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Differential response of barrier island dune grasses to species interactions and burial

April L. Harris · Julie C. Zinnert · Donald R. Young

Abstract Barrier islands are at the forefront of storms and sea-level rise. High disturbance regimes and sediment mobility make these systems sensitive and dynamic. Island foredunes are protective structures against storm-induced overwash that are integrally tied to dune grasses via biogeomorphic feedbacks. Shifts in dune grass dominance could influence dune morphology and susceptibility to overwash, altering island stability. In a glasshouse study, two dune grasses, *Ammophila breviligulata* and *Uniola paniculata,* were planted together and subjected to a 20 cm burial to quantify morphological and physiological responses. Burial had positive effects on both plants as indicated by increased electron transport rate and total biomass. *Ammophila breviligulata* performance declined when planted with *U. paniculata*. *Uniola paniculata* was not affected when planted with *A. breviligulata* but did have higher water use efficiency and nitrogen use efficiency. Planted in mixture, differential reallocation of biomass occurred between species potentially altering resource acquisition further. As *U. paniculata* migrates into *A. breviligulata* dominated habitat and *A. breviligulata* performance diminishes, biotic interactions between these and other species may affect dune formation and community structure. Our study emphasizes the importance of studying biotic interactions alongside naturally occurring abiotic drivers.

Keywords Ammophila breviligulata · Uniola paniculata · Biogeomorphic feedback · Species migration · Climate change

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Introduction

Barrier islands comprise ∼15% of world coastlines (van Heteren 2014; Zinnert et al. 2016). They protect the mainland from storms (Seabloom et al. 2013), protect back-barrier estuaries and wetlands, and provide habitat for rare and endangered plants and animals (Masterson et al. 2014). Barrier islands are sensitive and dynamic systems due to high disturbance frequency, sediment mobility, and biogeomorphic feedbacks (Stallins and Parker 2003; Brantley et al. 2014; Zinnert et al. 2016). Increased frequency in storms have the potential to alter biotic responses of vegetation through abiotic factors such as overwash (Durán and Moore 2013; Miller 2015). Species migrations could further shape dune-building through differentiated responses to overwash.

Within coastal research, biotic feedback and species migrations have largely been ignored in favor

of physical processes such as storm impacts and sea-level rise. Within terrestrial systems, large bodies of work have dealt with projected or expected species migrations and the effects on ecosystem process (Walther et al. 2002; Parmesan and Hanley 2015). This knowledge is currently lacking for coastal ecosystems. Climate change has the potential to alter coastal systems through increased global temperature (Wang et al. 2014) and increased frequency of storms (Hayden and Hayden 2003). Increased temperature could indirectly alter barrier islands through shifts in flora distribution patterns, while increased storms can result in overwash and sediment burial.

Semitropical plant species may experience a latitudinal expansion due to increased temperatures, which would shift plant community compositions in coastal systems (Gonzalez et al. 2010). On the North American Atlantic coast, specifically the barrier islands of Virginia, the semitropical dune grass *Uniola paniculata* has the potential to expand its range northward into the habitat of *Ammophila breviligulata*, the dominant dune grass species of mid-Atlantic coastlines. These two species currently co-occur on the Outer Banks, NC (Hodel and Gonzalez 2013) and sparse populations have been observed on the Virginia barrier islands (Young, personal observation). Expansion into the Virginia barrier islands represents the two species interacting on undeveloped barrier islands unlike the Outer Banks of North Carolina which are heavily managed to control island stability (Dolan 1972).

Rooting strategies of these two dune-building grasses result in different initial dune formations. Foredunes established by *A. breviligulata*, a C_3 or cool season species, are long and continuous along the shoreline (Ehrenfeld 1990; Brantley et al. 2014). *Ammophila breviligulata* is clonal and has "guerrilla root" morphology (Stallins 2005; Brantley et al. 2014). Connections between ramets are separated by long internodes resulting in widely spaced ramets that influence dune morphology (Ye et al. 2006; Emery and Rudgers 2013; Brantley et al. 2014). It is a dominant pioneer species of foredune habitat that once established, plays an important role capturing sand and creating tall foredunes (Emery and Rudgers 2014). *Ammophila breviligulata* can withstand very high rates of sand burial, up to 1 m of sand per year, which significantly contributes to foredune formation (Maun and Lapierre 1984).

In contrast, *U. paniculata*, a C_4 or warm season species, displays phalanx rhizome growth. Internode connections between ramets are very short which result in clumps of ramets that create hummocky dunes (Ye et al. 2006). Similar to *A. breviligulata*, *U. paniculata* is often the dominant species within its range and tolerates burial (Lonard et al. 2011). It is also very tolerant of sea spray (Lonard et al. 2011; Miller et al. 2003). The northern habitat range of *U. paniculata* on the southern barrier islands of Virginia is limited by winter temperatures (Lonard et al. 2011); however, recent climate data show warming during winter months on the Virginia barrier system (Zinnert et al. 2011).

