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ARTICLE

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Whole plant traits of coastal dune vegetation and implications for interactions with dune dynamics

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Abstract

Coastal dunes are important protective features against sea level rise and coastal storms. Interactions between dune plant aboveground structures and sediment trapping that allow for dune building and maintenance are well established. More recently, studies documenting belowground biomass for promoting erosion resistance in dominant dune species have been conducted, yet a knowledge gap remains regarding species-specific characterization of whole plants, specifically with respect to roots, rhizomes, and belowground stems. Our objective was to quantify above- and belowground traits of four dominant dune grasses to document the potential for species-specific effects on dune growth, maintenance, and erosion resistance. We examined above- and belowground traits among four prominent dune grasses of the Atlantic and Gulf Coasts of North America: *Ammophila breviligulata*, *Panicum amarum*, *Spartina patens*, and *Uniola paniculata*. Whole plant samples of each species were collected from the foredune at the US Army Engineer Research and Development Center's Field Research Facility in Duck, North Carolina, USA, and quantified for several above- and belowground traits (e.g., stem height, rhizome number and length, root surface area by diameter class, root tensile strength, and mycorrhizal percent infection). Belowground factors known to impact important dune processes, such as rhizome length, mycorrhizal percent infection, and root traits, differed substantially among species. When visualized in multivariate space, all species significantly differed in suites of above- and belowground traits. When considering belowground only, *Ammophila* and *Spartina* were similar, despite differences in biomass allocation. Species separated along axes related to mycorrhizal association, biomass allocation, and root construction. The four co-occurring dune grass species were dissimilar in suites of plant traits. Belowground trait differences were driven by those describing root construction, biomass allocation, and mycorrhizal infection.

Dissimilarity in above- and belowground suites of traits may demonstrate different approaches for surviving the dune environment. Incorporating belowground traits into modeling will enhance predictions of dune response to climate change through interactions between vegetation and dune dynamics that facilitate coastal resistance and resilience.

KEYWORDS

aboveground, *Ammophila breviligulata*, belowground, diameter class, dunes, erosion, mycorrhizae, *Panicum amarum*, root traits, *Spartina patens*, tensile strength, *Uniola paniculata*

INTRODUCTION

Coastal sand dune ecosystems serve many important roles in coastal protection, including attenuation of storm-driven wave energy (Carter, 1991; Hanley et al., 2020; Hesp, 1989; Morris et al., 2018). The role of vegetation in stabilizing dunes during collisional impacts (e.g., Feagin et al., 2015) and protection of dunes from interior flooding (e.g., Sallenger, 2000) has led to construction of sand dunes for coastal defense (Hanley et al., 2020; Morris et al., 2018; Nordstrom et al., 2002). Coastal ecosystems are experiencing a variety of disturbances due to the effects of sea level rise and changing storm characteristics, often leading to increased erosion (e.g., Moore et al., 2014; Hanley et al., 2020; Vousdoukas et al., 2020). Coastal dune ecosystems are expected to be particularly vulnerable as dune dynamics are driven in part by local and regional oceanography and storm disturbance, which are altered by changing climate (Brodie et al., 2019; Carter, 1991; Cohn et al., 2018; Feagin et al., 2005, 2015; Hanley et al., 2020; Hesp, 1989). Due to the ecological importance of dunes for protecting human and natural communities, understanding factors that influence resistance and resilience (i.e., dune recovery) to erosive forces are important for predicting coastal response to climate change.

It is well established that with adequate sediment supply, eolian and hydrologically transported sediments accumulate around dune vegetation through interception by leaves and stems (Hesp, 2002; Hesp et al., 2019; Zarnetske et al., 2015). Vegetation can also alter physical forces, leading to greater sediment deposition and reduced sediment loss, an important role in facilitating dune development and dune recovery (Feagin et al., 2015; Hesp, 2002; Maximiliano-Cordova et al., 2019; Silva et al., 2016). Dune vegetative aboveground structures, such as stem height and density, affect the capacity of different species to trap sediments and interact with wind and wave energies (Feagin et al., 2015; Hesp, 2002; Hesp et al., 2019; Zarnetske et al., 2015). When plants experience burial events, allocation of biomass and subsequent growth and expansion processes differ among dune grass species (Brown & Zinnert, 2018; Reijers et al., 2021). Certain dune building grasses such as *Ammophila breviligulata*, *Ammophila arenaria*, and *Uniola paniculata* accrete greater amounts of sediment than other species, attributed to growth response to burial, aboveground characteristics (i.e., stem density, height, and cover), and shifting allocation from belowground biomass to aboveground biomass (Brown & Zinnert, 2018; Hacker et al., 2019; Reijers et al., 2019; Zarnetske et al., 2015).

Although the importance of aboveground structures of vegetation in dune sediment dynamics is well established, less is known about the contribution of belowground factors. Most studies of belowground vegetative structures examine the role of clonal spread via rhizomes and species clonal growth rates with impacts on dune morphology (Godfrey, 1977; Goldstein et al., 2018; Hesp, 2002). Differences in above- and belowground allocation patterns have been studied in response to nutrient enrichment and sand burial (e.g., Brown & Zinnert, 2018; Day, 1996; Dech & Maun, 2021). More recently, studies of belowground structures have demonstrated that belowground biomass is important for stabilizing sediments and reducing wave-induced erosion, with species having different effects (Bryant et al., 2019; Charbonneau et al., 2017; De Battisti & Griffin, 2020; Feagin et al., 2019). Still, relatively little is known about variation in belowground structures among species (apart from biomass) and whether potential differences may influence species-specific effects on dune processes.

Roots are particularly understudied in dunes, though they are known to play an important role in sediment dynamics through several mechanisms in many other systems (Comino et al., 2010; Gyssels et al., 2005; Reubens et al., 2007). Although roots represent only a small proportion of the total belowground biomass of many dune plants, the capacity of roots to influence sediment properties is disproportionate to their biomass (De Battisti & Griffin, 2020; Feagin et al., 2015; Gregory, 2006; Moreno-Espíndola et al., 2007; Reubens et al., 2007). For example, 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; Gregory, 2006; Reubens et al., 2007). Root tensile strength, the amount of pulling force a root can withstand before breaking, and architecture may also provide biomechanical reinforcement to dunes and provide anchorage to plants (Davidson et al., 2020; Gregory, 2006; Klimešová et al., 2018; Reubens et al., 2007). Roots also modify surrounding sediment (known as the rhizosphere) by introducing organic material through decomposition, exuding carbonaceous compounds that may bind sediments, and through associations with microbes including mycorrhizal fungi (Gregory, 2006; Moreno-Espíndola et al., 2007; Rillig & Mummey, 2006; Unger et al., 2017).

