be important for understanding intra- and interspecific relationships that drive dune dynamics (Mardhiah et al., 2015; Mariotte et al., 2012; Burri et al., 2011; Rillig & Mummey, 2006; Gregory, 2000; Grime et al., 1987).

Natural dune ecosystems are highly complex and dynamic with many intra- and interspecific interactions existing in tandem with and in response to site-specific history and erosional forces. Erosional dynamics within dune systems are similarly complex, arising from interactions between morphology, sediment dynamics, vegetation, dominant forces, and storm activity (Brodie et al., 2019; Cohn et al., 2018; Biel et al., 2017; Goldstein et al., 2017; Feagin et al., 2015; Sigren et al., 2014). As illustrated by the foredune at Duck, FRF, the way in which abiotic and biotic components of natural dune systems ultimately drive the emergent characteristics of the system are highly complex. This is the first study to quantify belowground characteristics of dominant dune graminoids, however relatively little is known about how these characteristics may ultimately interact with erosional forces. Future studies will utilize these data in conjunction with dune coring to model species-specific interactions with dune erosion. Continuing investigation into these differences may provide critical information for understanding how both the above- and belowground interactions of dominant species affect erosional dynamics in these complex ecosystems.

Figures

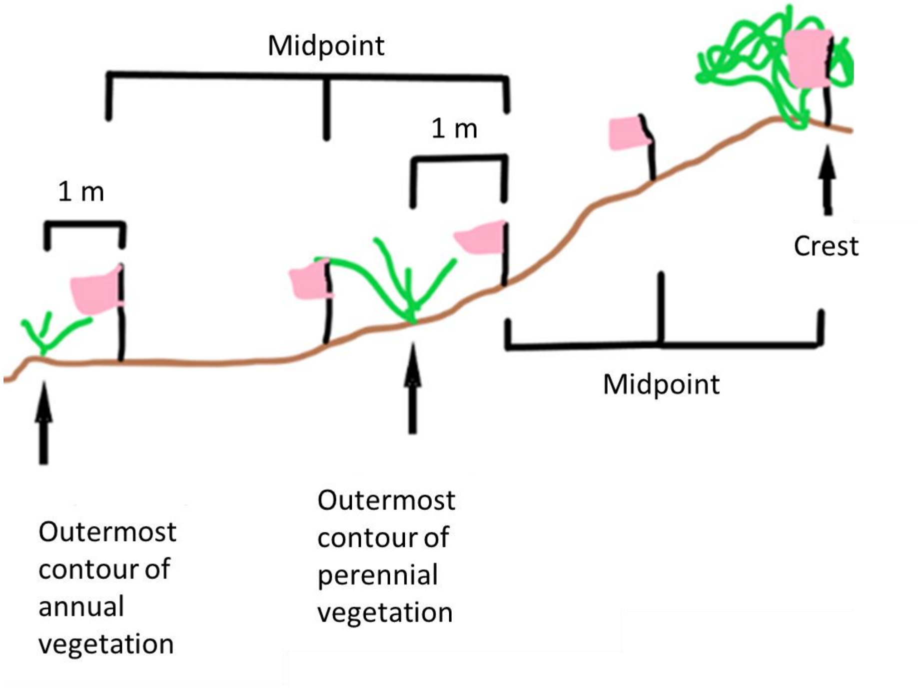

Figure 1. Illustration of plot locations along a given transect. Pink flags represent the location of the northwest corner for each plot.

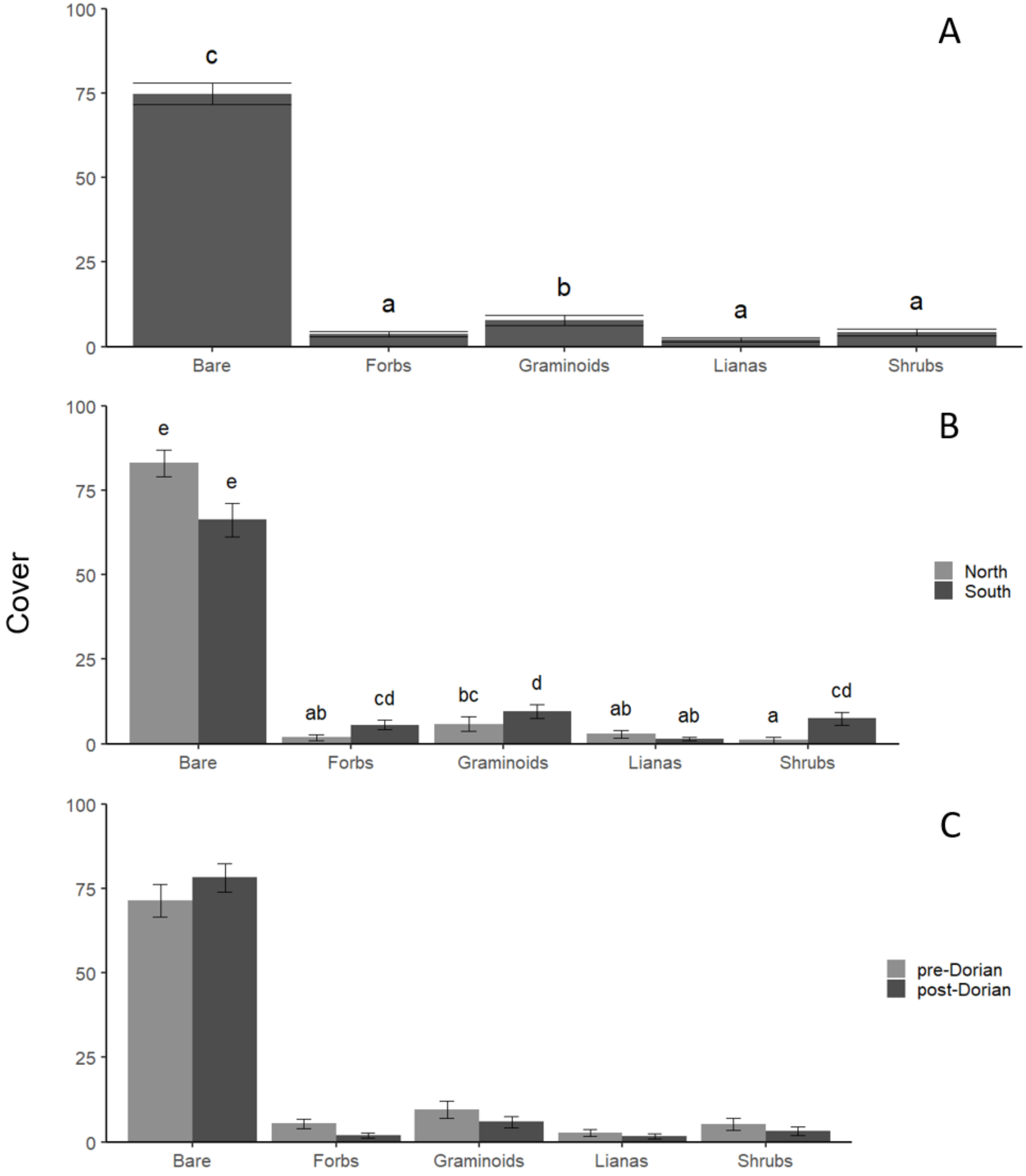

Figure 2. Bar graph (mean ± SE) of cover by functional group across the entire site (A), between north and south locations (B), and pre- and post-Hurricane Dorian (C). Letters denote post hoc differences across functional groups for the entire site (A) and of the significant interaction between location and functional group (B).

