

Article

Species-Specific Functional Morphology of Four US Atlantic Coast Dune Grasses: Biogeographic Implications for Dune Shape and Coastal Protection

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Abstract: Coastal dunes arise from feedbacks between vegetation and sediment supply. Species-specific differences in plant functional morphology affect sand capture and dune shape. In this study, we build on research showing a relationship between dune grass species and dune geomorphology on the US central Atlantic Coast. This study seeks to determine the ways in which four co-occurring dune grass species (*Ammophila breviligulata*, *Panicum amarum*, *Spartina patens*, *Uniola paniculata*) differ in their functional morphology and sand accretion. We surveyed the biogeography, functional morphology, and associated change in sand elevation of the four dune grass species along a 320-kilometer distance across the Outer Banks. We found that *A. breviligulata* had dense and clumped shoots, which correlated with the greatest sand accretion. Coupled with fast lateral spread, it tends to build tall and wide foredunes. *Uniola paniculata* had fewer but taller shoots and was associated with ~42% lower sand accretion. Coupled with slow lateral spread, it tends to build steeper and narrower dunes. *Panicum amarum* had similar shoot densities and associated sand accretion to *U. paniculata* despite its shorter shoots, suggesting that shoot density is more important than morphology. Finally, we hypothesize, given the distributions of the grass species, that foredunes may be taller and wider and have better coastal protection properties in the north where *A. breviligulata* is dominant. If under a warming climate *A. breviligulata* experiences a range shift to the north, as appears to be occurring with *U. paniculata*, changes in grass dominance and foredune morphology could make for more vulnerable coastlines.

Keywords: dune grass morphology; sand capture; foredune morphology; *Ammophila breviligulata* (American beachgrass); *Panicum amarum* (bitter panicum); *Spartina patens* (saltmeadow cordgrass); *Uniola paniculata* (sea oats); Outer Banks islands; North Carolina; distributional range shifts

1. Introduction

Over the last decade, there has been growing recognition that coastal interface habitats such as dunes provide important protection from the threats of extreme storms and chronic sea level rise [1,2]. Dunes, and thus the services they provide, arise from the feedback between vegetation and sediment supply [3–5]. This feedback process builds dunes, reducing vulnerability to coastal flooding and erosion [6,7], providing habitat for wildlife [8], and serving to sequester carbon [9]. One area of focus has centered on the role of species-specific biophysical feedbacks of dune plants in determining dune geomorphology [4,5,10–19]. These studies show that vegetation functional morphology and its interaction with windblown sand can contribute to the variability in dune geomorphology at local to landscape level scales.

The shape of coastal foredunes (i.e., linear ridges of sand parallel to the shoreline) is initially determined by the amount of sand delivered to the beach, which is dependent on sand availability, currents, waves, and sea level [20]. Wind moves sand from the beach to the backshore where vegetation plays a pivotal role in nucleating dunes; for example, Kuriyama et al. [21] found that plant cover as low as 28% reduced sand transport by 95%. Once vegetation captures sand, a positive feedback between plant growth and accretion occurs, eventually resulting in foredunes that vary in size and shape [5,10–13,18,19,22,23].

A recent study of US Pacific Northwest dunes explored the relative role of geological factors and the invasion of two grass species (European beachgrass *Ammophila arenaria* and American beachgrass *A. breviligulata*) in determining foredune variability along a 500-km stretch of coastline [19]. Using a Bayesian network analysis that compared foredunes at 20 sites, they found that ~50% of the variability in foredune crest height was explained by beach geomorphology, specifically backshore slope and shoreline change rate, both of which contribute to sand availability to the foredune. Density differences in invasive beachgrasses explained roughly 10% of the variability. In particular, steeper sloped beaches, positive shoreline change rates, and higher shoot densities of both beachgrass species were all associated with taller and wider dunes. In addition, Biel et al. [19] found that species-specific differences in sand capture of the two beachgrasses explained additional variability in dune shape, as had been hypothesized in other studies [11,12]. *Ammophila breviligulata*, which has less dense but thicker shoots, exhibited more lateral growth, resulting in greater sand deposition and widening of the foredune at the seaward margin. In contrast, *A. arenaria* had denser but thinner shoots and restricted lateral spread, resulting in comparatively more vertical sand deposition on the foredune face and crest. Over time, for a given sand supply regime, the differing growth forms of these beachgrasses have produced steep, narrow foredunes when dominated by *A. arenaria* and shallow, wide foredunes when dominated by *A. breviligulata*.

In general, the functional differences in sand capture among dune grass species are the result of variability in features of their growth form and morphology. These features are defined by the allocation of biomass to, and spatial arrangement of, two basic structures: belowground rhizomes (consisting of belowground stems with roots) and aboveground shoots (including the stems, leaves, and inflorescences). The length and specialized branching patterns of rhizomes of different dune grass species can produce more or less horizontal versus vertical growth patterns, as is seen for the two *Ammophila* congeners on the US Pacific coast [11]. In addition, dune grass species differ in the average number of shoots produced per rhizome, a factor that varies from a single shoot to multiple shoots. These two features, when combined, produce species-specific differences in aboveground shoot density and spacing (i.e., from evenly spaced to clumped) and differences in the relative amount of lateral versus vertical spread across the foredune, all of which directly affect sand capture and dune shape [4,5,10–12,18,19,24]. Overall, these studies show that sparse, evenly spaced, and/or laterally spreading growth forms produce shorter and wider dunes compared to dense, clumped, and/or vertical growing forms, which create taller, steeper, and narrower foredunes. Other morphological features of the shoots themselves, including their height, weight, blade number, and stiffness, can also affect sand

capture [5,12,21,25–27]. Overall, these studies show that short, thin, or flexible shoots capture less sand than tall, thick, or stiff shoots.

In this study, we build on previous research that has documented species-specific relationships between dune grasses and dune geomorphology on the Outer Banks islands of North Carolina, USA [4,10,28,29]. Four species of dune grasses, *Ammophila breviligulata* Fernald (American beachgrass), *Panicum amarum* Elliott (bitter panicum), *Spartina patens* (Aiton) Muhlenberg (saltmeadow cordgrass), and *Uniola paniculata* L. (sea oats) (Figure 1), overlap in their distribution in North Carolina and Virginia coastal sand dunes [30].