Associations with arbuscular mycorrhizal fungi (AMF) are nearly ubiquitous in the plant kingdom and thought to play a vital role in plant survival in dune ecosystems by increasing access to limited water and nutrient resources (Brundrett, 2002; Koske & Polson, 1984). The action of roots and AMF can stabilize sediments within the rhizosphere by increasing the cohesion among particles and adhering particles directly to root and hyphal structures (Gregory, 2006; Rillig & Mummey, 2006). These root system features alter key physical and chemical characteristics of the sediment (i.e., porosity, slope stability, and aggregation) and collectively may reduce the severity of dune scarping and resist uprooting of vegetation during disturbance events (Davidson et al., 2020; Gregory, 2006; Klimešová et al., 2018; Moreno-Espíndola et al., 2007).

Evaluating whole plant traits can provide quantitative measures of characteristics that may influence dune processes (e.g., plant height), and provide baseline measurements for modeling efforts (De Battisti, 2021; Temmerman et al., 2005). Our objective was to examine whole plant traits (aboveground and belowground) of four dominant dune species with a specific emphasis on root system traits due to lack of data. Our focal species, *A. breviligulata*, *Panicum amarum*, *Spartina patens*, and *U. paniculata*, hereafter referred to by their genera (Figure 1), are prevalent dune grasses in natural dunes of the Atlantic and Gulf Coasts of North America and frequently used in restoration efforts.

MATERIALS AND METHODS

Species

Ammophila (C3) has been long identified as the dominant dune building grass from North Carolina and northward along the Atlantic Coast of the United States (Goldstein et al., 2018; Figure 1). This species demonstrates a growth strategy in which long rhizomes or stolons allow for clonal units to be established farther from the parent plant. The rapid rhizomatous growth typical of this growth strategy may be important in facilitating the development of the generally linear dune ridges of the northern Atlantic coast (Godfrey, 1977; Goldstein et al., 2017). Along the southern Atlantic and Gulf Coasts, *Uniola* (C4) is known as the dominant dune building grass, with a northern range limit in North Carolina, USA (Godfrey, 1977; Goldstein et al., 2018). This species exhibits a phalanx growth strategy in which clonal units arise close to the parent plant resulting from

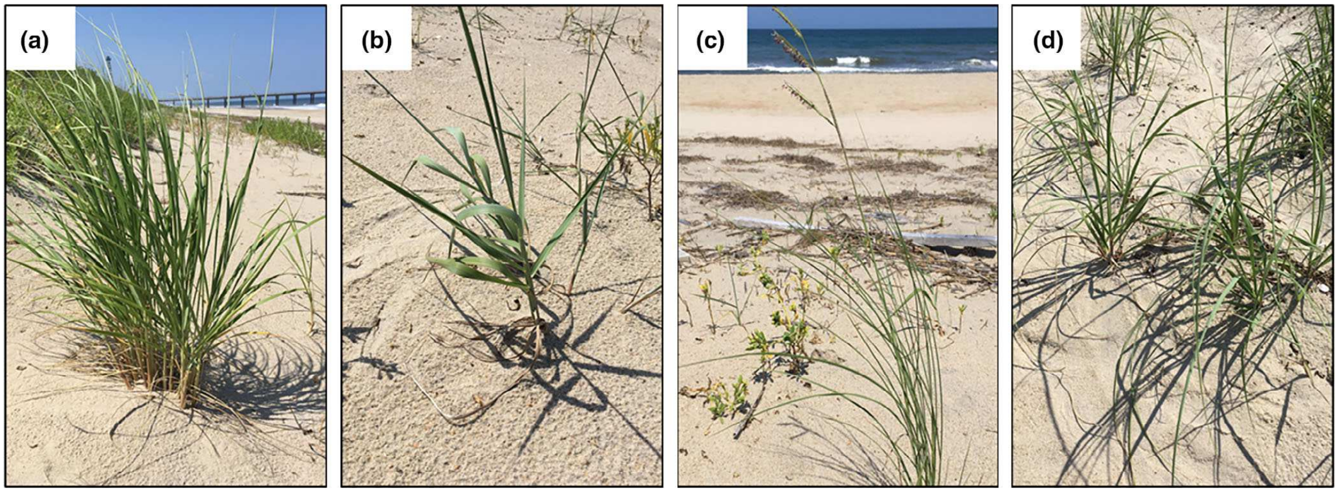

FIGURE 1 Images of focal species (a) *Ammophila breviligulata*, (b) *Panicum amarum*, (c) *Spartina patens*, and (d) *Uniola paniculata*. Images were taken on the foredune at the US Army Corps of Engineers Field Research Facility in Duck, North Carolina, USA (courtesy of Drew White)

slower rhizomatous expansion. This growth may lead to longer time to dune ridge coalescence leading hummocky dune fields rather than linear ridges (Godfrey, 1977; Goldstein et al., 2017; Stallins & Parker, 2003). *Uniola* is migrating northward due to warming temperatures, and the distributions of both *Uniola* and *Ammophila* overlap in North Carolina, USA, where sampling took place (Goldstein et al., 2018; Hacker et al., 2019). *Spartina* and *Panicum* are prevalent along both the Atlantic and Gulf Coasts. *Panicum* (C4) is frequently encountered on dune systems and can facilitate the development of small monocultural dunes with adequate sediment supply. *Spartina* (C4) is a generalist coastal grass species found in a variety of coastal habitats, including dunes, swales, and salt marshes (Godfrey, 1977). It has been identified as a moderate dune building grass, but also colonizes overwash flats (Brantley et al., 2014; Godfrey, 1977; Mullins et al., 2019).

Study site

Samples were collected from the US Army Engineer Research and Development Center (ERDC) Field Research Facility (FRF) located in Duck, North Carolina, USA (36.1820898, −75.7512527). The FRF is located on the Outer Banks chain of barrier islands on the US Atlantic seaboard. This microtidal system is frequently impacted by severe storms including hurricanes and Nor'easters, contributing to net negative shoreline changes in the region (Armstrong & Lazarus, 2019). The FRF contains a 1-km length of beach characterized by fine to coarse sand, with a median grain size of about 0.3 mm. A single foredune ridge was constructed in the 1930s and 1940s by the Civilian Conservation Corps and has since been unmanaged. Much of the Outer Banks is developed with frequent beach nourishment and dune planting projects, whereas the FRF property has been left in a natural state, a reason for selecting this particular site.

Field methods

Whole plant samples of *Ammophila* ($n = 10$), *Panicum* ($n = 18$), *Spartina* ($n = 13$), and *Uniola* ($n = 11$) were collected in June and July of 2019 by hand digging from the face of the main foredune ridge facing the Atlantic Ocean. Only plants that were located at least 0.5 m from the base of other species were collected to avoid interspecific interactions. Above- and belowground structures were separated in the field. Only roots and rhizomes directly attached to the base of a plant were collected which typically went to a depth of ~15–20 cm and within ~30 cm of each plant. Depth is approximate due to the unconsolidated nature of the sediment and subsequent difficulties with sand backfilling while digging. Subsamples of the root system intended for mycorrhizal percent infection were preserved in 70% EtOH, and those taken for tensile strength were preserved in 15% EtOH (Böhm, 1979). Samples were placed on ice while in the field. Upon returning from the field, subsampled roots were immediately refrigerated and remaining components of plant samples were frozen in water until further analysis.