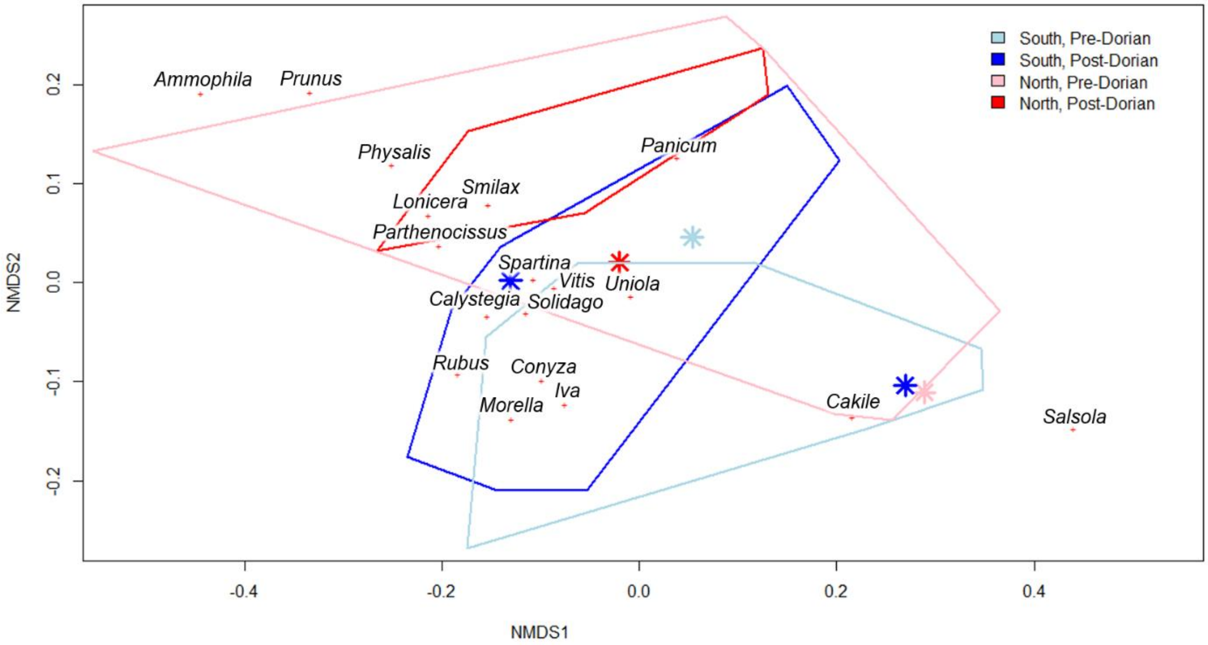

Figure 3. NMDS based on Bray-Curtis dissimilarity (k = 3, stress = 0.08) of species cover showing plots grouped by north and south locations as well as pre- and post-Hurricane Dorian. Species are denoted by their genus.

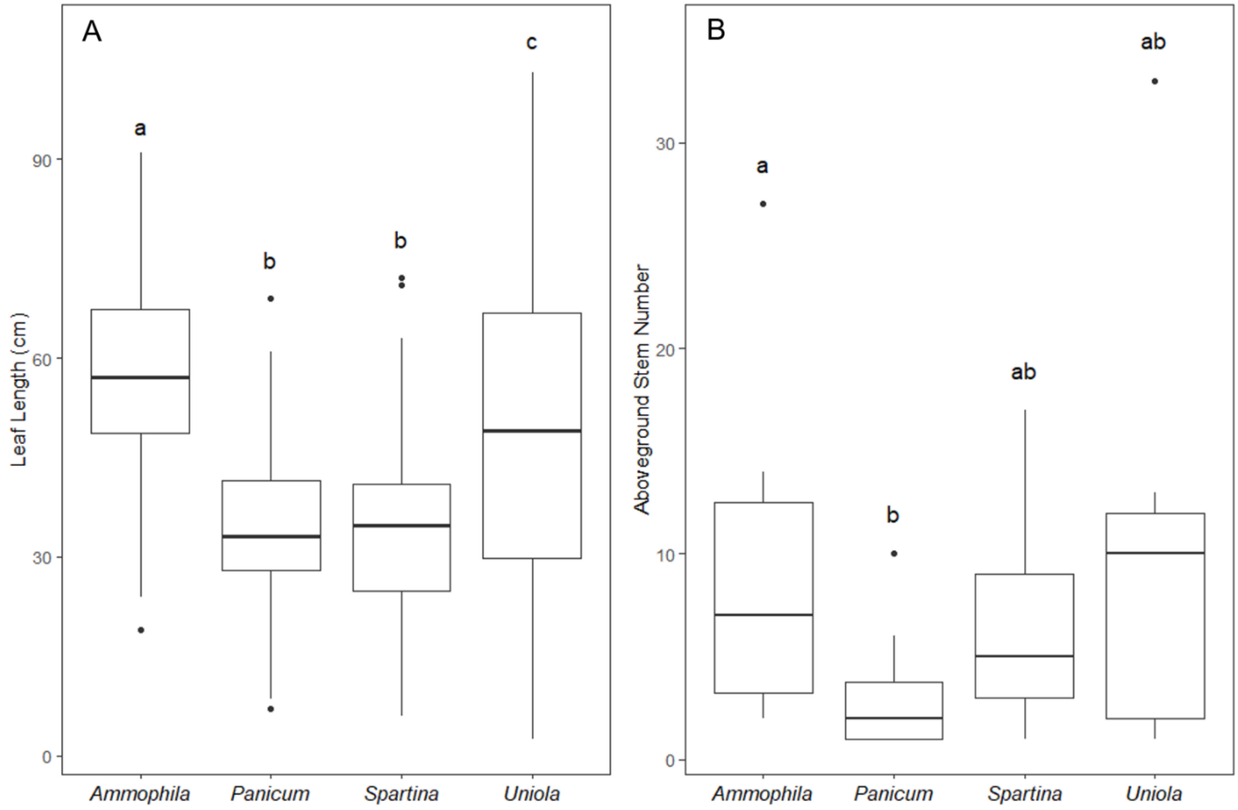

Figure 4. Leaf length (cm) (A) and aboveground stem number (B) differ significantly among focal species.