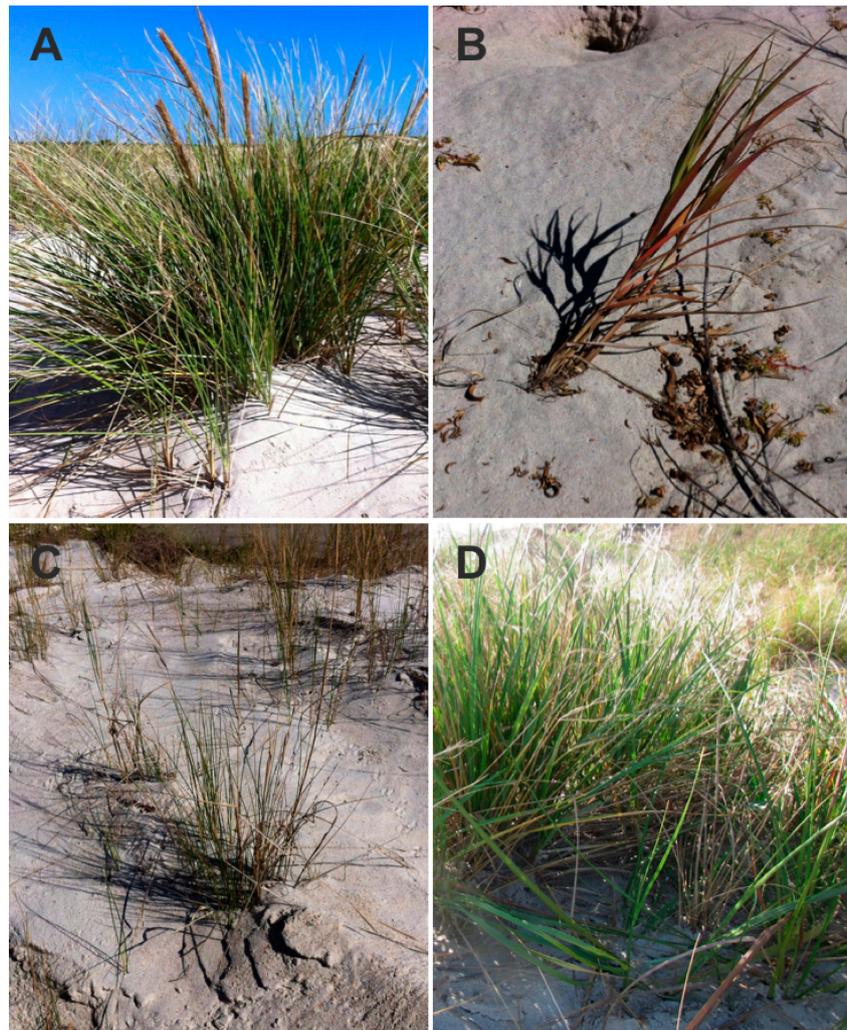


Figure 1. Photographs of the four most common dune grass species (A) *Ammophila breviligulata* (American beachgrass), (B) *Panicum amarum* (bitter panicum), (C) *Spartina patens* (saltmeadow cordgrass), and (D) *Uniola paniculata* (sea oats) in foredunes of the Outer Banks islands from Virginia to North Carolina, USA. Photos by S. D. Hacker.

As part of a revegetation project started in the 1960s, experimental plantings were conducted on Ocracoke and Portsmouth Islands to determine whether the three most dominant dune grass species in the region (*A. breviligulata*, *P. amarum*, and *U. paniculata*) varied in their dune-building capabilities [4,10,28,29]. The experiments showed that, after 8 years, separate foredunes with monocultures of either *A. breviligulata*, *P. amarum*, or *U. paniculata* grew to similar crest heights but *A. breviligulata* established and spread more quickly (lateral spread of ~2–3 m per year) than *U. paniculata* (~0.6 m per year) or *P. amarum* (no data), resulting in an overall wider and larger volume foredune. The *U. paniculata* and *P. amarum* monocultures built foredunes that were narrower and

steeper. Interestingly, dunes with polycultures of all three species did not differ appreciably from those with monocultures of *A. breviligulata*. Nonetheless, the authors recommended that even though *A. breviligulata* appears to be the superior dune builder, planting foredunes with polycultures should provide insurance against the observation that *A. breviligulata* is shorter lived. Taken together, previous research describes how species of dune grasses vary in their utility as dune builders, but generally lack mechanistic explanations of dune-building capacity based on quantitative measures of their functional morphology and sand capture.

Here we report on measurements of the functional morphology, and associated changes in sand elevation, of the four most common dune grass species (*A. breviligulata*, *P. amarum*, *S. patens*, and *U. paniculata*; Figure 1) on the US central Atlantic coast. In particular, we surveyed foredunes along the Outer Banks islands for the distribution, abundance, growth form, morphology, and sand accretion patterns of the four dune-building grass species in this region. We asked the following questions:

1. How do the four dominant dune grass species compare in their distribution and abundance with latitude and location on the foredune profile?
2. How do the four species of dune grasses differ in their functional morphology and sand accretion in the field?

We further discuss, using a conceptual model, how the functional morphology of dune grass species in this study compare to those of species from the US West Coast. We end the paper by considering the potential consequences of species-specific differences to dune morphology, especially given the current and projected latitudinal distribution patterns of these US East Coast dune grass species. We suggest that determining the functional role of dune grass species to dune geomorphology at regional scales will ultimately require quantitative analyses that partition the relative contributions of sand supply, beach geomorphology, and dune grass species abundance.

2. Materials and Methods

2.1. Field Setting

The study was conducted along foredunes of the Outer Banks islands, a 320-kilometer barrier island chain extending from the northern tip of False Cape (Virginia, USA) in the north to the western tip of Bogue Banks (North Carolina, USA) in the south (Figure 2, Table S1). The micro-tidal region is characterized by a moderately energetic seasonal wave and wind climate, with regional average annual significant wave heights of ~1.2 m and wind speeds of ~6.8 m/s [31]. Throughout the region, wave and wind energy is lowest in boreal spring and summer. The most energetic conditions are associated with tropical hurricane systems, occurring between June and November, and nor'easters, which typically occur between September and April.

The study site includes heavily developed regions with residential and commercial development adjacent to and on the dunes, as well as undeveloped and unmanaged areas, including two national seashores and multiple national wildlife refuges and state parks. On average, the entire stretch of the Outer Banks coastline region is eroding ~0.7 m/year [32] with alongshore variation in the shoreline change rate influenced by local shoreline angles, sediment grain size, and the underlying geologic framework [33]. Trends in beach evolution are additionally confounded by the common use of beach nourishment along the North Carolina coastline [34], with implications of these management interventions on subsequent dune dynamics [35]. Beach driving, which is seasonally permitted across most of the study region, except for on Shackleford Banks within Cape Lookout National Seashore and Pea Island National Wildlife Refuge, may also influence dune geomorphology.