Warmer temperatures associated with climate change could enhance the northern expansion of *U. paniculata* further into the Virginia barrier island system due to its C_4 photosynthetic pathway (Lonard et al. 2011). Expansion would most likely occur during an overwash event where waves transport sand across the strand and over the foredune creating an overwash fan (Brantley et al. 2014). Within deposited sand on overwash fans, propagules of *U. paniculata* and *A. breviligulata* could establish alongside one another (Maun 1984; Lonard et al. 2011) resulting in potential for biotic interactions. Although both *A. breviligulata* and *U. paniculata* are adapted to strandline conditions such as salt spray, sand deposition, and high solar radiation, the difference in photosynthetic pathway (C_3 vs. C_4) could give *U. paniculata* a competitive advantage due to its tolerance for higher temperatures and higher water use efficiency (WUE) when grown with *A. breviligulata* (Way et al. 2014).
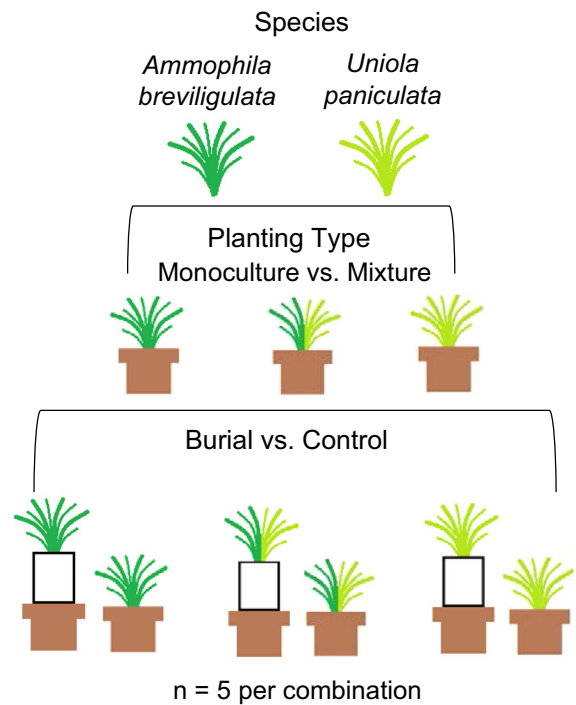
Vegetation change on foredune habitats of barrier islands resulting from range expansion of a species can alter plant responses to burial due to species interactions. Foredune vegetation has a strong impact on dune morphology through influences on sediment deposition and mobility (Stallins and Parker 2003; Hacker et al. 2012; Zarnetske et al. 2012; Miller 2015; Charbonneau et al. 2016). Differences in dune morphology can occur over relatively short time scales (Stallins and Parker 2003) and influence island susceptibility to overwash events (Wolner et al. 2013). This becomes even more important in the future as climate change alters the intensity, frequency, and track of hurricanes (Masselink and Heteren 2014) as well as sea-level rise (Mousavi et al. 2011; Williams 2013).

Quantifying biotic interactions of dune grasses under abiotic drivers is essential when predicting plant response as both can act together as influencing factors (Zarnetske et al. 2013; He and Bertness 2014). However, there are relatively few studies that examine both biotic interaction and abiotic drivers in an experimental setting. The objective of our study was to determine how growth of the dominant dune grasses *A. breviligulata* and *U. paniculata* respond when grown in monoculture or mixture planting under burial, a common abiotic driver. Specifically, we quantified physiological and morphological responses of these dune grasses related to growth and productivity. We hypothesized that *U. paniculata* will outperform *A. breviligulata* due to the advantages associated with having a C_4 photosynthetic pathway.

Methods

Experimental design

Ammophila breviligulata (American beachgrass) is a perennial dune grass native to the Atlantic coast with a range from North Carolina, USA to Newfoundland, CA and shorelines of the five Great Lakes (Emery and Rudgers 2013). *Uniola paniculata* (sea oats) is perennial, semitropical grass that occurs on dunes in the Bahamas, Cuba, and from eastern Mexico northward to southern Virginia (Hodel and Gonzalez 2013). For our glasshouse study *A. breviligulata* and *U. paniculata* ramets ($\sim$25 and 30 cm, respectively) were obtained from Cape Coastal Nursery, South Dennis, MA and Coastal Transplants, Bolivia, NC, respectively. Distance between ramet sources was driven by availability constraints. Vegetative propagules of *A. breviligulata* can survive ocean transport for some distance (Maun 1984) resulting in variable source location. Species were planted in three combinations: *A. breviligulata* alone, *U. paniculata* alone, and in a 50:50 mixture with one another ($n = 5$ per combination) (Fig. 1). A total of 6 individual stems were planted per 15 $\times$ 15 cm pot containing 1.8 kg of sand. Sand was a 3:1 mixture of unsterilized sand collected from a Virginia barrier island (Hog Island) and commercial sand. The experiment was conducted from late May 2015 to early July 2015 (9 weeks). Glasshouse photosynthetic photon flux density was $\sim$1300 μmol m^{-1} s^{-1} with a mean temperature

Species

Ammophila breviligulata   *Uniola paniculata*

Planting Type
Monoculture vs. Mixture

Burial vs. Control

n = 5 per combination

Fig. 1 Multifactorial design consisting of two dune-building grasses, two planting types, and burial treatment (20 cm) or control (0 cm)

of 31.3 °C and a mean daily high of 40 °C (Thermodata ibutton data logger). Glasshouse temperatures are characteristic of those on Hog Island, VA, during the summer (Thompson et al. 2017).