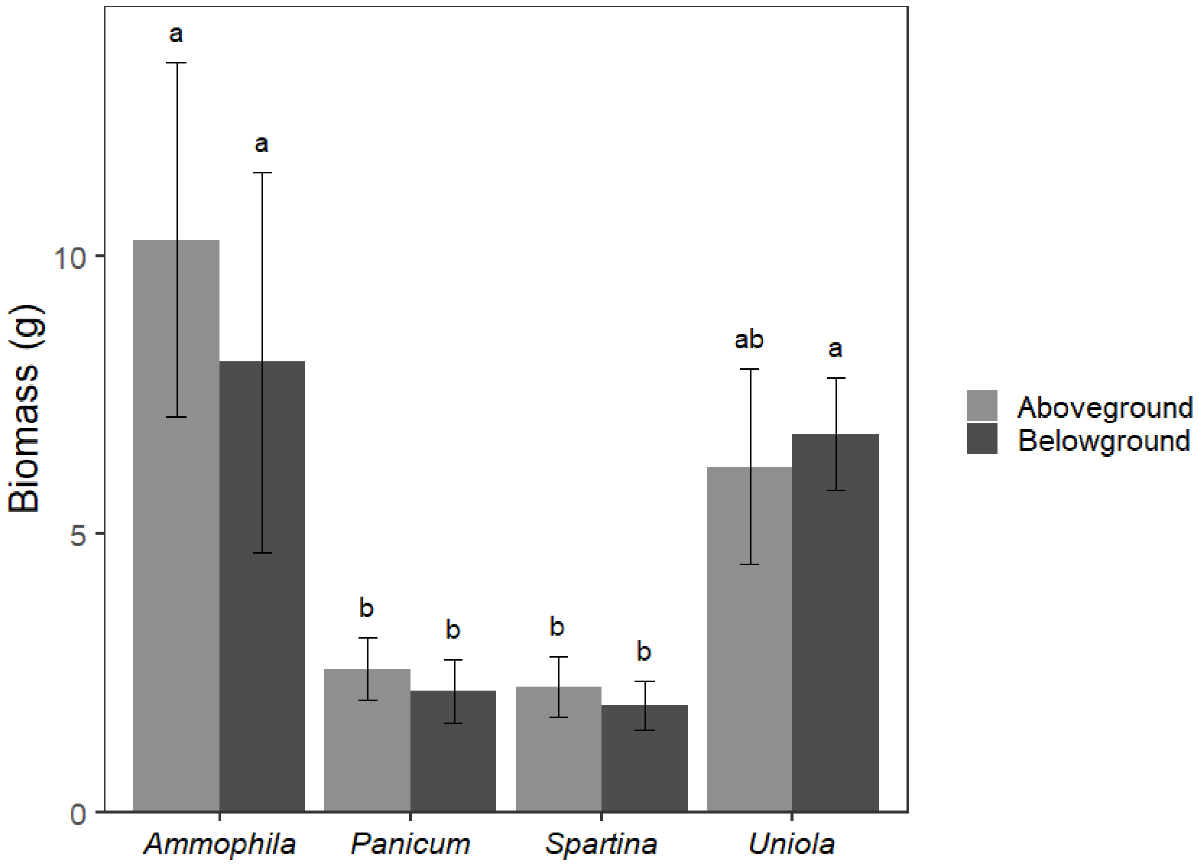

Figure 5. Above- (light grey) and belowground biomass (dark grey) for focal species (mean ± SE). Compact letter display (CLD) shows differences between species in above- and belowground biomass allocation.

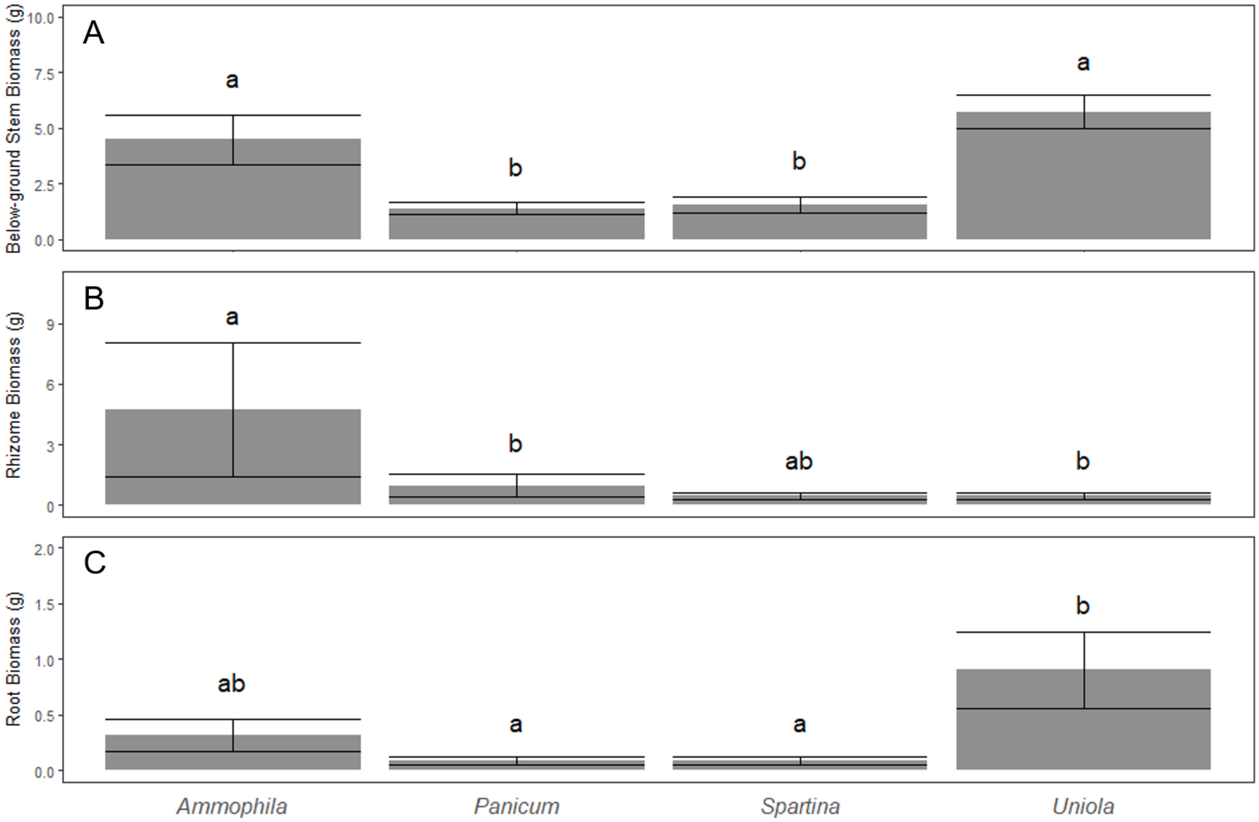

Figure 6. Belowground biomass (mean ± SE) for focal species divided into the three major components—belowground stems (A), rhizomes (B), and roots (C).