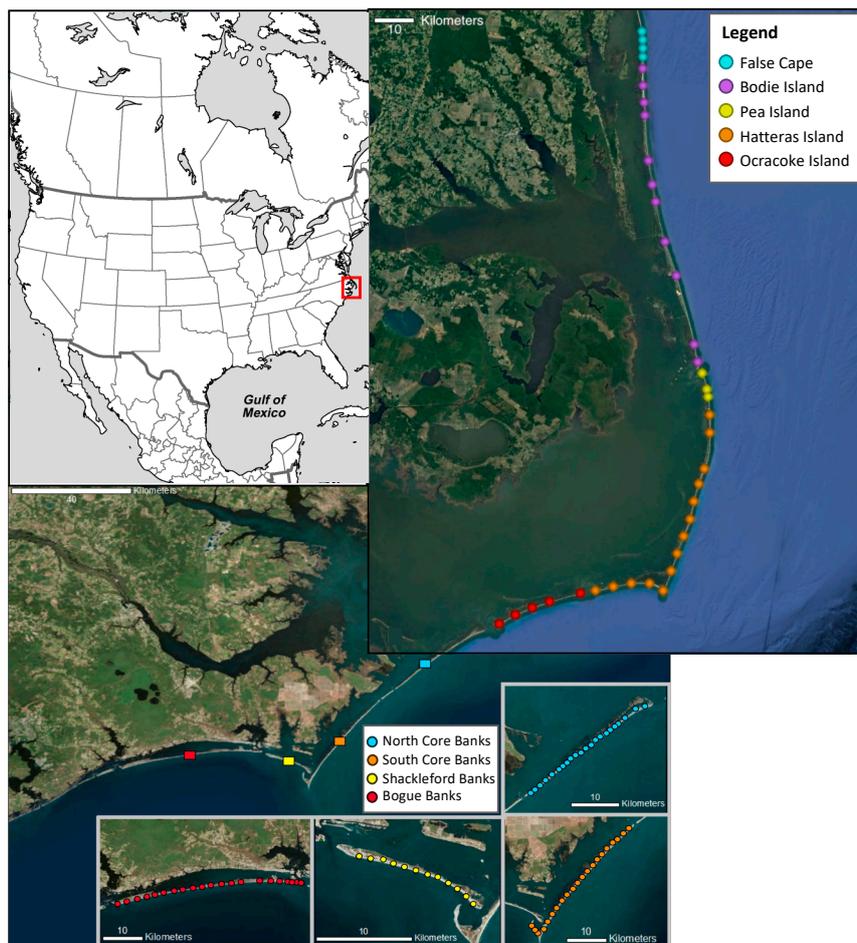


Figure 2. Map of the transect locations used to survey the distribution and abundance of foredune vegetation and the growth form and morphology of dune grass species along the barrier islands of the Outer Banks from False Cape, Virginia, to Bogue Banks, North Carolina, USA. Note that the transect locations for the southern islands are in the inset boxes at the bottom of the map.

2.2. Foredune Plant and Grass Distribution and Abundance Along the US Outer Banks Islands

From October 2016–June 2017, we documented the distribution and abundance of foredune plant species by established 112 cross-shore transects along the islands, separated by distances ranging from 0.4–20.4 km (most were 1–5 km apart), depending on the island and beach access (Figure 2, Table S1). The cross-shore transects started at approximately mean lower low water (MLLW) and moved onshore capturing the beach and then toe, crest, and heel of the foredune, and ending at the low point of the back dune. We visually estimated percent areal cover of all plant species and counted the number of shoots of the dune grass species contained within 0.25-m² quadrats at 5-m intervals along the cross-shore transects (see [11] for methods). Topography was also measured along the transects using a Network Real-Time Kinematic Differential Global Positioning System (R7 unit, Trimble, Sunnyvale, CA, USA). We resampled the plant community and topography along each of the 112 cross-shore transects a year later from October 2017–June 2018.

2.3. Dune Grass Growth Form, Morphology, and Changes in Sand Elevation

We measured the growth form and morphology of the four dominant dune grass species, *Ammophila breviligulata*, *Panicum amarum*, *Spartina patens*, and *Uniola paniculata* (Figure 1). We extracted one haphazardly chosen individual plant sample (defined as all the shoots attached to a single rhizome) of each grass species (when present) from the toe/face, crest, and heel/face of the foredune near each transect for both years of sampling. We included at least 15 cm of the rhizome and as many roots

as possible. We air-dried the plant samples to a constant mass and, for each, measured plant height (cm), plant weight (g per aboveground plant), shoot number (per plant), shoot weight (g per shoot), leaf number (per plant), leaf width (mm), ligule length (mm), rhizome internode length (cm), and root number (per node).

We estimated sand capture for the four dune grass species by measuring the change in elevation of the sand surface from one year to the next using our topographic data. The differences in elevation were calculated from quadrats that were at the face of the foredune and that had monocultures of each of the grass species (*A. breviligulata*, $n = 32$ quadrats; *P. amarum*, $n = 16$ quadrats; *S. patens*, $n = 2$ quadrats; and *U. paniculata*, $n = 85$ quadrats). The field-based change in sand elevation included natural variability in shoot density as well as differences in sand supply that could affect elevation and thus should be interpreted as correlative in nature.

2.4. Data and Statistical Analyses

Data were analyzed using R [36]. From our transect surveys, we calculated the (1) relative abundance of four plant functional groups (proportional cover for shrubs, vines, forbs, and grasses; percent cover per total percent cover for each transect) and the (2) relative abundance of the four most common dune grass species (proportional shoot density for *A. breviligulata*, *P. amarum*, *S. patens*, and *U. paniculata*; number of shoots per total number of shoots for each transect) for each of the islands in the study region. We used one-factor ANOVAs (and Tukey's Honest Significant Difference (HSD) post hoc tests) to separately test for differences in the relative abundance of each plant functional group and each dune grass species across the islands. We also calculated the relative abundance of the four most common dune grass species across the dune profile (i.e., dune toe, crest, and heel) using data from transects that had all four species present ($n = 9$). We used one-factor ANOVAs (and Tukey's HSD post hoc tests) to test for differences in the relative abundance of each dune grass species across the foredune profile.