A 1 cm sand addition was given to all plants at the beginning of the experiment to promote vigor and stimulate growth, and all plants were trimmed to 35 cm to standardize height. For burial treatment, one half of each planting type received an additional 20 cm burial to simulate overwash (Fig. 1). A 20 cm burial was chosen because this represents possible sand deposition from a single storm event on the Virginia barrier islands (Harris, personal observation). Reference plants did not receive additional burial.

To limit nutrient stress, each pot was treated with 25 ml of Hoagland's solution (Hoagland and Arnon 1950) diluted to 50 ml with tap water, twice during the study. Plants were kept well watered throughout the experiment. Instant Ocean by Aquarium Systems, mixed to a diluted concentration of sea water (20 ppt), was sprayed on all plants once weekly to simulate sea spray. Sea spray solution was rinsed off leaves through

watering 24 h later to ensure leaf necrosis did not occur.

Measurements

Physiological measurements were conducted at the end of the experiment on one leaf from each species in each pot. Measurements were taken at midday (1100–1300 h) on cloudless days. Stomatal conductance to water vapor diffusion (g_s mmol H_2O m^{-2} s^{-1}) was quantified using a porometer (SC-1 Leaf Porometer, Decagon Devices Inc., USA). Electron Transport Rate (ETR), a measure of photosynthetic potential, was measured using the miniPAM (Walz, Germany).

At the end of the experiment, plant height was measured with a meter stick from the pre-burial sand surface to the tip of the longest leaf. Relative growth rate (RGR) was calculated from height measurements using the following equation: RGR = ($\ln \cdot L_2 - \ln \cdot L_1$)/ ($t_2 - t_1$) where L_1 and L_2 are starting height and final height and t_1 and t_2 are start and end of experiment in days. Number of alive leaves were counted. Aboveground and belowground biomass were separated, oven dried at 60 °C for 72 h, and weighed on a digital scale. Change in contribution (CC) is the amount of biomass, a species attained in a mixture divided by the expected amount from monoculture plantings minus one (Williams and McCarthy 2001). This gives the proportional change in contribution of biomass in mixture versus monoculture plantings, allowing a comparison of species in different planting combinations (Williams and McCarthy 2001). CC was calculated from biomass weight using the following set of equations:

$$CC_A^D = \left(Y_{AB}^D / \left(Y_{AB}^D + Y_{BA}^D\right)\right) / \left(\left(p_A Y_A^D\right) / \left(p_A Y_A^D + p_B Y_B^D\right)\right) - 1$$

$$CC_B^D = \left(Y_{BA}^D / \left(Y_{AB}^D + Y_{BA}^D\right)\right) / \left(\left(p_B Y_B^D\right) / \left(p_A Y_A^D + p_B Y_B^D\right)\right) - 1$$

obtained from Williams and McCarthy (2001), where CC_A^D is the change in contribution of species A at density D, CC_B^D is the change in contribution of species B at density D, Y_{AB}^D is the yield of species A in the presence of species B at density D, Y_{BA}^D is the yield of species B in the presence of species A at density D, Y_A^D is the yield of species A in monoculture at density D, Y_B^D is the yield of species B in monoculture at density

D, and p_A is the proportion with which species A was sown, and p_B is the proportion with which species B was sown such that $p_A + p_B = 1$ is always true (Williams and McCarthy 2001). CC > 1.0 indicates that a species grew better in an interspecific mixture than in monoculture. In contrast, CC < 1.0 indicates that species grew better in monoculture than with another species. Increases or decreases in CC indicate the percent increase or decrease in biomass (Williams and McCarthy 2001).

$\delta^{13}C$, %N, %C, C:N measurements were obtained from each plant to provide insight into nutrient and water use efficiency. Plant leaves were dried at 60 °C for 72 h and ground into a fine powder with a handheld electric grinder. Further processing (i.e., weighing and encapsulating), nutrient, and isotope analysis were conducted at the Cornell University Stable Isotope Lab, Ithaca, New York, USA.