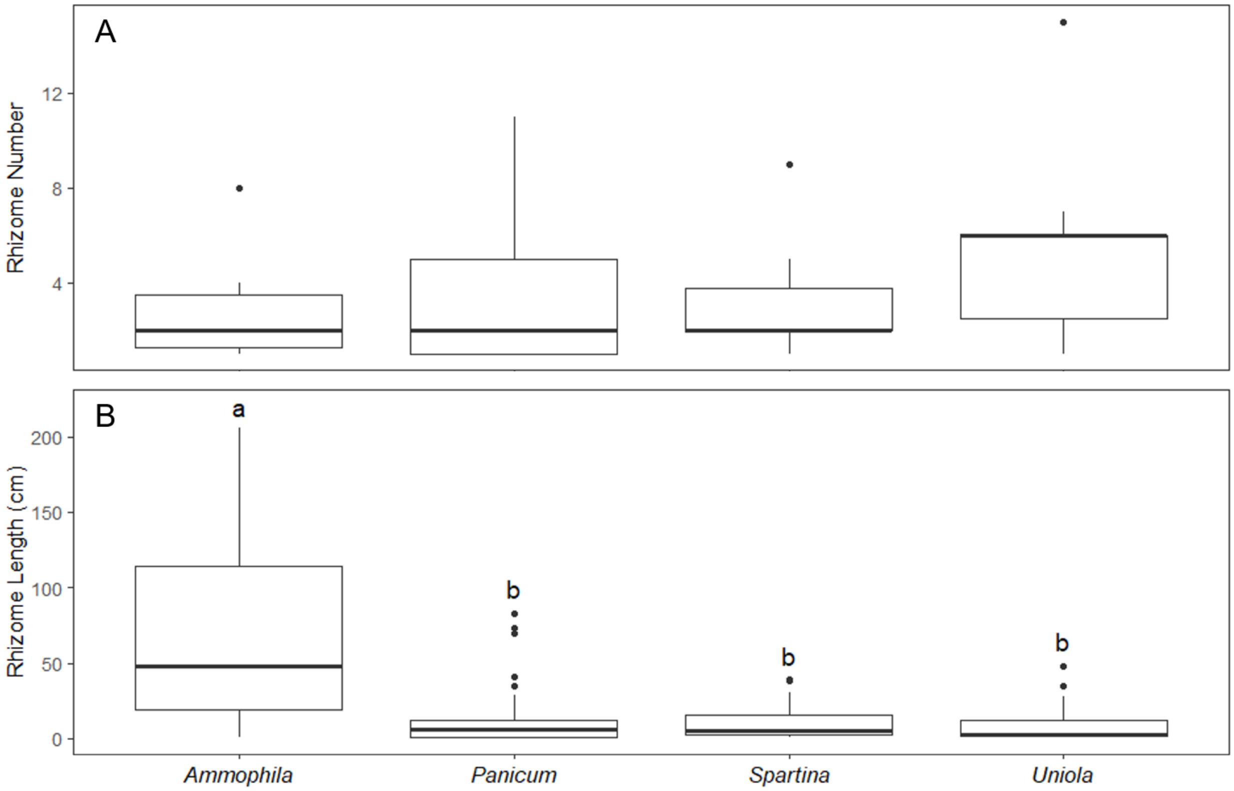

Figure 7. Rhizome number (A) and length (cm) (B) for each species. *Ammophila* possessed significantly longer rhizomes than the other species.

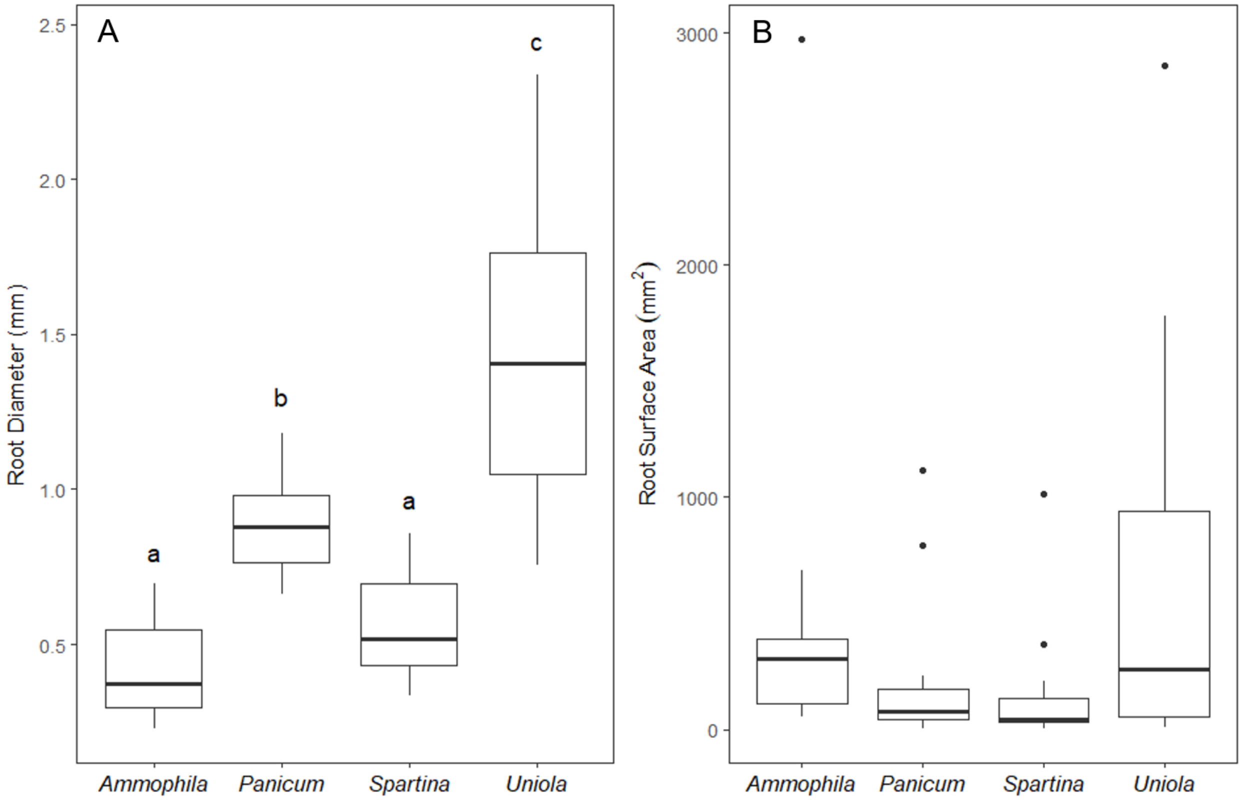

Figure 8. Root average diameter (A) and surface area per species (B).