Above- and belowground traits

Aboveground components were assessed for stem number and maximum leaf length per stem. Belowground components were separated into belowground stems (buried portions of vertical stems), rhizomes (lateral stems), and roots. Rhizomes were counted and measured for length, and roots were scanned using WinRHIZO. All above- and belowground components were then dried in an oven at 60°C for 48 h and weighed for dry biomass. Care was taken to sample roots from a variety of diameter classes for each sample to examine root traits by diameter. In WinRHIZO, roots were grouped into five, 0.5-mm categories of root diameter for analysis (0.0–0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0, and >2.0 mm). 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. Root tissue density is the ratio of total root biomass to total volume for a given sample. Specific root length is the ratio of total root length to total biomass. As not all individuals possessed roots at the time of sampling or had extremely few roots, root sample sizes per species are as follows: *Ammophila* ($n = 9$), *Panicum* ($n = 12$), *Spartina* ($n = 9$), and *Uniola* ($n = 9$).

Tensile strength

Subsampled tensile strength roots were rehydrated in distilled water for 30 min. Root diameter was taken using digital calipers. Due to lack of roots in some samples, additional roots were included from sampled individuals on Hog Island, part of the Virginia Coast Reserve Long-Term Ecological Research (LTER) Network and spare root samples collected from target species not directly associated with a sample individual. Tensile strength tests were conducted using an MTS Insight 30 Universal Testing Machine (MTS Systems Corporation, Eden Prairie, MN, USA) with 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.

Mycorrhizal percent infection

Root samples of individual plants were cut into 1-cm segments and root diameter determined using the ocular reticle of a compound microscope. Root segments were classified into one of four diameter classes (0.0–0.5, 0.5–1.0, 1.0–1.5, and 1.5–2.0 mm). Root subsamples were placed in beaker of distilled water and gently agitated to remove EtOH and sediment particles. Staining for fungal structures followed modified methods of Phillips and Hayman (1970). Samples were moved to hot 10% KOH for between 5 and 15 min depending on species. Time in 10% KOH was adjusted by species to prevent disintegration of the delicate roots (Rabatin, 1979). Samples were then briefly rinsed in distilled water and moved to 3.5% HCl for 15 min. Root samples were stained overnight in 0.04% trypan blue and preserved in glycerin prior to mounting on slides.

Species were assessed for hyphal, vesicular, and arbuscular colonization using a modified, magnified intersect method in which five intersections, 1 mm apart, were assessed per 1-cm root segment (McGonigle et al., 1990). Mycorrhizal hyphae were identified as morphotypes that had been characterized following observations of direct hyphal connections to arbuscules and vesicles for each plant species following root staining as detailed in Gooden et al. (2020). Only arbuscules with clear dichotomously branched structures were considered. Because of the possibility of AMF hyphal infection without direct mycorrhizal relationships facilitated via arbuscules and the possibility of mycorrhizal relationships without the presence of arbuscules, all three structures typical of AMF were characterized for this study (Brundrett, 2004). Sample sizes for mycorrhizal percent infection were limited as some individuals did not have enough root length to assess for mycorrhizal percent infection (*Ammophila* [$n = 8$], *Panicum* [$n = 10$], *Spartina* [$n = 8$], and *Uniola* [$n = 8$]).

Statistical analyses

Analyses were conducted in RStudio (R Core Team, R version 4.0.1, 2020). Above- and belowground traits were compared among species using ANOVA or Kruskal–Wallis analyses. Post hoc comparisons were made using either Tukey's honestly significant difference or Tukey–Nemenyi tests. Data were either log or square root transformed to meet assumptions of parametric statistical tests. Nonparametric tests were used when transformation did not satisfy assumptions. A two-way ANOVA was used to assess how root surface area was allocated across roots of different diameter size classes. Due to high variability in total root surface area, the percentage of the total surface area falling within the root diameter classes was used for each sample. Relationships among above- and belowground traits and species were visualized using principal components analysis (PCA) ordinations of the standardized correlation matrix using the prcomp() function from the vegan R package. Species groups were compared using a permutational multivariate analysis of variance (PERMANOVA) of the Euclidean distances, and p values were adjusted using the FDR method. Vectors of trait variables were fitted to the ordination using the envfit() function within R. Only individuals that had records for all metrics evaluated in the PCA were included in these analyses. Tensile strength data were assessed using analysis of covariance where root diameter was averaged across 0.5-mm bins (to account for sampling effort) and included the interaction between root diameter and species. Multiple comparisons of slopes were conducted in JMP using Indicator Parameterization Estimates. Individual linear models were created for each species.

RESULTS

Aboveground measurements

Individuals of *Ammophila*, *Panicum*, *Spartina*, and *Uniola* were assessed for above- and belowground features. Both leaf length ($X^2 = 77.18$, $p < 0.0001$) and stem number ($X^2 = 10.71$, $p = 0.01$) differed among species (Table 1). *Ammophila* had the longest leaves (58.3 ± 2.8 cm) followed by *Uniola* (48.7 ± 2.5 cm). *Uniola* exhibited considerable variation in leaf length, ranging from 2.5 to 103.0 cm. *Spartina* and *Panicum* were similar in leaf length (~35 cm), and ~30–40% shorter than *Uniola* and *Ammophila*. Both *Ammophila* and *Uniola* exhibited the highest stem numbers (approximately eight stems per plant), but stem number was variable within species (Table 1).

Biomass

Above- and belowground biomass differed among species. *Ammophila* and *Uniola* had the highest aboveground biomass, consistent with other aboveground measurements ($F = 5.97$, $p = 0.002$; Table 1). Patterns in aboveground biomass were similar belowground, though

Uniola did not differ significantly from *Spartina* and *Panicum* ($F = 11.29$, $p < 0.0001$). Above- to belowground biomass ratios were highest for *Ammophila* (1.5 ± 0.2), *Panicum* (1.6 ± 0.3), and *Spartina* (1.4 ± 0.2) and lowest for *Uniola* (0.9 ± 0.2). When belowground biomass was partitioned among roots, rhizomes, and belowground stems, distinctive allocation patterns were observed among species (Figure 2). Patterns of belowground stem biomass followed with total above- and belowground biomass ($F = 11.29$, $p < 0.0001$). Rhizome

TABLE 1 Species above- and belowground traits (mean ± SE)