Statistical analysis

Three-factor analysis of variance (ANOVA) quantified variations in measurement variables due to burial, species, and planting scheme (monoculture vs. mixture). For significant three-way interactions, two-factor analysis of variance was used to further examine planting type x burial interactions within each species. Two-factor analysis of variance was also used to quantify variations in burial and species for change in contribution. Drawing broad conclusions from multiple individual measures that are correlated with one another, e.g., plant morphological and physiological traits, can be difficult. Multivariate analysis aids in the interpretation of multiple correlated measures by expressing them in fewer dimensions through data reduction. Principal components analysis (PCA, PC-ORD software v. 5.10) of all measurement variables were used to separate species and treatments and determine which traits were most important for influencing separation. Measurement variables were standardized using a correlation matrix. Axes were retained if observed eigenvalues exceeded broken-stick eigenvalues (Jackson, 1993). Resulting PCA groups were compared using multiple response permutation procedures (MRPP) with the same measurement variables as in the PCA. Measurement variables were standardized using Z-scores.

Table 1 Three-way ANOVA results (f,p) of electron transport rate (ETR), stomatal conductance (g_s), $\delta^{13}C$, %N, %C, C:N, total biomass, relative growth rate (RGR), and number of alive leaves for the independent variables species (S), planting (P), and Burial (B)

	S	P	B	S × P	S × B	P × B	S × P × B
ETR	7.9, **0.008**	1.9, 0.174	19.1, **0.0001**	2.3, 0.140	0.6, 0.437	1.3, 0.266	0.2, 0.631
g_s	1.7, 0.206	5.2, **0.029**	2.2, 0.145	8.2, **0.007**	1.2, 0.277	0.2, 0.625	0.2, 0.623
$\delta^{13}C$	7587.5, **<0.0001**	1.1, 0.310	1.3, 0.257	10.7, **0.0025**	0.2, 0.651	1.5, 0.224	2.2, 0.145
% N	39.8, **<0.0001**	1.0, 0.318	9.2, **0.0001**	18.2, **0.0001**	0.8, 0.387	0.2, 0.632	0.8, 0.372
% C	0.1, 0.775	1.4, 0.248	4.1, 0.051	2.3, 0.136	0.4, 0.514	3.2, 0.082	0.2, 0.700
C:N	38.0, **<0.0001**	7.2, **0.011**	11.4, **0.002**	24.9, **<0.0001**	3.3, 0.078	2.5, 0.123	3.8, 0.061
Total biomass	4.4, **0.044**	17.7, **0.0002**	4.2, **0.048**	8.7, **0.006**	0.4, 0.537	0.1, 0.789	0.3, 0.569
AGB	3.4, 0.075	0.6, 0.434	0.8, 0.379	0.2, 0.688	7.3, **0.011**	2.6, 0.119	5.9, **0.021**
BGB	16.5, **0.0003**	36.3, **<0.0001**	0.8, 0.392	7.6, **0.009**	1.0, 0.323	0.1, 0.801	0.6, 0.460
RGR	227.8, **<0.0001**	5.4, **0.027**	26.4, **<0.0001**	11.2, **0.002**	8.4, **0.007**	0.3, 0.568	6.4, **0.016**
# of Alive leaves	52.9, **<0.0001**	1.8, 0.183	0.1, 0.766	25.0, **<0.0001**	17.5, **0.0002**	8.1, **0.008**	2.7, 0.111

Bold indicates significance at α = 0.05. Degrees of freedom are 7, 34 for all measures

Results

Physiology

There were no significant species x planting type x burial interactions for physiological measurements (ETR, g_s, $\delta^{13}C$, %N, C:N) (Table 1). There were no interactions for electron transport rate (ETR) but there was an effect of species and burial; ETR was enhanced for both species with burial. *Uniola paniculata* had a higher mean ETR than *A. breviligulata* under both burial regimes (Fig. 2). While not significant, there was a trend of *A. breviligulata* monoculture planting mean ETR being higher when compared to being grown in mixture with *U. paniculata* (Fig. 2).

All other physiological measurements (g_s, $\delta^{13}C$, %N, C:N) had a significant species x planting type interaction (Table 1). Stomatal conductance was significant among planting type (Table 1). When planted with *A. breviligulata*, *U. paniculata* stomatal conductance experienced a 34.8% increase with burial compared to control, whereas buried monoculture plantings only increased 18.4%. Stomatal conductance of *A. breviligulata* grown in monoculture was higher than mixture plantings (Table 2). $\delta^{13}C$ was higher for *U. paniculata* than *A. breviligulata* (Table 1). Percent nitrogen was higher for *A. breviligulata* than *U. paniculata* and burial was higher than controls (Table 1; Fig. 2). Percent nitrogen had a significant

species x planting type interaction where *A. breviligulata* had higher percent nitrogen in monoculture relative to mixture plantings and *U. paniculata* showed the opposite response with higher nitrogen in mixture plantings than monoculture (Fig. 2). C:N was higher for *U. paniculata* than *A. breviligulata* and buried plants had an 18.1% lower C:N than controls (Tables 1, 2).