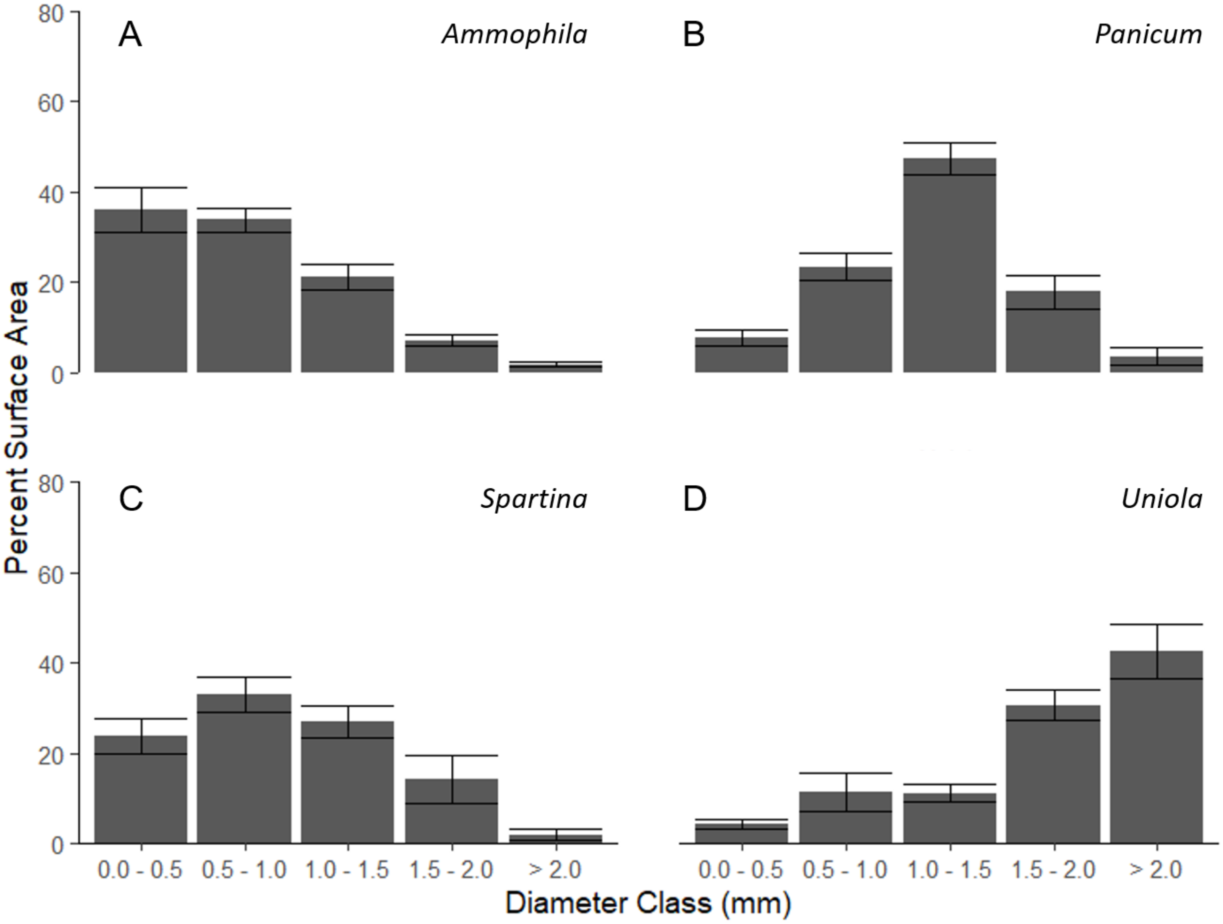

Figure 9. The percent root surface area (mean ± SE) divided into five diameter size classifications for *Ammophila* (A), *Panicum* (B), *Spartina* (C), *and Uniola* (D).

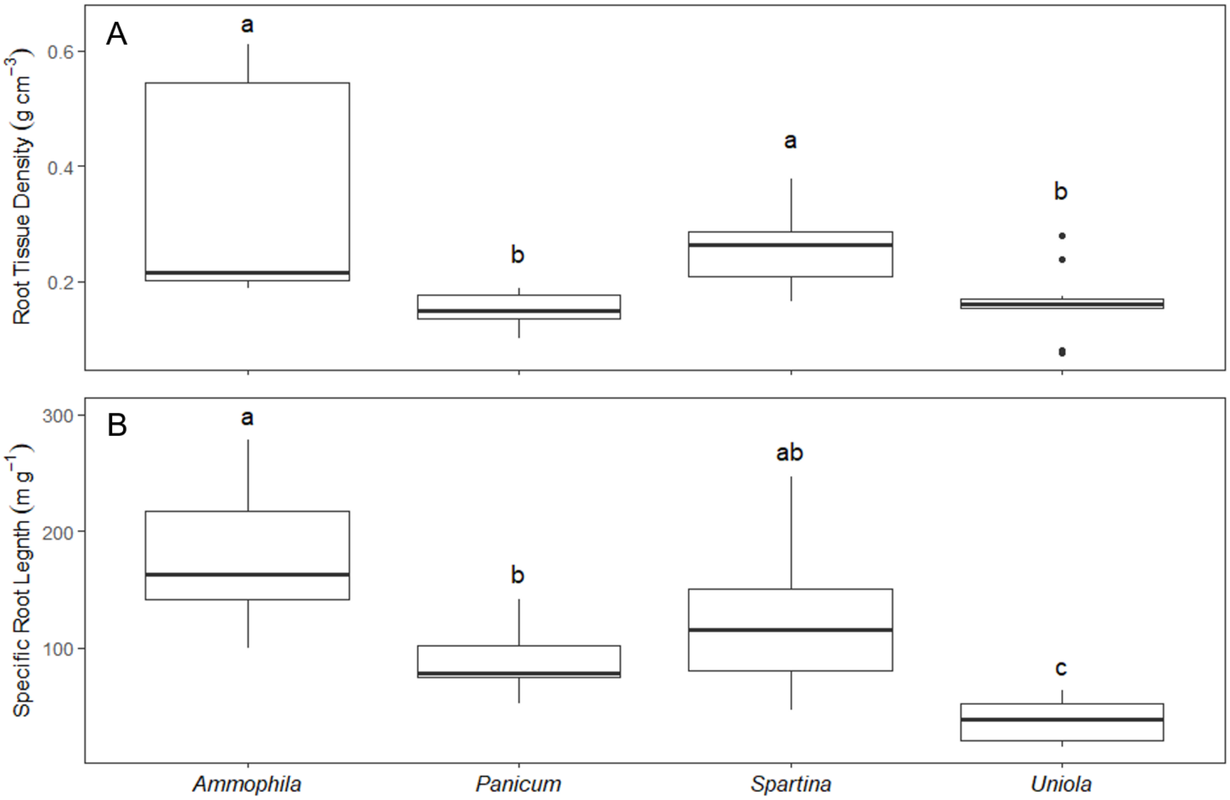

Figure 10. Root tissue density (RTD; gcm^{-3}) (A) and specific root length (SRL; mg^{-1}) (B) for the four focal species.