Characteristic	*Ammophila*	*Panicum*	*Spartina*	*Uniola*	*F*	X^2	*p*
Leaf length (cm)	58.3 ± 1.8^{a}	34.6 ± 2.1^{b}	34.5 ± 1.5^{b}	48.7 ± 2.5^{c}	...	77.18	<0.0001
Stem number	8.8 ± 2.5	2.7 ± 0.5	6.6 ± 1.4	8.3 ± 2.9	...	10.71	0.01
Aboveground biomass (g)	10.3 ± 3.2^{a}	2.6 ± 0.6^{b}	2.3 ± 0.5^{b}	6.2 ± 1.7^{ab}	5.97	...	0.002
Belowground biomass (g)	8.1 ± 3.4^{a}	2.2 ± 0.6^{b}	1.9 ± 0.4^{b}	7.1 ± 1.2^{a}	11.29	...	<0.0001
Rhizome number	2.3 ± 0.8	2.7 ± 0.7	2.3 ± 0.7	5.1 ± 1.2	n.s.	...	n.s.
Rhizome length (cm)	69.7 ± 12.3^{a}	11.3 ± 2.7^{b}	10.6 ± 2.0^{b}	10.0 ± 2.5^{b}	...	39.17	<0.0001
Average root surface area (mm^2)	573.7 ± 306.8	250.4 ± 98.9	219.2 ± 105.6	1741.9 ± 923.6	n.s.	...	n.s.
Average root diameter (mm)	0.41 ± 0.05^{a}	0.90 ± 0.04^{b}	0.53 ± 0.05^{a}	1.43 ± 0.17^{c}	30.61	...	<0.0001
Root tissue density (RTD; g cm^{-3})	0.35 ± 0.06^{a}	0.15 ± 0.01^{b}	0.25 ± 0.02^{a}	0.17 ± 0.02^{b}	9.66	...	<0.0001
Specific root length (SRL; m g^{-1})	177.2 ± 19.5^{a}	82.7 ± 5.6^{b}	136.4 ± 19.8^{ab}	36.9 ± 6.6^{c}	27.16	...	<0.0001

Note: Superscripted compact letter display denotes significant pairwise differences (α = 0.05) following post hoc analyses.

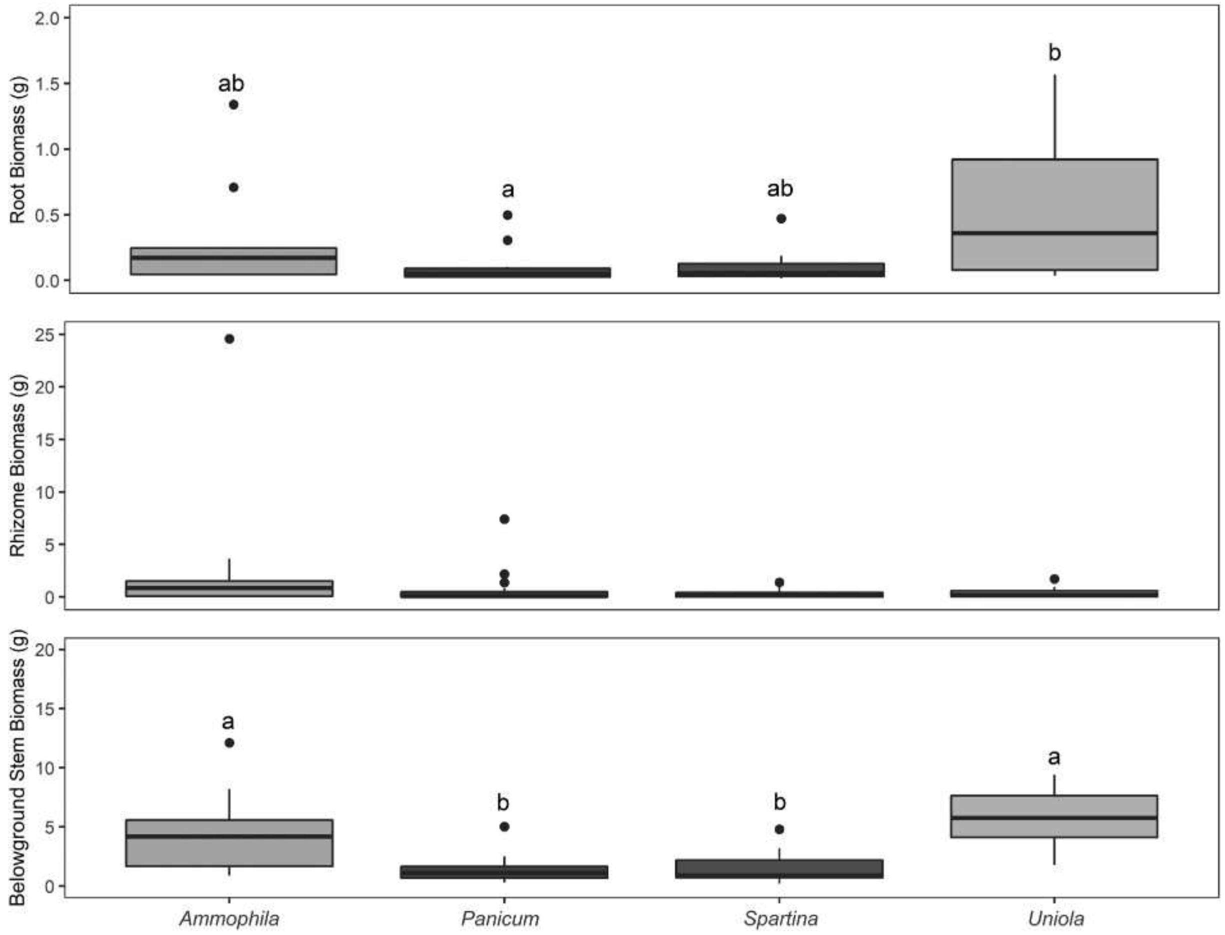

FIGURE 2 Belowground biomass partitioned into belowground structures. Species display significant differences in allocation to belowground structures (α = 0.05). Compact letter display (CLD) represents significant differences among species

biomass did not differ among species, but *Ammophila* had significantly longer rhizomes than the other species (69.7 ± 12.3 cm, $X^2 = 39.17$, $p < 0.0001$; Table 1). Root biomass differed significantly among groups, with *Panicum* having the lowest values ($X^2 = 9.47$, $p = 0.02$; Figure 1).

Root traits

Species root traits diverged from patterns in total biomass. *Ammophila* and *Spartina* had the smallest average root diameter, followed by *Panicum* and *Uniola* ($F = 30.61$, $p < 0.0001$; Table 1). Total root system surface area did not differ among species due to high variability within species. Percent root system surface area was then examined to determine allocation of root surface area by diameter class independently of raw root system surface area, which was highly variable (Table 1). Percent root surface area allocation across root diameter classes differed significantly among species, with *Ammophila* and *Spartina* allocating most surface area to fine roots ≤1.5 mm in diameter (diameter class × species $F_{12,175} = 23.7$, $p < 0.0001$; Figure 3). *Panicum* allocated a large proportion of the root system surface area (50%) to a single diameter class (1.0–1.5 mm), demonstrating that its root system was largely composed of roots of similar diameter. Most of *Uniola* surface area was distributed among larger roots (≥1.5 mm). Species differed in RTD ($F = 9.66$, $p < 0.0001$) and SRL ($F = 27.16$, $p < 0.0001$), with *Ammophila* and *Spartina* having the highest values for both (Table 1). Tensile strength also differed among species with a significant interaction between species and root diameter ($F_{3,55} = 16.72$, $p = 0.0012$; Figure 4). Both *Spartina* and *Ammophila* exhibited high maximum tensile strength values (4314 and 2879 MPa, respectively) and steepest slopes with diameter (Table 2).