Morphology

Total biomass had a significant species x planting type interaction (Table 1). Total biomass for monoculture plantings for both species was higher than for mixture plantings and burial yielded higher biomass than controls (Table 1). *Ammophila breviligulata* total biomass was higher than *U. paniculata* (Table 1). Change in contribution for aboveground biomass (CCAB) had a significant species x planting type interaction ($F_{3,16} = 11.2$, $p = 0.004$) where *A. breviligulata* decreased in aboveground biomass when not buried but and increased when buried in relation to monoculture plantings (Fig. 3). *Uniola paniculata* showed the opposite response where aboveground biomass increased when not buried but decreased when buried (Fig. 3). Change in contribution for belowground biomass (CCBB) had a significant effect of species ($F_{3,16} = 4.4$, $p = 0.009$) where *A. breviligulata* belowground biomass decreased and *U.*
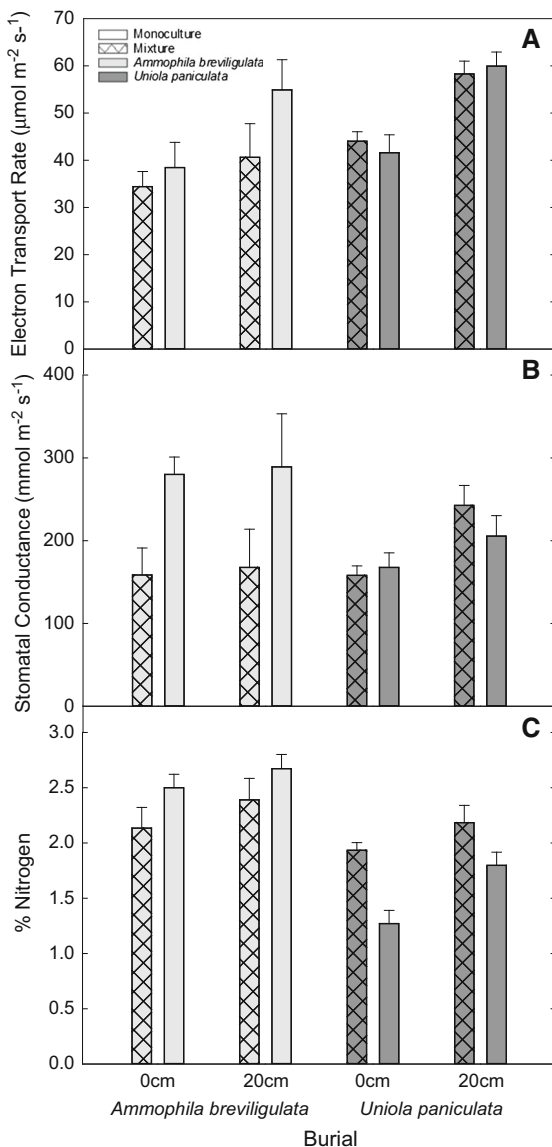
Fig. 2 *Ammophila breviligulata* and *Uniola paniculata* electron transport rate, stomatal conductance, and % nitrogen for control/buried treatment and monoculture/mixture planting type. Values are means ±1 standard error

paniculata increased when compared to respective monoculture plantings (Fig. 3).

Relative growth rate (RGR) exhibited significant species × planting type × burial interaction (Table 1). *Ammophila breviligulata* monoculture planting RGR was higher than mixture planting; however, burial had no effect (Table 2). *Uniola paniculata* displayed an opposite pattern where RGR was higher for buried treatment but planting type had no effect (Table 2).

Number of alive leaves exhibited a significant species × planting type interaction (Table 1). *Uniola paniculata* mixture planting had more leaves than monoculture planting and *A. breviligulata* monoculture planting had more leaves than mixture plantings (Table 2). It also exhibited a significant species × burial interaction, where burial increased leaf number of *U. paniculata* (Table 2), and planting type × burial interaction (Table 1). *Uniola paniculata* was higher than *A. breviligulata* with the exception of *A. breviligulata* control monoculture (Table 2).

Combined traits

Principal components analysis axis 1 explained 32.8% of the variation with $\delta^{13}C$ ($r = -0.94$) and RGR (-0.81) being most influential in providing separation (Table 3). Axis 2 explained 28.5% of data variation. Total biomass ($r = 0.83$) and ETR ($r = 0.68$) were most influential in providing separation (Table 3). The four resulting groups (*A. breviligulata* monoculture vs. mixture, *U. paniculata* buried vs. control) from PCA were significantly different (MRPP, $t = -16.89$, $A = 0.47$, $p < 0.0001$; Fig. 4). *Uniola paniculata* separated completely from *A. breviligulata*. *Ammophila breviligulata* grouping further divided into monoculture plantings versus mixture plantings, while *U. paniculata* separated based on burial level (Fig. 4).