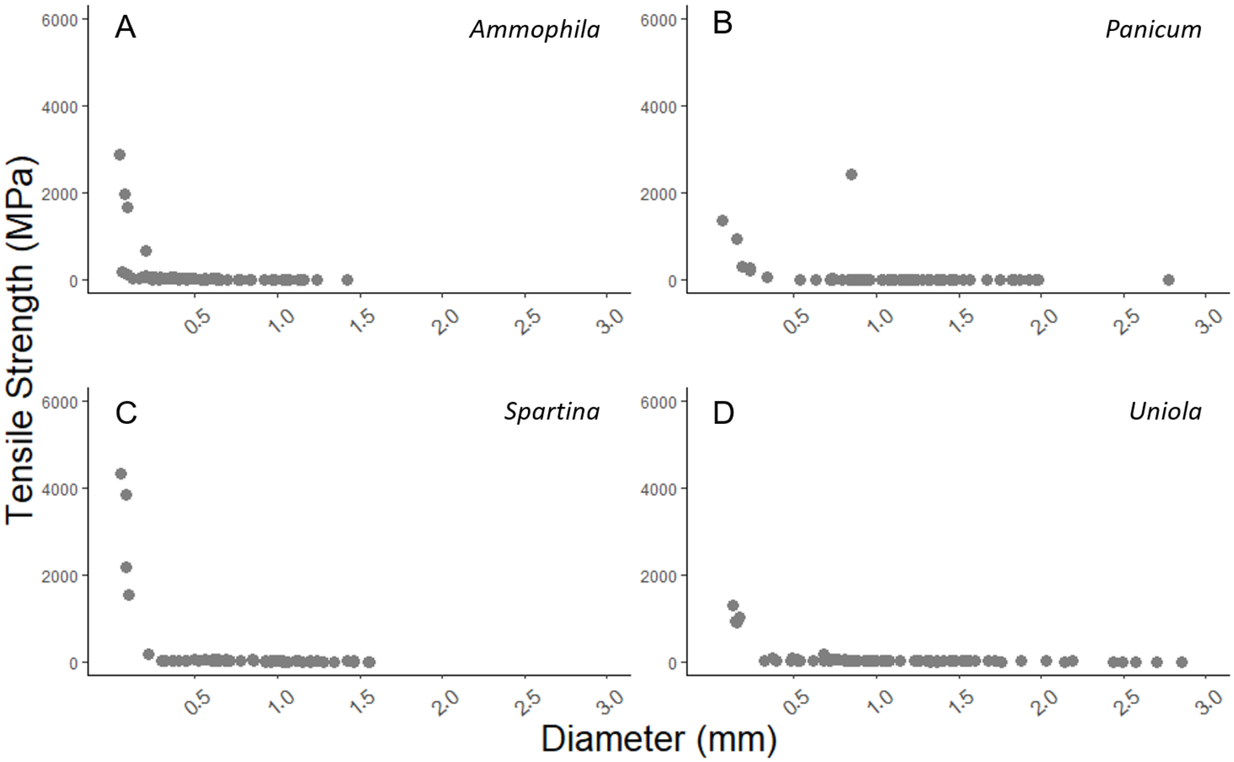

Figure 11. Tensile strength (MPa) of roots by diameter (mm) for *Ammophila* (A), *Panicum* (B), *Spartina* (C), and *Uniola* (D). Roots follow a logarithmic trend from large to small diameter, with the greatest tensile strength values in roots less than 0.5 mm in diameter. *Ammophila* and *Spartina* exhibit the highest maximum tensile strength values of the four species.

Tables

Table 1. Overall species cover and functional group identity for all species and bare sand along transects. Species not present in a location are denoted with NA.

Species	Functional Group	Overall Mean Cover (%)	Overall SE	North Mean Cover (%)	North SE	South Mean Cover (%)	South SE
Bare sand	NA	74.8	3.2	83.1	3.9	66.2	4.9
Spartina patens	Graminoid	4.5	1.0	3.3	1.4	5.7	1.3
Uniola paniculata	Graminoid	1.6	0.7	0.2	0.2	2.9	1.3
Panicum amarum	Graminoid	1.6	0.5	2.1	0.9	1.0	0.5
Ammophila breviligulata	Graminoid	0.1	0.1	0.2	0.1	> 0.1	> 0.1
Iva imbricata	Shrub	3.6	1.0	NA	NA	7.3	1.9
Prunus serotina	Shrub	0.5	0.5	1.1	0.9	NA	NA
Morella pensylvanica	Shrub	0.1	0.1	NA	NA	0.2	0.2
Solidago sempervirens	Forb	1.6	0.6	0.6	0.5	2.7	1.1
Cakile edentula	Forb	1.5	0.6	0.8	0.6	2.2	0.9
Physalis walteri	Forb	0.3	0.1	0.5	0.3	0.1	0.1
Calystegia soldanella	Forb	0.2	0.1	NA	NA	0.3	0.2
Conyza canadensis	Forb	0.1	0.1	NA	NA	0.1	0.1
Salsola kali	Forb	0.0	0.0	NA	NA	> 0.1	> 0.1
Smilax bona-nox	Liana	1.3	0.4	1.9	0.7	0.6	0.3
Lonicera japonica	Liana	0.5	0.2	0.6	0.4	0.4	0.3
Vitis labrusca	Liana	0.1	0.1	NA	NA	0.2	0.2
Parthenocissus quinquefolia	Liana	0.3	0.2	0.4	0.3	0.1	0.1
Rubus trivialis	Liana	0.0	0.0	NA	NA	0.1	0.1

Table 2. 3-way ANOVA results of log-transformed cover where Functional Group = functional groups (grasses, forbs, lianas, and shrubs), Location = north and south locations on the foredune, and Sampling = pre- and post-Dorian collection times. Significant p-values are given in bold.

Effects	DF	SS	F-value	p-value
Functional Group	4	386.22	147.20	< **0.0001**
Location	1	11.68	17.80	< **0.0001**
Sampling	1	2.06	3.14	0.08
Functional Group X Location	4	14.54	5.54	**0.0002**
Functional Group X Sampling	4	5.24	2.00	0.09
Location X Sampling	1	0.49	0.74	0.40
Functional Group X Location X Sampling	4	0.61	0.23	0.92
Residuals	470	308.30		

Table 3. 2-way ANOVA results of square-root-transformed percent root surface area. Significant p-values are given in bold.

Effects	DF	SS	F-value	p-value
Diameter Class	4	224.74	31.28	< **0.0001**
Species	3	1.28	0.24	0.87
Species X Diameter Class	12	539.62	25.03	< **0.0001**
Residuals	215	386.22		

Table 4. Linear regression model components for log-transformed tensile strength data. Significant p-values are given in bold. CLD shows the results of ANCOVA interaction between species and root diameter with differences in slope between species evaluated using a Tukey's HSD post hoc.