Mycorrhizal percent infection

Mycorrhizal colonization was highly variable within species. Although not significant, *Panicum* had the highest

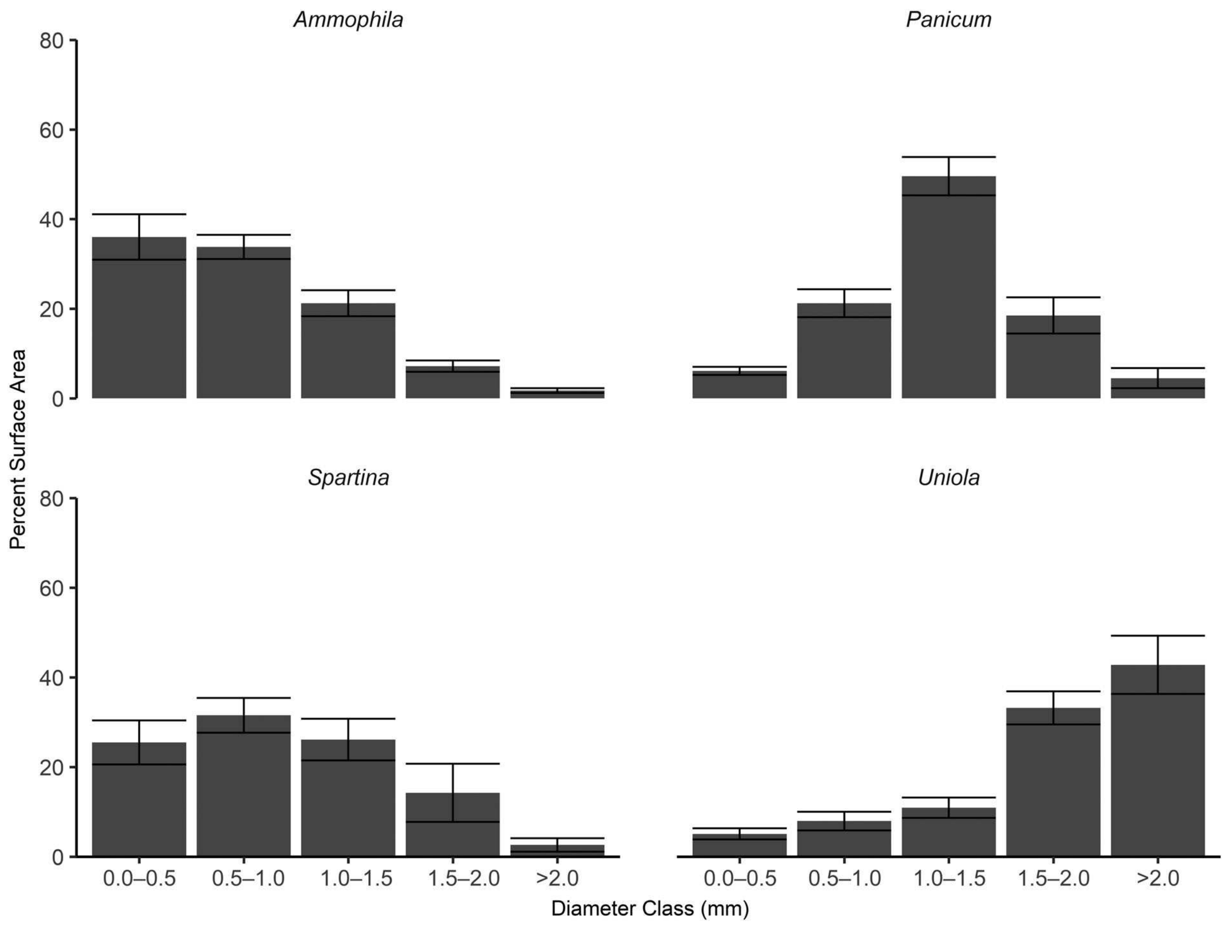

FIGURE 3 Percent root surface area distributed into five, 0.5-mm root diameter classifications. *Ammophila* and *Spartina* distributed a greater proportion of their root surface area in smaller diameter roots, *Panicum* distributed a large amount in a single root diameter class (1.0–1.5 mm), and *Uniola* distributed most surface area in the larger diameter roots