Discussion

Coastal drivers, such as storms and sea-level rise, that alter sediment movement have gained attention because of their ability to restructure coastlines (Roelvink et al. 2009). Biotic interactions also play an important role in the structure and function of barrier islands (Stallins 2005; Feagin et al. 2015). As climate change alters abiotic conditions and range expansion of species occurs, it is crucial to understand biotic interactions with present species. *Uniola paniculata* has the potential to expand northward along the Atlantic coast into *A. breviligulata* dominated habitat. This has been documented on the Virginia barrier islands (Young, personal observation). The relationship between *A. breviligulata* and *U. paniculata*, and response both morphologically and physiologically, to environmental factors such as burial may have ecosystem consequence based on root growth strategy

Table 2 $\delta^{13}C$, %C, C:N, total biomass, aboveground biomass (AGB), belowground biomass (BGB), # of alive leaves, relative growth rate (RGR), mean ± standard error

	A-MX-NB	A-MX-B	A-MO-NB	A-MO-B	U-MX-NB	U-MX-B	U-MO-NB	U-MO-B
$\delta^{13}C$	−27.0 ± 0.3[bc]	−26.5 ± 0.8[b]	−27.2 ± 0.1[bc]	−27.3 ± 0.1[c]	−16.6 ± 0.1[a]	−16.5 ± 0.1[a]	−16.3 ± 0.1[a]	−16.2 ± 0.1[a]
%C	43.3 ± 0.3[ab]	45.9 ± 0.3[ab]	46.6 ± 0.5[ab]	45.5 ± 0.40[b]	45.5 ± 0.3[ab]	45.8 ± 0.4[ab]	46.9 ± 0.5[a]	45.9 ± 0.1[ab]
C:N	22.3 ± 1.6[c]	19.8 ± 1.6[abc]	18.8 ± 0.8[ab]	17.2 ± 0.8[a]	23.7 ± 0.7[bc]	21.5 ± 1.9[abc]	38.4 ± 3.2[bc]	26.9 ± 1.8[abc]
Total biomass	1.1 ± 0.1[c]	1.3 ± 0.2[abc]	2.0 ± 0.1[a]	2.0 ± 0.1[a]	1.2 ± 0.2[c]	1.4 ± 0.2[abc]	1.3 ± 0.1[bc]	1.6 ± 0.2[abc]
AGB	0.8 ± 0.0[bc]	1.0 ± 0.2[abc]	1.1 ± 0.0[ab]	0.8 ± 0.1[c]	1.0 ± 0.1[abc]	1.2 ± 0.2[a]	0.8 ± 0.1[c]	1.2 ± 0.1[a]
BGB	0.3 ± 0.0[cd]	0.4 ± 0.0[cd]	0.8 ± 0.1[b]	1.3 ± 0.0[a]	0.2 ± 0.1[d]	0.2 ± 0.0[cd]	0.5 ± 0.1[c]	0.4 ± 0.1[cd]
# of Alive leaves	1.5 ± 0.2	1.5 ± 0.6	4.7 ± 0.4	2.0 ± 0.5	4.4 ± 0.5	5.9 ± 0.7	3.7 ± 0.1	4.5 ± 0.1
RGR	0.2 ± 0.1[e]	0.5 ± 0.1[de]	0.8 ± 0.02[d]	0.7 ± 0.05[d]	1.3 ± 0.1[bc]	1.7 ± 0.1[ab]	1.1 ± 0.1[c]	1.7 ± 0.1[a]

A Ammophila breviligulata, *U* Uniola paniculata, *MX* Mixture planting, *MO* Monoculture planting, *B* Burial, *NB* Not buried

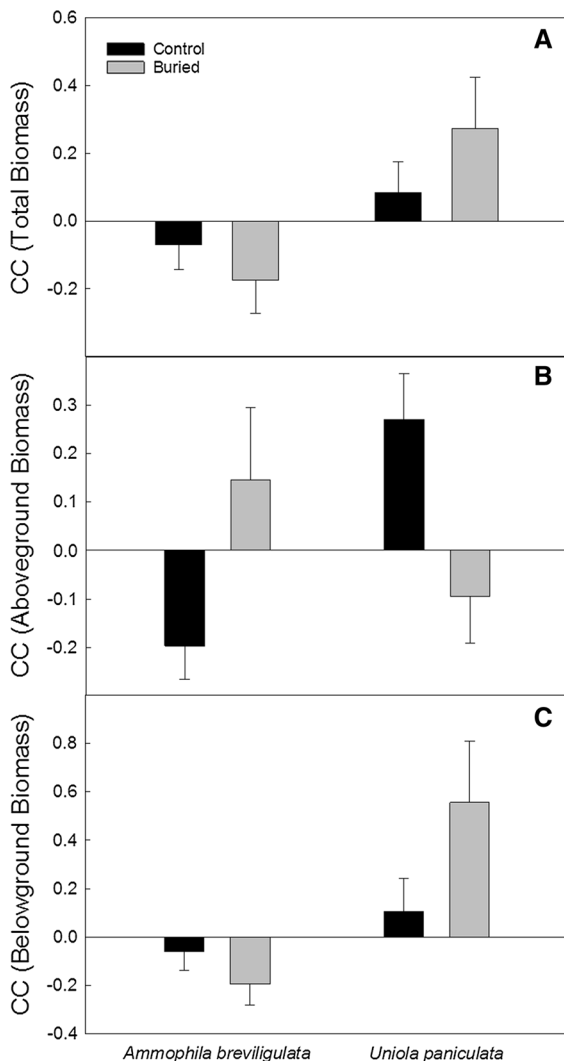[abcd] denote significant differences among treatments