Species	Slope	Y - Intercept	r^2	p-value	Post hoc
Ammophila	-1.57	2.28	0.62	< **0.0001**	a
Panicum	-1.06	2.24	0.51	< **0.0001**	b
Spartina	-1.65	2.7	0.65	< **0.0001**	a
Uniola	-0.64	1.99	0.56	< **0.0001**	c

References

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological monographs, 81*(2), 169-193. https://doi.org/10.1890/10-1510.1

Biel, R. G., S. D. Hacker, Ruggiero, P., Cohn, N., & Seabloom E. W. (2017). Coastal protection and conservation on sandy beaches and dunes: context-dependent tradeoffs in ecosystem service supply. *Ecosphere, 8*(4). https://doi.org/10.1002/ecs2.1791

Birkemeier, W., Dolan, R., & Fisher, N. (1984). The evolution of a barrier island: 1930–1980. *Shore Beach, 52*, 2–12.

Böhm W. (1979). *Methods of studying root systems*. New York: Springer-Verlag.

Brantley, S. T., Bissett, S. N., Young, D. R., Wolner, C. W. V., & Moore, L. J. (2014). Barrier island morphology and sediment characteristics affect the recovery of dune building grasses following storm-induced overwash. *PLOSone, 9*(8), 1-12. https://doi.org/10.1371/journal.pone.0104747

Brodie, K., Conery, I., Cohn, N., Spore, N., & Palmsten, M. (2019). Spatial variability of coastal foredune evolution, part A: timescales of months to years. *Journal of Marine Science and Engineering, 7*(5), 124. https://doi.org/10.3390/jmse7050124

Brown, J. K., & Zinnert, J. C. (2018). Mechanisms of surviving burial: Dune grass interspecific differences drive resource allocation after sand deposition. *Ecosphere, 9*(3), p.e02162. https://doi.org/10.1002/ecs2.2162

Bryant, D. B, Bryant, M. A., Sharp, J. A., Bell, G. L., & Moore, C. (2019). The response of vegetated dunes to wave attack. *Coastal Engineering, 152*, 1-8. https://doi.org/10.1016/j.coastaleng.2019.103506

Burri, K., Gromke, C., & Graf, F. (2011). Mycorrhizal fungi protect the soil from wind erosion: a wind tunnel study. *Land Degradation & Development, 24*, 385-392. https://doi.org/10.1002/ldr.1136

Charbonneau, B. R., Wootton, L. S., Wnek, L. P., Langley, J. A., & Posner, M. A. (2017). A species effect on storm erosion: invasive sedge stabilized dunes more than native grass during Hurricane Sandy. *Journal of Applied Ecology, 54*(5), 1385-1394. https://doi.org/10.1111/1365-2664.12846

Charbonneau, B. R., Wnek, J. P., Langley, J. A., Lee, G., & Balsamo, R. A. (2016). Above vs. belowground plant biomass along a barrier island: implications for dune stabilization. *Journal of Environmental Management, 182*, 126-133. https://doi.org/10.1016/j.jenvman.2016.06.032

Charbonneau, B. R. (2015). A Review of Dunes in Today's Society. *Coastal Management, 43*(5), 465-470. https://doi.org/10.1080/08920753.2015.1051419

Cohn, N., Ruggiero, P., de Vries, S., & Kaminsky, G. M. (2018). New insights on coastal foredune growth: the relative contributions of marine and aeolian processes. *Geophysical Research Letters, 45*, 4965-4973. https://doi.org/10.1029/2018GL077836

Comino, E., Marengo, P., & Rolli, V. (2010). Root reinforcement effect of different grass species: A comparison between experimental and model results. *Soil & Tillage Research, 110*, 60-68. https://doi.org/10.1016/j.still.2010.06.006

Day, F. P., Crawford, E. R., & Dilustro, J. J. (2001). Aboveground plant biomass change along a coastal barrier island dune chronosequence over a six-year period. *The Journal of the Torrey Botanical Society, 128*(3), 197-207. https://doi.org/10.2307/3088711

De Baets, S., Poesen, J., Reubens, B., Wemans, K., De Baerdemaeker, J., & Muys, B. (2008). Root tensile strength and root distribution of typical Mediterranean plant species and their contribution to soil shear strength. *Plant Soil, 305*, 207-226. https://doi.org/10.1007/s11104-008-9553-0

De Battisti, D., & Griffin, J. N. (2019). Below-ground biomass of plants, with a key contribution of buried shoots, increases foredune resistance to wave swash. *Annals of Botany, 125*(2), 325-334. https://doi.org/10.1093/aob/mcz125

Durán, O., & Moore, L. J. (2013). Vegetation controls on the maximum size of coastal dunes. *PNAS, 110*(43), 17217-17222. https://doi.org/10.1073/pnas.1307580110

Feagin, R.A., Figlus, J., Zinnert, J.C., Sigren, J., Martínez, M.L., Silva, R., Smith, W.K., Cox, D., Young, D.R. & Carter, G. (2015). Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. *Frontiers in Ecology and the Environment, 13*(4), 203-210. https://doi.org/10.1890/140218

Feagin, R. A., Sherman, D. J., & Grant, W. E. (2005). Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. *Frontiers in Ecology and the Environment, 3*(7), 359-364. https://doi.org/10.1890/140218

Goldstein, E. B., Mullins, E. V., Moore, L. J., Biel, R. G., Brown, J. K., Hacker, S. D., Jay, K. R., Mostow, R. S., Ruggiero, P., & Zinnert, J. C. (2018). Literature-based latitudinal distribution and possible range shifts of two US east coast dune grass species (*Uniola paniculata* and *Ammophila breviligulata*). *PeerJ, 6*, e4932. https://doi.org/10.7717/peerj.4932

Goldstein, E. B., Moore, L. J., & Orencio D. V. (2017). Lateral vegetation growth rates exert control on coastal foredune "hummockiness" and coalescing time. *Earth Surface Dynamics, 5*, 417-427. https://doi.org/10.5194/esurf-5-417-2017

Gregory, P. J. (2000). Physical changes in the rhizosphere and their significance for plant-soil interactions. *Acta Agronomica Hungarica, 48*(1), 107-112. https://doi.org/10.1556/AAgr.48.2000.1.12

Grime, J. P., Mackey, J. M. L., Hillier, S. H., & Read, D. J. (1987). Floristic diversity in a model system using experimental microcosms. *Nature, 328*, 420-422.