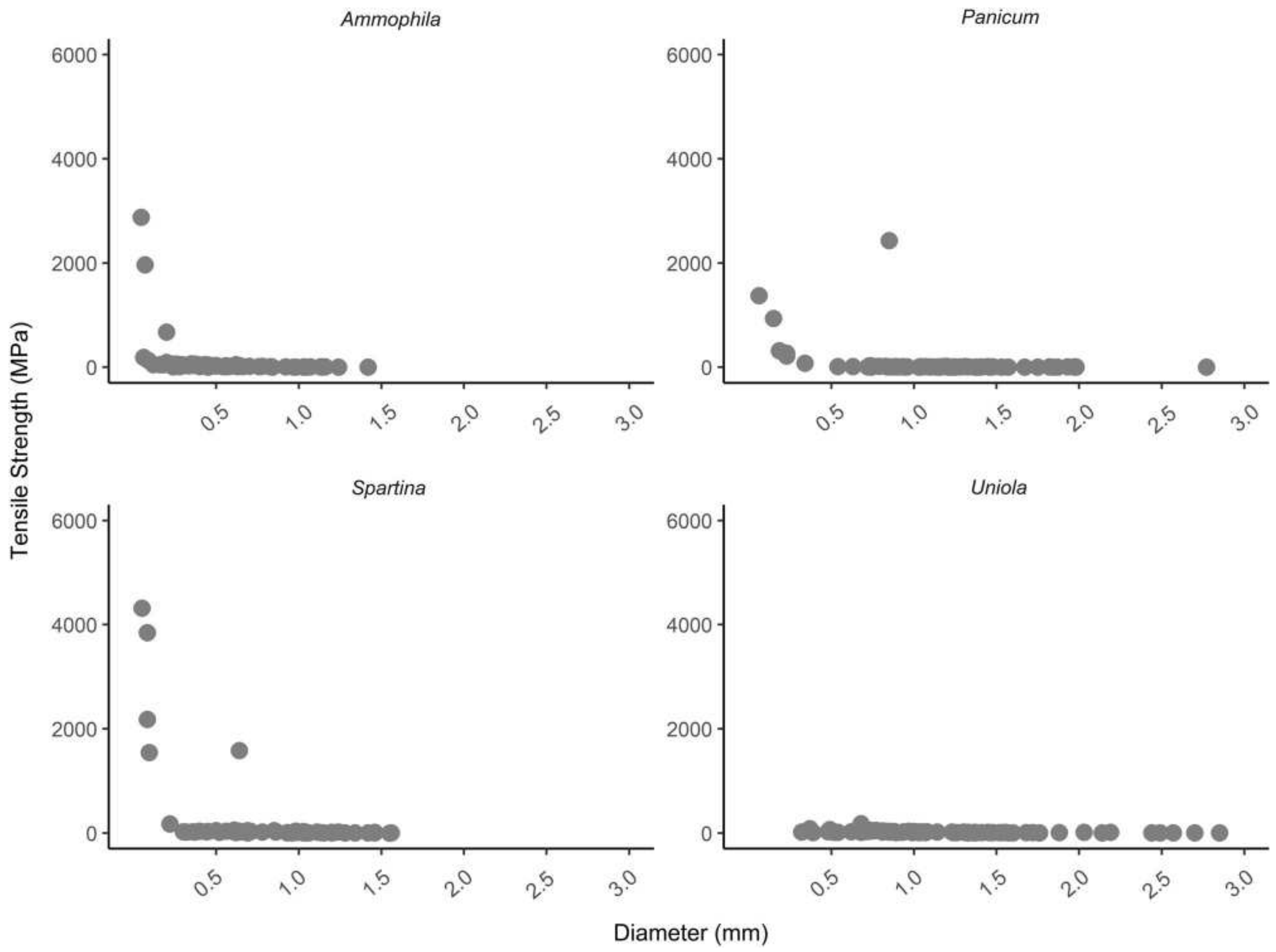

FIGURE 4 Tensile strength measurements for roots of each species. Tensile strength measurements for roots of each species. Data show the tensile strength measurements and root diameter for each root sample, which follows a typical logarithmic curve that reflects an inverse relationship. *Spartina* and *Ammophila* had greatest maximum tensile strength values, and *Uniola* had a significantly lower slope (Table 2)

TABLE 2 Linear regression model for log-transformed slopes of root tensile strength

Species	Slope	*y* Intercept	r^2	*p*	Post hoc
Ammophila	−3.20	5.25	0.68	**<0.0001**	A
Panicum	−2.97	6.06	0.66	**0.0002**	A
Spartina	−3.13	6.04	0.57	**0.0073**	A
Uniola	−0.80	3.89	0.63	**0.0006**	B

Note: Significant *p* values are given in bold. Compact letter display shows the results of analysis of covariance interaction between species and root diameter with differences in slopes.

percent hyphal colonization (62.3 ± 7.6%) and vesicular colonization (17.0 ± 3.6%) of the species (Table 3). *Spartina*, *Ammophila*, and *Uniola* all had hyphal percent infection values below 50%. *Panicum* exhibited significantly greater arbuscular colonization than the other species (22.3 ± 4.5%, $X^2 = 15.7$, $p = 0.001$). Colonization did not differ by diameter class within species (Appendix S1: Figure S1).

Plant traits PCA

Above- and belowground traits were then considered in multivariate space. Species formed distinctive groups, with axes PC1 and PC2 explaining 56.7% variation (Figure 5). Principal component 1 (36.4%) described differences in biomass allocation, aboveground traits, and mycorrhizal interactions. Principal component 2 (20.3%)

TABLE 3 Mycorrhizal percent infection of arbuscules (AC), hyphae (HC), and vesicles (VC) for the four focal species (data show the mean ± SE)

Structure	*Ammophila*	*Panicum*	*Spartina*	*Uniola*	Test statistic	*p*
AC	0.4 ± 0.3%^{a}	22.3 ± 6.3%^{b}	1.9 ± 1.3%^{a}	1.8 ± 1.0%^{a}	$X^2 = 15.7$	0.001
HC	36.2 ± 10.2%	62.3 ± 7.6%	43.2 ± 10.6%	36.7 ± 11.9%	n.s.	n.s.
VC	9.0 ± 4.2%	17.0 ± 3.6%	7.8 ± 4.9%	4.8 ± 3.5%	n.s.	n.s.

Note: Superscripted letters denote α = 0.05.

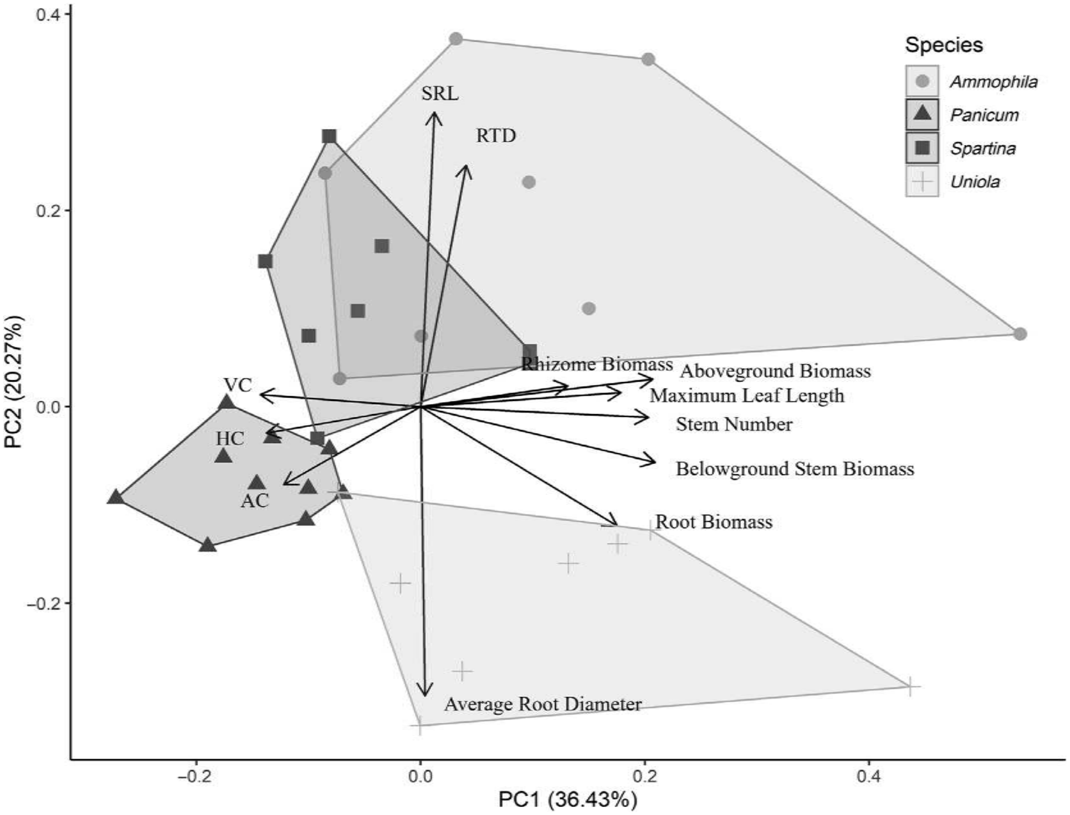

FIGURE 5 Principal components analysis (PCA) of above- and belowground traits grouped by species. Individuals of different species are denoted by symbol shape and grayscale color. Axis correlations for vector variables are given in Appendix S1: Table S1. All species groups differed significantly following a permutational multivariate analysis of variance (Appendix S1: Table S2). AC, arbuscular colonization; HC, hyphal colonization; RTD, root tissue density; SRL, specific root length; VC, vesicular colonization

described aspects of root construction (i.e., average root diameter, SRL, and RTD). Pearson's correlations for all traits and axis correlations are given in Appendix S1: Tables S1 and S2. All species groups differed significantly ($F_{3,33} = 5.67$, $p = 0.001$; Appendix S1: Table S3).