(Stallins and Parker 2003; Charbonneau et al. 2016). Understanding potential biotic interactions between these two dune grasses and response to burial is the first step in predicting future dune communities which may affect dune morphology under climate change scenarios (Stallins and Parker 2003). Our study demonstrates that *A. breviligulata* and *U. paniculata*, species adapted to withstand foredune environmental conditions, differentially respond when planted in a mixture vs. monoculture and when buried.

Uniola paniculata exhibited more robust physiology relative to *A. breviligulata* as evidenced in higher electron transport rate (ETR). This was expected given the C_4 photosynthetic pathway of *U. paniculata* (Taylor et al. 2010). Burial had a positive effect on both species through higher ETR and total biomass relative to controls. Our results of higher *A. breviligulata* ETR agree with previous findings of positive response to burial (Disraeli 1984; Maun and Lapierre 1984; Yaun et al.1993). *Uniola paniculata* physiological response to burial is less documented (Wagner 1964). We report *U. paniculata* having higher ETR and relative growth rate (RGR) when buried. Positive responses are needed as survival mechanisms in foredune environments in order to recover from frequent burial by overwash events.

Relative to monoculture plantings, our results indicate *A. breviligulata* physiological and morphological performance declined when planted with *U. paniculata*. Conversely, *U. paniculata* did not appear to be affected when planted with *A. breviligulata*. This can be seen at a physiological level which predicates whole plant responses to stressors. ETR and relative growth rate (RGR) for *A. breviligulata* mixture plantings were reduced and directly contributed to lower total biomass seen in the change in contribution. This demonstrates that *A. breviligulata* vigor is reduced in the presence of *U. paniculata*. *Uniola paniculata* ETR and RGR did not decrease vigor when planted with *A. breviligulata*.

Change in contribution showed that when grown together, total biomass was reduced for *A. breviligulata* and stimulated for *U. paniculata* relative to monoculture plantings, and resources were reallocated under control and burial conditions. Under control conditions, *A. breviligulata* aboveground biomass was reduced relative to monoculture and *U. paniculata* aboveground biomass increased. Burial stimulated *A. breviligulata* allocation of resources aboveground in

Fig. 3 *Ammophila breviligulata* and *Uniola paniculata* mixture paintings change in contribution for total (**a**), aboveground (**b**), and belowground biomass (**c**) when compared to monoculture plantings. Values are means ±1 standard error

Table 3 Pearson correlation of measurement variables with principal component axes 1 and 2

Variables	PCA 1	PCA 2
ETR	−0.33	0.68
g_s	0.27	0.61
$\delta^{13}C$	−0.94	−0.01
%N	0.74	0.41
%C	−0.07	−0.02
C:N	−0.66	−0.42
AGB	−0.36	0.67
BGB	0.54	0.52
Total biomass	0.21	0.83
RGR	−0.81	0.46
# Alive leaves	−0.65	0.58

per water use) is important due to low water holding capacity of sandy soils (Uzoma et al. 2011). High nitrogen use efficiency (NUE; carbon gain per nitrogen use) is essential in the strand environment due to lack of nutrients in sandy soils (Dilustro and Day 1997).

WUE can be determined through $\delta^{13}C$ due to the ability of carbon isotopes to integrate eco-physiological measures associated with gas exchange through time (Esquivias et al. 2015). *Uniola paniculata* was more water and nitrogen efficient than *A. breviligulata*, based on *U. paniculata* having higher $\delta^{13}C$ and carbon to nitrogen ratio compared to *A. breviligulata*. This was expected due to stomatal regulation and less ribulose-1,5-bisphosphate carboxylase/oxygenase (RUBISCO; which reduces nitrogen content) in *U. paniculata*, a C_4 plant (Taylor et al. 2010). These traits allowed *U. paniculata* to sustain a greater number of living leaves than *A. breviligulata*. *Ammophila breviligulata* monoculture planting sustained the highest number of leaves, whereas *U. paniculata* sustained the highest number of leaves when planted in mixture with *A. breviligulata*. The number of living leaves combined with the allocation of biomass seen in change in contribution could allow for greater success of *U. paniculata* within the foredune system as it migrates northward along the Atlantic seaboard into *A. breviligulata* dominated habitat.