We tested for differences in dune grass species growth form (i.e., plant number (per 0.25 m²), total shoot number (per 0.25 m²), and total aboveground biomass (g per 0.25 m²)) and plant and shoot morphology (i.e., plant height (cm), plant weight (g), shoot number (per plant), shoot weight (g), leaf number (per shoot), leaf width (mm), ligule length (mm), rhizome internode length (cm), and root number (per node)) using one-factor ANOVAs (Tukey's HSD post hoc tests).

To test for the changes in sand elevation associated with the four dune grass species, we used one-factor ANOVAs (and Tukey's HSD post hoc tests) for (1) all values of elevation change (i.e., accretion and erosion), and (2) those values with positive elevation change (i.e., accretion). There were only two elevation values for *S. patens*, so we did not include them in our statistical analyses.

3. Results

3.1. Foredune Plant and Grass Distribution and Abundance Along the Outer Banks Foredues

We found that foredues along the Outer Banks islands had a total of 53 plant species (Table S2): 14 grass species, 27 forb species, 8 vine species, and 5 shrubs and trees species. The islands differed in plant species richness, with Bodie Island and Hatteras Island having as much as double the number of plant species compared to the other islands (Figure 3). The relative abundance of plant functional groups also varied among the islands, with grasses dominating on all foredues, but especially on False Cape, North Core Banks, and Hatteras Island (Figure 3, Table S3A).

The four most common dune grass species were *A. breviligulata*, *P. amarum*, *S. patens*, and *U. paniculata* (Figures 1 and 4). Overall, of those species, *U. paniculata* was the most abundant, *A. breviligulata* and *P. amarum* had intermediate abundance, and *S. patens* was the least abundant, but this depended on the island (Figure 4). The northern islands generally had more *A. breviligulata* and *P. amarum* compared to the southern islands, which had more *U. paniculata* (Figure 4, Table S3B). Interestingly, Shackleford Banks lacked both *A. breviligulata* and *P. amarum*, and had low abundance of *S. patens*.

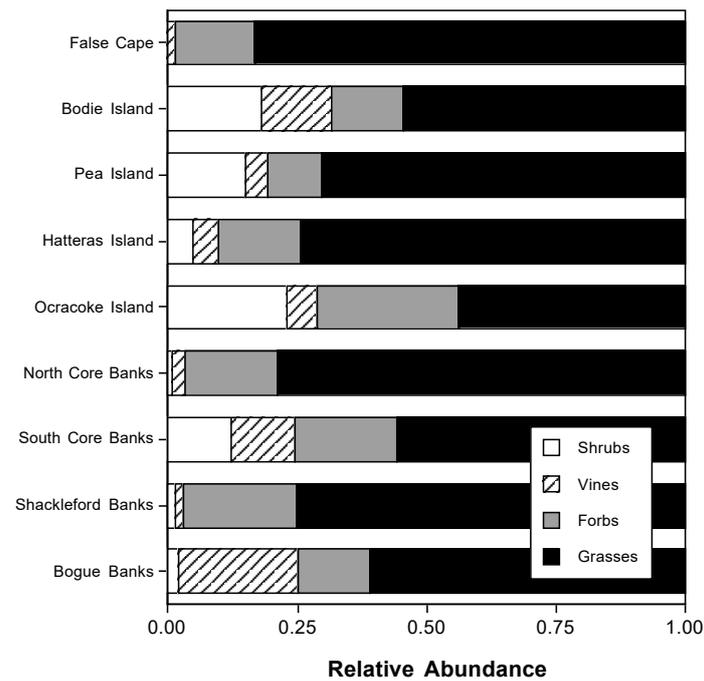


Figure 3. Distribution and relative abundance (proportional cover; percent cover per total percent cover of all functional groups) of plant functional groups (grasses, forbs, vines, and shrubs/trees) found in foredunes of the Outer Banks islands, USA (see Table S3A for statistics). Species richness for each island was the following: False Cape = 15 species, Bodie Island = 29 species, Pea Island = 10 species, Hatteras Island = 32 species, Ocracoke Island = 16 species, North Core Banks = 18 species, South Core Banks = 20 species, Shackleford Banks = 19 species, and Bogue Banks = 21 species. A plant species list for each functional group is given in Table S2.

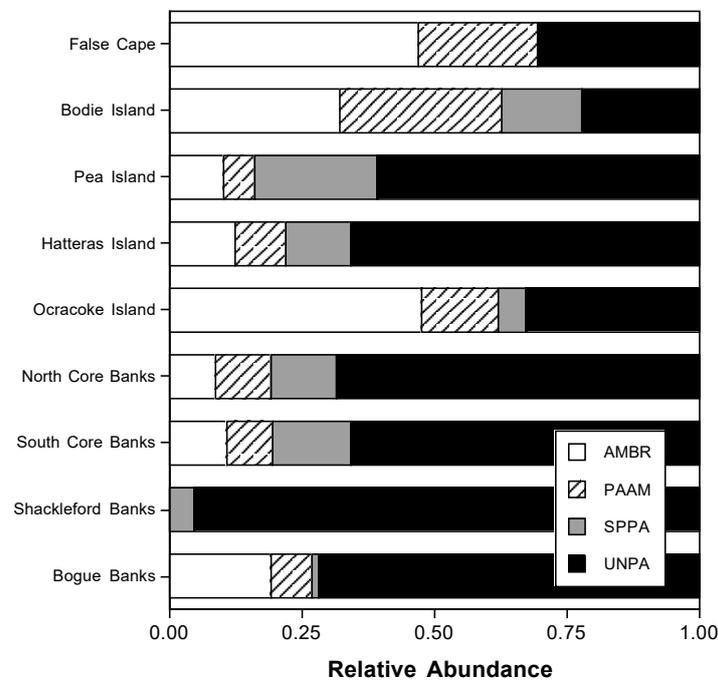


Figure 4. The distribution and relative abundance (proportional shoot density; number of shoots per total number of shoots for all dune grass species) of the dominant dune grass species (AMBR = *Ammophila breviligulata*, PAAM = *Panicum amarum*, SPPA = *Spartina patens*, UNPA = *Uniola paniculata*) found in the foredunes of the Outer Banks islands, USA (see Table S3B for statistics).