When considering belowground features alone, species *Ammophila* and *Spartina* grouped separately from *Uniola* and *Panicum* in multivariate space (PERMANOVA $F_{3,30} = 5.81$, $p = 0.001$; Figure 6, Appendix S1: Table S4). Separation along PC1 (31.7%) described differences in root construction, while separation along PC2 (26.9%) described differences in both mycorrhizal associations and biomass allocation (Figure 5, Appendix S1: Table S4).

DISCUSSION

Understanding trait differences among dominant dune grass species can provide context for species interactions with the dune environment. Rather than demonstrating convergence in traits, our results show the four co-occurring dominant dune grasses displayed trait dissimilarity, even when considering belowground alone (Figure 7). This was largely driven by root construction, biomass allocation, and mycorrhizal infection. Dissimilarity in whole plant traits may indicate that that functionally similar species have different approaches for surviving the dune environment (De Battisti, 2021;

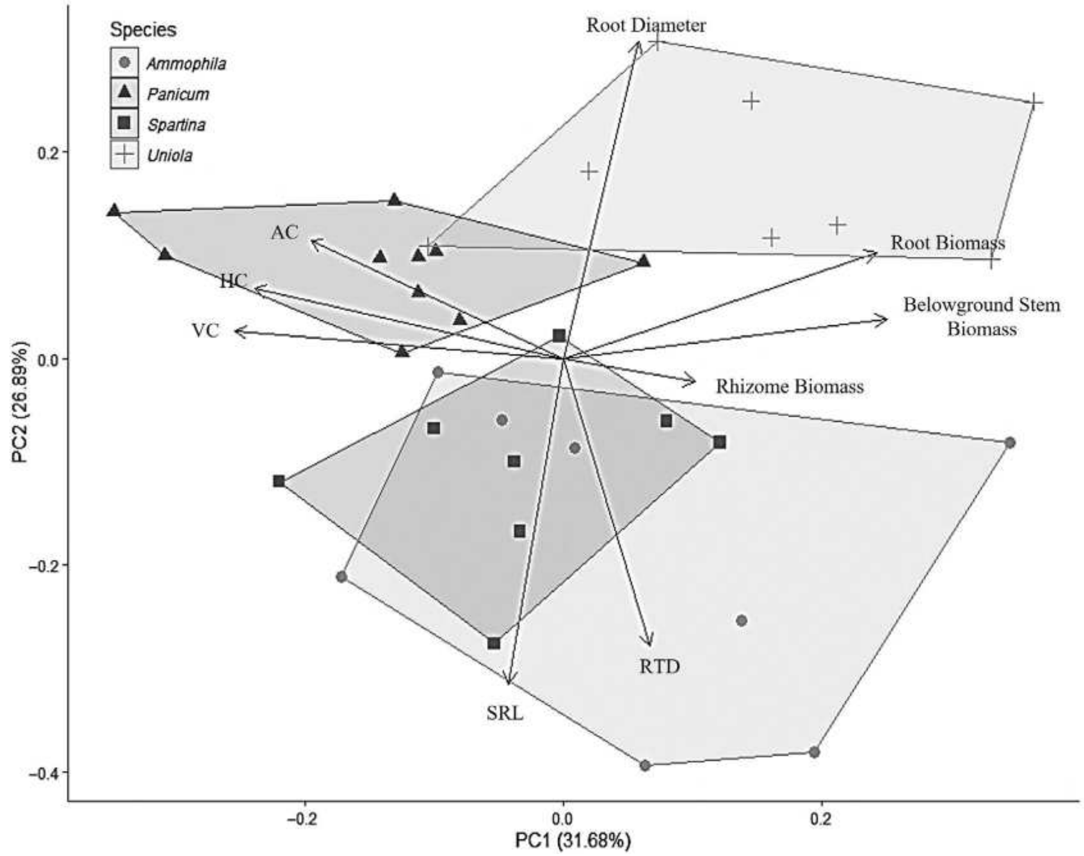

FIGURE 6 Principal components analysis (PCA) of belowground traits only grouped by species. Axis correlations for vector variables are given in Appendix S1: Table S3. *Ammophila* and *Spartina* were similar in belowground traits following permutational multivariate analysis of variance (Appendix S1: Table S4). AC, arbuscular colonization; HC, hyphal colonization; RTD, root tissue density; SRL, specific root length; VC, vesicular colonization

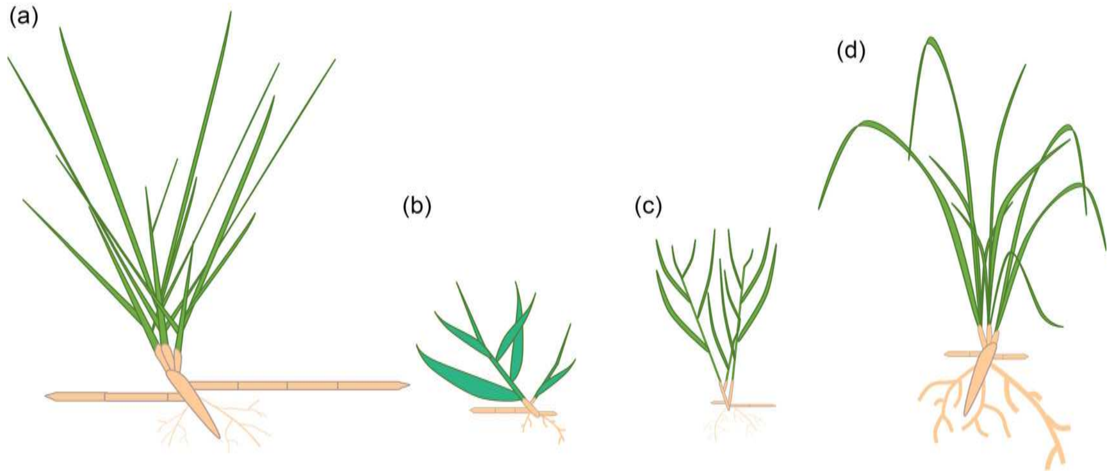

FIGURE 7 Schematic of species similarities and differences above and below ground. (a) *Ammophila breviligulata*, (b) *Panicum amarum*, (c) *Spartina patens*, and (d) *Uniola paniculata*

Reich, 2014; Tavares et al., 2020; Westoby et al., 2002; Wright et al., 2004). Species with different individual traits may tolerate similar environmental conditions through unique combinations of trait that cumulatively provide similar whole plant fitness (Marks & Lechowicz, 2006; Pivovaroff et al., 2016; Tavares et al., 2020; Westoby et al., 2002). Many root trait studies assess only fine roots, which may not take whole plant functioning into account

(Freschet & Roumet, 2017). Here, we evaluate whole root systems in order to capture the breadth of plant functioning including strategic differences in growth patterns and tensile strength of dominant dune species.