Hacker, S. D., Jay, K. R., Cohn, N., Goldstein, E. B., Hovenga, P. A., Itzkin, M., Moore, L. J., Mostow, R. S., Mullins, E. V., & Ruggiero, P. (2019). Species-specific functional morphology of four US Atlantic coast dune grasses: biogeographic implications for dune shape and coastal protection. *Diversity, 11*(5), 82. https://doi.org/10.3390/d11050082

Klimešová, J., Martínkova, J., & Ottaviani, G. (2018). Belowground plant functional ecology: Towards an integrated perspective. *Functional Ecology, 32*, 2115-2126. https://doi.org/10.1111/1365-2435.13145

Kuriyama, Y., Mochizuki, N., & Nakashima, T. (2005). Influence of vegetation on aeolian sand transport rate from a backshore to a foredune at Hasaki, Japan. *Sedimentology, 52*, 1123-1132. https://doi.org/

Lazell, J. D., & Auger, P. J. (1981). Predation on Diamondback Terrapin (Malaclemys terrapin) Eggs by Dunegrass (Ammophila breviligulata). *Copeia*, *1981*(3), 723-724. https://doi.org/10.2307/1444585

Mardhiah, U., Caruso, T., Gurnell, A., & Rillig, M. C. (2015). Arbuscular mycorrhizal fungal hyphae reduce soil erosion by surface water flow in a greenhouse experiment. *Applied Soil Ecology, 99*, 137-140. https://doi.org/10.1016/j.apsoil.2015.11.027

Mariotte, P., Meugnier, C., Johnson, D., Thébault, A., Spiegelberger, T., & Buttler, A. (2012). Arbuscular mycorrhizal fungi reduce the differences in competitiveness between dominant and subordinate plant species. *Mycorrhiza, 23*, 267-277. https://doi.org/10.1007/s00572-012-0465-8

Maximiliano-Cordova, C., Salgado, K., Martínez, M. L., Mendoza, E., Silva, R., Guevara, R., & Feagin, R. A. (2019). Does the functional richness of plants reduce wave erosion on embryo coastal dunes? *Estuaries and Coasts, 42*, 1730-1741. https://doi.org/10.1007/s12237-019-00537-x

Moore, L. J., Patsch, K., List, J. H., & Williams, S. J. (2014). The potential for seal-level-rise-induced barrier island loss: insights from the Chandeleur Islands, Louisiana, USA. *Marine Geology, 355*, 244-259. https://doi.org/10.1016/j.margeo.2014.05.022

Moreno-Espíndola, I. P., Rivera-Becerril, F., de Jesús Ferrara-Guerrero, M., & De León-González, F. (2007). Role of root-hairs and hyphae in adhesion of sand particles. *Soil Biology & Biochemistry, 39*, 2520-2526. https://doi.org/10.1016/j.soilbio.2007.04.021

Mullins, E., Moore, L. J., Goldstein, E. B., Jass, T., Bruno, J., & Vinent, O. D. (2019). Investigating dune-building feedback at the plant level: Insights from a multispecies field experiment. *Earth Surface Processes and Landforms, 44*(9), 1734-1747. https://doi.org/10.1002/esp.4607

Nordstrom, K. F., Jackson, N. L., Bruno, M. S. and de Butts, H. A., 2002. Municipal initiatives for managing dunes in coastal residential areas: a case study of Avalon, New Jersey, USA. *Geomorphology, 47*(2-4), 137-152. https://doi.org/10.1016/S0169-555X(02)00084-3

Ranasinghe, R. (2016). Assessing climate change impacts on open sandy coasts: A review. *Earth-Science Reviews, 160*, 320-332. https://doi.org/10.1016/j.earscirev.2016.07.011

Reijers, V. C., Lammers, C., de Rond, A. J. A., Hoetjes, S. C. S., Lamers, L. P. M., & van der Heide, T. (2020). Resilience of beach grasses along a biogeomorphic successive gradient: resource availability vs. clonal integration. *Oecologia, 192*, 201-212. https://doi.org/10.1007/s00442-019-04568-w

Reubens, B., Poesen, J., Danjon, F., Geudens, G., & Muys, B. (2007). The role of fine and coarse roots in shallow slope stability and soil erosion control with a focus on root system architecture: a review. *Trees*, *21*, 385-402. https://doi.org/10.1007/s00468-007-0132-4

Rillig, M. C. & Mummey, D. L. (2006). Tansley review: micorrhizas and soil structure. *New Phytoloist, 171,* 41-53. https://doi.org/10.1111/j.1469-8137.2006.01750.x

Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrignon-Brenas, S., Cao, K., & Stokes, A. (2016). Root structure-function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. *New Phytologist*, *210*, 815-826. https://doi.org/10.1111/nph.13828

Stallins, J. A., & Parker, A. J. (2003). The influence of complex systems interactions on barrier island dune vegetation pattern and process. *Annals of the Association of American Geographers*, *93*(1), 13-29. https://doi.org/10.1111/1467-8306.93102

Sigren, J. M., Figlus, J., & Armitage, A. R. (2014). Coastal sand dunes and dune vegetation: restoration, erosion, and storm protection. *Shore & Beach*, *82*(4), 5-12.

Silva, R., Martínez, M. L., Odériz, I., Mendoza, E., & Feagin, R. A. (2016). Response of vegetated dune-beach systems to storm conditions. *Coastal Engineering*, *109*, 53-62. https://doi.org/10.1016/j.coastaleng.2015.12.007

Vousdoukas, M. I., Ranasinghe, R., Mentaschi, L., Plomaritis, T. A., Athanasiou, P., Luijendijk, A., & Feyen, L. (2020). Sandy coastlines under threat of erosion. *Nature Climate Change*, *10*, 260-263. https://doi.org/10.1038/s41558-020-0697-0

Zarnetske, P. L., Ruggiero, P., Seabloom, E. W., & Hacker, S. D. (2015). Coastal foredune evolution: the relative influence of vegetation and sand supply in the US Pacific Northwest. *Journal of the Royal Society Interface*, *12*(106), 20150017. https://doi.org/10.1098/rsif.2015.0017

Vita

Shannon Louise Walker was born in Richmond, VA in 1995 to Susan and David Walker. She graduated from Hancock High School, Hancock Co., MS in 2013. She received a Bachelor of Science in Biological Science, emphasis in Environmental Biology, with a Minor in Chemistry, Summa Cum Laude, from The University of Southern Mississippi in 2017. From 2015 to 2017, she worked at Lake Thoreau Environmental Center assisting with research projects, community outreach programs, and management of native Longleaf Pine habitat. While pursuing her B.S., she completed an undergraduate Honors Thesis which characterized an unusual population of an endangered, semi-aquatic plants native to the southeastern United States. While pursuing her undergraduate thesis work, she was awarded the USM Eagle Scholars Program for Undergraduate Research Award. She then worked as an intern at Weeks Bay National Estuarine Research Reserve in Fairhope, AL from 2017 to 2018. During the internship, she collected and managed data for the System Wide Monitoring Program (SWMP), assisted with outreach programs and research projects, and initiated a microplastics monitoring program. She will receive her Master of Science in Biology from Virginia Commonwealth University in 2020 and anticipates continuing to pursue her education and research in plant ecology.