Of the foredunes where all the four dune grass species were present, species varied in their abundance along the cross-shore profile (Figure 5, Table S3C). *Uniola paniculata* and *A. breviligulata* were co-dominants at the foredune toe/face and *U. paniculata* was dominant at the foredune crest. *Spartina patens* was most abundant at the foredune back/heel, where it was co-dominant with *U. paniculata*. *Panicum amarum* had relatively low abundance across the profile.

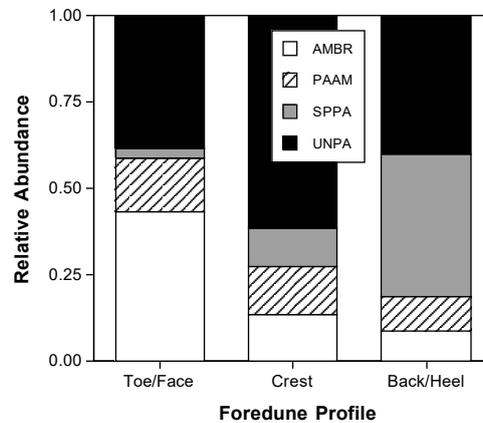


Figure 5. The distribution and relative abundance (proportional shoot density; number of shoots per total number of shoots for all dune grass species) of the dominant dune grass species (abbreviations in Figure 4) found along cross-shore profiles of foredunes that included all dune grass species within the Outer Banks islands, USA (see Table S3C for statistics).

3.2. Dune Grass Growth Form and Morphology and Changes in Sand Elevation

The four dune grass species had characteristic growth forms and morphologies. For a given 0.25-m² area, *A. breviligulata*, *P. amarum*, and *U. paniculata* had similar plant densities (~5 plants per 0.25 m²) but varied in total shoot density, with *A. breviligulata* having almost double the number of shoots than the other two species (Figure 6A,B, Table S4). *Spartina patens* had less than half the plant density (~2 plants per 0.25 m²) of the other species but the highest shoot density. Given the differences in shoot density and morphological measurements given below, total plant biomass (per 0.25 m²) decreased in the following order: *U. paniculata* > *A. breviligulata* > *P. amarum* = *S. patens* (Figure 6C).

For a given plant and shoot, *U. paniculata* was taller and weighed more on a per plant and per shoot basis than the other three species despite having similar or lower numbers of shoots per plant and leaves per shoot (Figure 7, Table S4). *Ammophila breviligulata* was somewhat shorter (by ~10 cm, on average), weighed less (especially on a per shoot basis), and had slightly fewer leaves per shoot than *U. paniculata*, but it also had one more shoot per plant on average (Figure 7, Table S4). Compared to the other species, *P. amarum* was considerably shorter, had fewer shoots per plant, and weighed less overall despite having a greater number of leaves, which were also wider than the other species (Figure 7, Table S4). *Spartina patens* had many more shoots and leaves than the three other species, but they were considerably thinner and intermediate in height, resulting in an overall plant weight just below *A. breviligulata* (Figure 7, Table S4). Finally, the plant species varied in ligule length, with *P. amarum* and *U. paniculata* having the longest ligules, *A. breviligulata* having intermediate ligules, and *S. patens* having the shortest ligules (Table S4; ANOVA $F_{3, 769} = 103.5, p < 0.0001$).

The four dune grass species differed in some characteristics of their rhizomes (Table S4). *Ammophila breviligulata* and *S. patens* had the shortest internodes compared to *P. amarum* and *U. paniculata*, which were slightly longer (Table S4; Internode length: ANOVA $F_{3, 2969} = 3.1, p < 0.01$). Only *A. breviligulata* and *P. amarum* internodes differed significantly from one another ($p = 0.026$); however, the difference between *A. breviligulata* and *U. paniculata* internodes bordered on significant ($p = 0.058$). Finally, *S. patens* had more than double the number of roots per node compared the other three grass species (Table S4; ANOVA $F_{3, 793} = 23.5, p < 0.0001$). *Ammophila breviligulata* had more roots than *P. amarum* and *U. paniculata*, which did not differ.

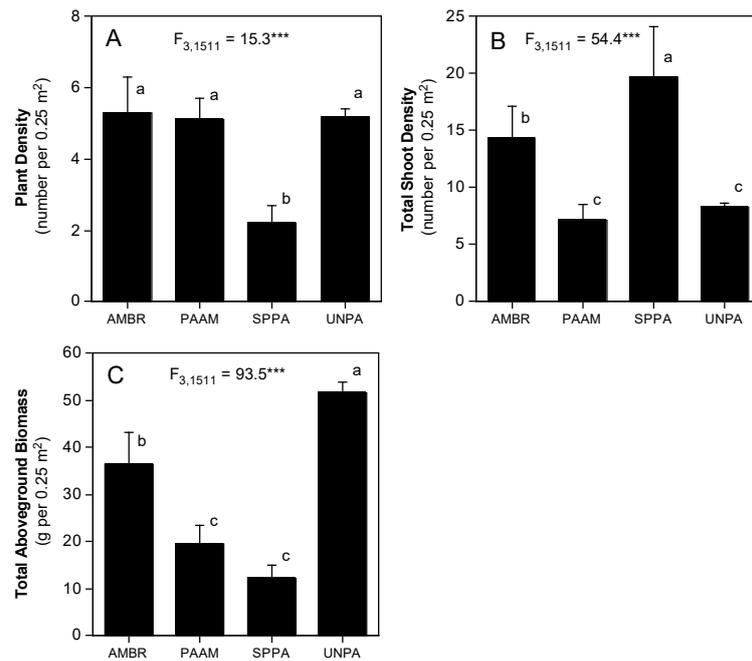


Figure 6. Comparisons (mean \pm 95% CI per 0.25 m²) of species growth form, measured as (A) plant density, (B) total shoot density, and (C) total plant biomass of the four most common dune grass species (abbreviations in Figure 4). One-factor ANOVA results are given in plots. Bars that do not share letters are significantly different (Tukey's HSD $p \leq 0.05$). *** $p < 0.0001$.