Our study species exhibited similarities in several root traits associated with anchoring and sediment reinforcement (Davidson et al., 2020; Gregory, 2006; Klimešová et al., 2018; Reubens et al., 2007). For example, *Ammophila* and *Spartina* had similar average root diameters, with greater root surface area distributed in smaller size classes of higher tensile strength (Figures 3–5). These two species also had maximum tensile strength values that were two and three times greater, respectively, than *Uniola* (1373 MPa) and *Panicum* (1281 MPa), which may confer advantage for sediment reinforcement and anchorage during disturbance events. However, species with greater belowground biomass have also been shown to reduce sediment loss under both wave and wind erosional regimes (Bryant et al., 2019; Charbonneau et al., 2017; De Battisti & Griffin, 2020). In our study, *Ammophila* and *Uniola* were similar in belowground biomass despite clear differences in root traits, while *Spartina* and *Panicum* were ~70% less massive belowground. These unique combinations of belowground features may confer different levels of erosional resistance depending on local context and affect patterns of dune erosional. Both long-term, in situ experiments evaluating individual and plant community traits with accretional and erosional dynamics and ex situ experiments that allow for more precise manipulation and measurement of these relationships are essential for understanding how these traits interact with dune processes.

Rooting traits may also be used to infer general plant strategies based on a whole plant economic spectrum related to carbon economy first identified in leaves (the leaf economic spectrum) such that species with traits indicating fast, acquisitive growth are thought to also exhibit high relative growth rates overall (Reich, 2014; Wright et al., 2004). In the Poaceae family, which encompasses the species studied here, RTD and SRL may be indicative of plant physiological stress tolerance, with high RTD and low SRL associated with greater drought tolerance (Fort et al., 2013). Although our traits were measured on whole plant systems, the majority of rooting material was <2 mm (the upper boundary for root trait measurements; Cornelissen et al., 2003) for all species except *Uniola*. Using traits in this way provides information about general plant behaviors and responses to stressors in the dune environment. These factors are key for understanding vegetation establishment, proliferation, and distribution, which are known to impact both accretional and erosional dune processes.

Ammophila and *Spartina* both demonstrated high SRL, which may indicate higher root foraging capacity than *Panicum* and possibly *Uniola*, but high observed RTD may allow for drought tolerance with resource acquisition. Low SRL, low RTD, relatively low root biomass, and general lack of roots in the smallest diameter classes indicate slow growth, a resource conservation strategy, drought tolerance, and low root foraging capacity in *Panicum*. *Uniola* also exhibited low SRL and RTD values, but high root biomass and high root diameter. *Uniola* also had high root surface area, which was driven by larger diameter roots and root biomass production. These traits may allow *Uniola* to forage belowground effectively despite greater carbon cost and may even compensate for other factors such as low tensile strength for anchorage and sediment reinforcement.

All species in this study demonstrated AMF colonization, indicating that mycorrhizal fungi are prevalent (e.g., Corkidi & Rincón, 1997; Koske & Polson, 1984). *Panicum* had significantly greater AMF colonization than the other species in this study and low SRL. Recent global examinations of belowground trait relationships have found that SRL is negatively related to mycorrhizal “outsourcing” of resource acquisition (Bergmann et al., 2020; Weigelt et al., 2021). These data indicate that *Panicum* relies strongly on mycorrhizal partners for resource acquisition. High colonization by arbuscules, the fungal structures thought to facilitate water and nutrient exchanges between AMF and host plant, and root traits related to drought tolerance may allow *Panicum* to persist in the harsh dune environment despite other traits that indicate low root foraging capacity and overall low root biomass (Brundrett, 2004; Fort et al., 2013; Rillig & Mummey, 2006; Unger et al., 2017). Similar patterns in root traits have also been observed in other sand dune species that are typically highly colonized by mycorrhizal fungi, an indication of trait syndromes related to resource conservation and drought tolerance in dune plants (Unger et al., 2017).

A variety of trait combinations confers differing plant contributions to ecosystem services and processes, with whole plant contributions related to both above- and belowground traits. Quantifying suites of plant traits is important when evaluating whole plant species and community contributions to these processes. For example, examining *Ammophila* above- and belowground features can be used to understand known impacts on dune processes. Significantly longer rhizomes of *Ammophila*, root traits linked to rapid growth (e.g., small root diameter and high SRL), and high biomass production allow this species to initially colonize dune systems. High belowground biomass with greater root tensile strength further reinforce sediments and promote erosional resistance in the rhizosphere of *Ammophila* (Davidson et al., 2020; De Battisti & Griffin, 2020). Combining these belowground features with aboveground traits such as greater leaf length and known biomass allocation behaviors such as dune building may be key in understanding the capacity of *Ammophila* to rapidly colonize recently disturbed areas, drive rapid dune coalescence, and promote greater sediment capture and retention relative to other species. Using *Ammophila* as an example, it can be seen that evaluating whole plant traits provide a mechanistic understanding of plant behaviors. Trait evaluations further provide data that can be applied to modeling efforts as they are quantitative descriptors of plant characteristics that have direct impacts on specific dune processes such as erosion.

Plant traits are inherently variable, and quantifying this variability is important for accurately modeling and understanding relationships between vegetation and the environment (Westerband et al., 2021). We demonstrate clear differences in whole plant traits among prominent dune species, which varied differentially, possibly due to ontogeny, genetics, seasonality, and adaptation to localized biotic and abiotic conditions (Henn & Damschen, 2021; Lum & Barton, 2020; Tavares et al., 2020; Westerband et al., 2021). Three of the species studied here—*A. breviligulata*, *U. paniculata*, and *S. patens*—are known to vary above- and belowground traits in response to sediment burial (Brown & Zinnert, 2018). In this study, *Panicum* individuals were less dissimilar in their combinations of above- and belowground traits in multivariate space relative to the other species. Plasticity of plant traits and variation in multiple trait response to disturbance and sediment supply ultimately influence dune dynamics. Evaluating multiple plant traits can provide a mechanistic understanding of plant–environment interactions that influence dune features as have been done in other ecosystems such as coastal marshes (e.g., Bouma et al., 2007; Temmerman et al., 2005). Additional studies of belowground structures are specifically important as these features have been hypothesized to influence dune resistance but remain understudied.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Zinnert & Walker, 2022) are available from Dryad: https://doi.org/10.5061/dryad.2jm63xsqv.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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