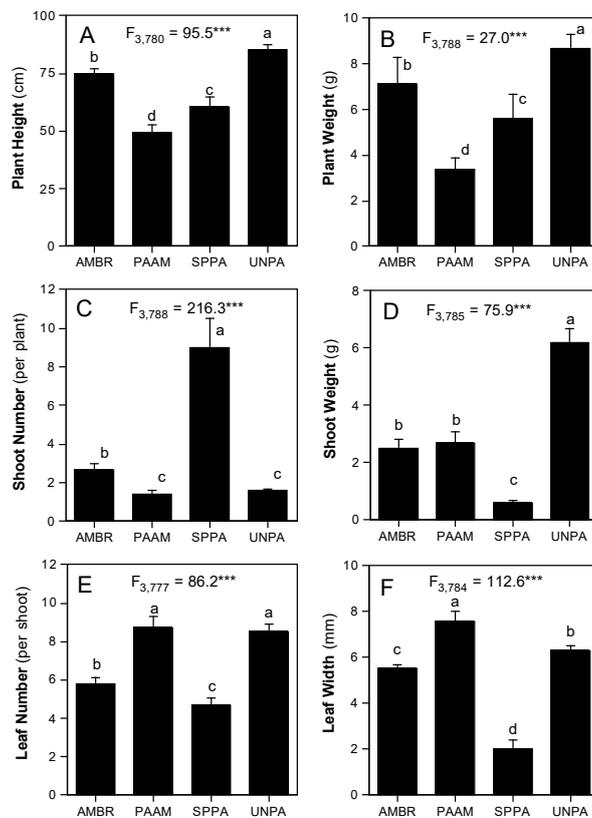


Figure 7. Comparisons (mean \pm 95% CI) of plant morphology, including (A) plant height, (B) plant weight, (C) shoot number, (D) shoot weight, (E) leaf number, and (F) leaf width of the four common dune grass species (abbreviations in Figure 4). One-factor ANOVA results are given in plots. Bars that do not share letters are significantly different (Tukey's HSD $p \leq 0.05$). *** $p < 0.0001$.

The average change in sand elevation on the foredune face ranged from approximately 0.10 to 0.35 m during the year (Figure 8). As might be expected, change in elevation was highly variable, with the greatest values found in plots with *A. breviligulata* (0.28 ± 0.09 m per year) and *P. amarum* (0.16 ± 0.14 m per year) (Figure 8A), which did not differ (Tukey's HSD $p \leq 0.05$). *U. paniculata* had the lowest values (0.09 ± 0.07 per year). If only positive elevation changes (i.e., sand accretion) are considered, *A. breviligulata* was associated with the greatest sand accretion (0.35 ± 0.06 m per year), followed by *U. paniculata* (0.24 ± 0.04 m per year) and *P. amarum* (0.22 ± 0.05 m per year) (Figure 8B), which did not differ (Tukey's HSD $p \leq 0.05$). We only had two elevation change measurements for *S. patens*, both of which showed accretion (0.22 and 0.21 m per year; the average is plotted in Figure 8B but was not included in the ANOVA analyses).

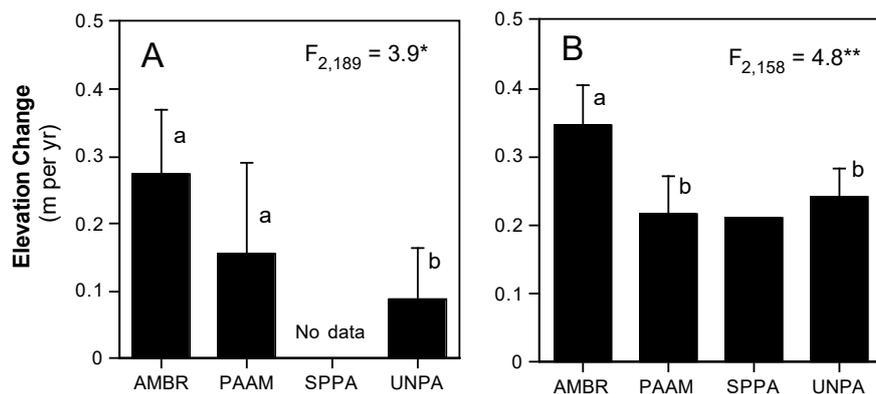


Figure 8. Comparisons (mean \pm 95% CI) of changes in sand elevation (m per year) in the field for (A) all values (sand accretion and erosion) and (B) only positive values (sand accretion) for quadrats with monocultures of the four dune grass species (abbreviations in Figure 4). One-factor ANOVA results are given in the plots. Bars that do not share letters are significantly different (Tukey's HSD $p \leq 0.05$). SPPA values in (B) are based on two values (0.22, 0.21) and were not included in the ANOVA analyses. * $p < 0.01$, ** $p < 0.001$.

4. Discussion

In this study, we found that a suite of dune grass species, which overlap in their distributions along the Outer Banks islands of the US Atlantic Coast, vary significantly in their patterns of functional morphology and sand accretion. The species-specific differences in dune grass functional morphology and bioengineering capabilities provide support for the differences in foredune morphology documented in previous planting experiments [4] and dune-building models [18] for this region. In particular, we found that *A. breviligulata* had functional morphology characteristics, including dense and clumped shoots, which are consistent with an ability to capture more sand than the other species. The dense growth form of *A. breviligulata* coupled with its propensity for lateral spread ($\sim 2\text{--}3$ m per year; [4]) likely allows it to build both relatively tall and wide foredunes, as was seen in a study by Woodhouse et al. [4]. On the other hand, *U. paniculata*, the most abundant foredune grass species on the Outer Banks islands, had the tallest and most robust shoots of all the species but as much as 42% less sand accretion compared to *A. breviligulata*. It appears that the sparser and more evenly spaced growth form of *U. paniculata*, coupled with its slow lateral spread (~ 0.6 m per year; [4]) is likely responsible for the narrower and more hummocky dunes seen in the results of Woodhouse et al. [4] and Goldstein et al. [18]. Finally, *P. amarum* had similar shoot densities and sand accretion values to *U. paniculata*, despite its shorter shoots (i.e., ~ 35 cm shorter than *U. paniculata*). Again, this sparser growth form, combined with potentially slower lateral spread, would tend to produce steeper, narrower foredunes similar to *U. paniculata*, supporting the hypothesis that the two grass species are functional equivalents in their dune-building capabilities [4].

Below we describe in more detail the species-specific functional morphology of the four dune grass species, compare these functional differences to those of US West Coast dune grass species, and discuss the potential consequences for foredune geomorphology and coastal protection given the current and projected latitudinal distribution patterns of these grasses along the US East Coast.

4.1. Species-Specific Functional Morphology and Associated Changes in Sand Elevation

We have shown that the specific growth form and morphological differences in four US East Coast dune grass species are associated with different changes in sand elevation in field settings. For example, comparing *A. breviligulata*, *P. amarum*, and *U. paniculata*, we found that while all had roughly the same plant density (Figure 6A, Table S4), *A. breviligulata* had two-fold greater shoot densities than *P. amarum* and *U. paniculata* (Figure 7, Table S4). In addition, even though *U. paniculata* shoots were taller and thicker than *A. breviligulata* shoots (~10 cm and 2.5-fold, respectively) or *P. amarum* (~25 cm and 2.3-fold, respectively) shoots (Figure 7, Table S4), *A. breviligulata* monocultures were associated with ~15 cm (or ~42%) more sand accretion over a year long period than the other two species, which did not differ (Figure 8). Interestingly, *Spartina patens* had up to 6-fold greater numbers of shoots per plant than the other species (Figure 7C), but plant densities were so low (~2 per m²) that shoot densities were only slightly greater than that of *A. breviligulata* (Figure 6B). *Spartina patens* shoots were also relatively short and very thin compared to the other species, likely explaining the lower sand accretion values similar to *P. amarum* and *U. paniculata* (Figure 8). Interestingly, a recent field experiment by Mullins et al. [37] demonstrated that although *S. patens* is less efficient in accreting sand than *A. breviligulata* and *U. paniculata*, it, too, functions as a dune builder, contrary to previous thought [38,39].

Taken together, the relationships between functional morphology and sand accretion suggest that the dense, clumped growth form of *A. breviligulata* in field settings is a more important factor than the fairly wide variation in shoot morphology that we document here. This result is similar to field and wind tunnel studies that compared sand accretion of three US West Coast dune grass species (*Ammophila arenaria*, *A. breviligulata*, and *Elymus mollis*; [11,12]). In particular, Zarnetske et al. [12] found a positive relationship between shoot density and sand accretion, irrespective of how individual shoot morphology affected sand capture efficiency for the three species. For example, even though the Pacific Northwest native American dune grass *Elymus mollis* had tall and thick shoots (similar to *U. paniculata*), and the greatest sand capture efficiency on a per shoot basis in the wind tunnel trials, its low field densities resulted in very poor sand accretion compared to the two non-native *Ammophila* congeners. In fact, although *A. arenaria* had the lowest sand capture efficiency on a per shoot basis of all the species, it had the highest sand accretion in field settings simply because of its dense tussock-like growth form.

We can use a conceptual model to expand our mechanistic understanding of the range of functional morphological differences in sand accretion among a suite of common dune grass species (Figure 9). Borrowing from the literature [11,12], the model integrates morphological and growth form variability for six species of dune grasses in North America (non-native European beachgrass *Ammophila arenaria*, American beachgrass *Ammophila breviligulata*, sea oats *Uniola paniculata*, bitter panicum *Panicum amarum*, American dune grass *Elymus mollis*, saltmeadow cordgrass *Spartina patens*) and hypothesizes the relative effects on sand capture. We suggest that dune grass species with a combination of dense plants, dense shoots, and clumped dispersion (e.g., the two *Ammophila* species) capture more sand than species with sparse plants, sparse shoots, and/or more evenly spaced dispersion (e.g., *E. mollis*; Figure 9). Dune grasses with some combination of, but not all, characteristics of higher density and/or clumped dispersion are associated with intermediate sand capture (e.g., *U. paniculata*, *P. amarum*, and *S. patens*; Figure 9). In addition, it is possible that differences in shoot characteristics such as height or weight play a mitigating role, albeit less than that of shoot density, which seems to be universal in its effects (this study, [11,12,19]).

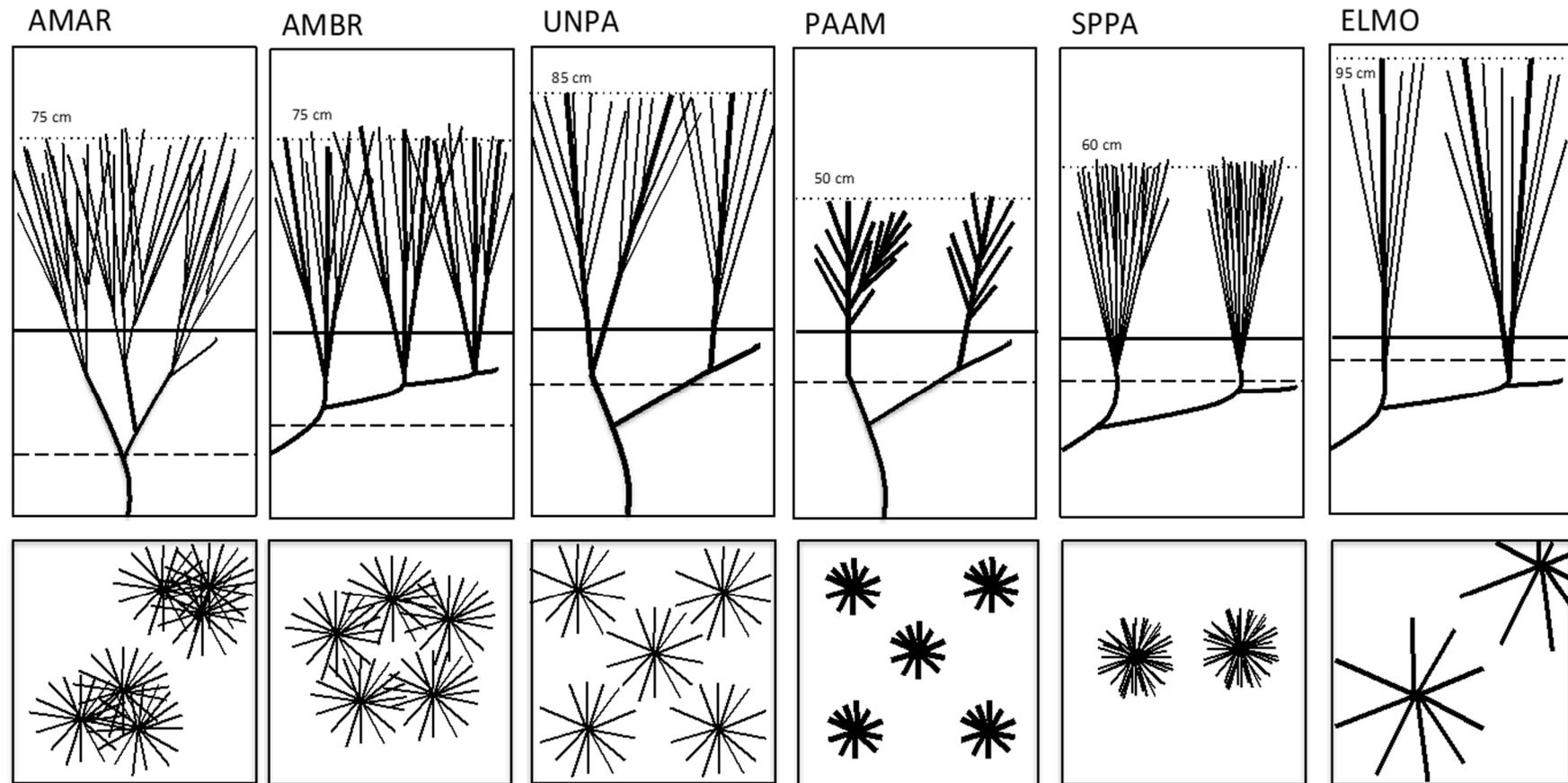


Figure 9. Diagram integrating growth form and morphological differences, as well as hypothesized relative differences in sand capture (represented by the distance from the solid line and the lower dashed line), among six species of dune grasses (AMAR = *Ammophila arenaria*, AMBR = *Ammophila breviligulata*, ELMO = *Elymus mollis*, PAAM = *Panicum amarum*, SPPA = *Spartina patens*, UNPA = *Uniola paniculata*) from US East Coast and West Coast foredunes. The stippled line and value represent average plant height (from this study and Hacker et al. [11]). The lower boxes represent 0.25-m² quadrats.

4.2. Dune Grass Distributions and the Consequences for Foredune Geomorphology and Coastal Protection Along the Outer Banks

It is important to consider the current and projected distributions of the four dune grass species and whether the associated species-specific changes in sand accretion we report here could play a role in dune geomorphology and coastal vulnerability along the Outer Banks islands and US Atlantic coast more generally. A recently published literature-based survey showed that *A. breviligulata* dominates foredunes north of Virginia and that *U. paniculata* dominates to the south [30]. The southern limit for *A. breviligulata* was determined to be Cape Fear, NC, and the northern range limit for *U. paniculata* was Assateague Island on the Maryland and Virginia border. These large-scale distributional differences are associated with physiological responses to climate. *Ammophila breviligulata* is a C₃ grass that prefers temperate climates, with plants susceptible to mortality above 35 °C [40,41]. *Uniola paniculata* is a C₄ grass that prefers warmer climates and appears to be limited by cold winter temperatures [42,43]. Although distributional information is less up-to-date, both *P. amarum* and *S. patens* are present from New England south to Florida and the Gulf Coast, with *P. amarum* more common to the south ([10,44,45]; although note that it is more abundant to the north in our surveys, Figure 4). Goldstein et al. [30] also noted that there is evidence for a northern range expansion of *U. paniculata* (but not a northward shift in the southern extent of *A. breviligulata*), possibly as a consequence of warming trends to the north.

Taken together, the current and projected distributions of US East Coast dune grass species suggest that, all other factors being equal (e.g., shoreline change rate, sand supply to the beach and dune, wave regime, and relative sea level rise), foredunes should be inherently taller and wider, and have better coastal protection properties, along coastal dunes north of Virginia where *A. breviligulata* is the dominant dune builder. In addition, if under warming conditions *A. breviligulata* experiences a range shift to the north, as appears to be occurring with *U. paniculata*, changes in grass dominance and foredune morphology could make coastal regions more vulnerable to erosion and overtopping. Interestingly, in an observational study in the Great Lakes region, Emery and Rudgers [41] found that *A. breviligulata* plants were taller at lower latitudes but shoot densities did not vary with any climate variables. Thus, while shifts in dune grass species' ranges are important to document, focusing on the physiological and morphological changes of dune grasses with changing climate is likely to be equally important to predicting foredune landscapes in the future.

Within the Outer Banks region, our surveys verify that all four species of dune grasses overlap in their distribution, but *U. paniculata* is the most abundant overall and *A. breviligulata* and *P. amarum* decrease somewhat in abundance to the south (Figure 4). Interestingly, Shackleford Banks is overwhelmingly dominated by *U. paniculata* and completely lacking in *A. breviligulata* and *P. amarum*. This island is part of Cape Lookout National Seashore and has the most restricted access of the islands within the park (which also includes North and South Core Banks). Shackleford Banks protects a remnant population of wild horses, whose grazing pressure might be a factor in the lack of dune grass species diversity found there. While the slight latitudinal pattern in dune grass species distribution and abundance that we observed along the Outer Banks islands could be a consequence of physiological range limits, species interactions (e.g., *A. breviligulata* was found to be an inferior competitor compared to *U. paniculata* in manipulative experiments [46,47]) and/or intentional planting for foredune restoration are also likely important. The distributional legacy of dune grass management could be especially important on the highly developed island of Bogue Banks, where *A. breviligulata* has been intentionally planted in restoration projects.

Finally, whether the large-scale distributional patterns of the four dune grass species within the Outer Banks islands, and the Atlantic coast more generally, have consequences for dune geomorphology and coastal vulnerability remains, as yet, an unanswered question. Determining the functional role of dune grass species to dune geomorphology at regional scales will require quantitative analyses that partition the relative contribution of sand supply, beach geomorphology, and dune grass species abundance, similar to the studies of Zarnetske et al. [13] and Biel et al. [19] for beachgrasses on the US Pacific Northwest coast. However, this and other recent research on dune grasses, and their

species-specific effects on foredune geomorphology, make it clear that understanding these relationships is critical to the management of these important and vulnerable coastal ecosystems now and in the future.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/11/5/82/s1>: Table S1: Transect locations, north to south, used to survey the distribution and abundance of vegetation along foredunes of the Outer Banks islands from False Cape, Virginia, to Bogue Banks, North Carolina, USA (see Figure 2), Table S2: List of the 53 plant species found in foredune surveys of the Outer Banks islands from False Cape, Virginia, to Bogue Banks, North Carolina, USA, Table S3: One-way ANOVAs and associated Tukey's post hoc tests ($p \leq 0.05$) for the abundance of (A) plant functional groups (grasses, forbs, vines, and shrubs) on different islands (abbreviations in Table S1), (B) dune grass species (abbreviations in Table S2) on different islands, and (C) dune grass species across the dune profile (toe/face, crest, and heel/back) in foredunes of the Outer Banks islands from Virginia to North Carolina, USA, Table S4: Mean (\pm 95% CI) growth form and morphological differences of the four dominant dune grass species (abbreviations in Table S2) in foredunes of the Outer Banks islands, USA.

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