When all measures were integrated together, it was clear that *A. breviligulata* was most affected by planting type. *Uniola paniculata* responded inversely, with burial contributing more to grouping than

the presence of *U. paniculata*. In the presence of *A. breviligulata*, burial positively affected *U. paniculata* belowground biomass. Reallocation of resources into aboveground traits allows for quick response to sand deposition and is important in dune-building. However, the overall reduction in total biomass and resulting reallocation can affect the mechanisms by which these dune grasses utilize fresh water and nutrients. This is important due to limited availability of both within the strand environment (Frosini et al. 2012). High water use efficiency (WUE; carbon gain
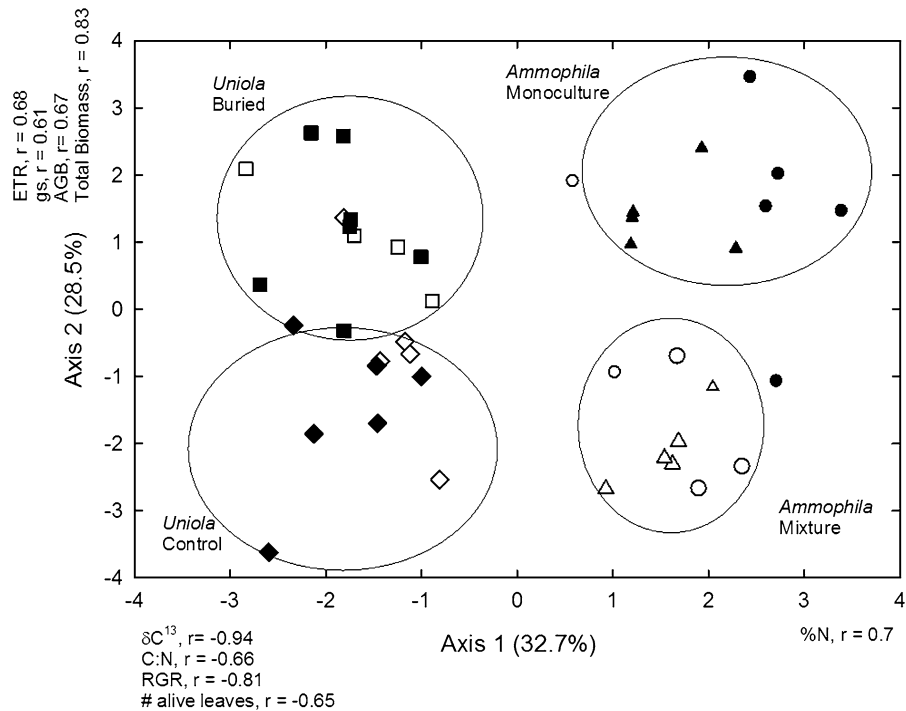
Fig. 4 Principal Component Analysis (PCA) ordination for species, planting type, and burial. PCA axis 1 and 2 are shown. *Circles* are buried *Ammophila breviligulata*, *triangles* are control *A. breviligulata*, *squares* are buried *Uniola paniculata*, and *diamonds* are control *U. paniculata*. *Open symbols* indicate mixture planting, and *solid symbols* indicate monoculture planting. Four significantly different groups were observed

planting type. These alterations in responses indicate that *A. breviligulata* has a diminished performance capacity in the presence of *U. paniculata*. Stallins (2002) observed at the Core Banks of North Carolina, USA, that *U. paniculata* had greater absolute species cover (17%) than *A. breviligulata* (1%). Only one site out of five had a greater *A. breviligulata* absolute species cover than *U. paniculata* (Stallins 2002). At the other four sites, *U. paniculata* had a higher absolute species cover (Stallins 2002). Our results, which suggest that *A. breviligulata* performance diminishes when planted with *U. paniculata*, correspond with these field species cover observations because in areas of high *U. paniculata* cover, *A. breviligulata* cover is reduced. Although we used a northern population of *A. breviligulata* in our glasshouse study, these corresponding observations from plants growing together in the field indicate that plant source may not be a contributing factor in the results presented.

Potential island impacts due to climate change shifts in dominant dune grass species and the results of this study documenting *A. breviligulata* and *U. paniculata* interactions, underscores the importance of understanding dune grass biotic interactions (Zarnetske et al. 2013). These ecosystem engineers are at the forefront of barrier island change as foredune morphology has the ability to influence disturbance regimes through susceptibility to overwash (Wolner et al. 2013; Brantley et al. 2014). Migrating species interaction with local host communities has to be examined alongside co-occurring environmental drivers, as species interactions could shift with altered abiotic conditions (Zarnetske et al. 2013; He and Bertness 2014). Plant communities on barrier island systems, which cope with multiple abiotic drivers simultaneously such as sea spray, burial, high radiation, salt water intrusion, and limited access to nutrients, demonstrate the need for species interactions and environmental drivers to be studied together. It is through differential dune grass interactions that feedbacks with foredune morphology could be altered, shifting the future of barrier island stability and community composition.

Conclusion

Barrier island systems are important to study because they are at the forefront of storms and sea-level rise, and provide valuable services. To understand how barrier island dune grasses will respond in the future, it is essential to study the biogeomorphic relationship between dune species in response to sediment manipulation. As dune grass species shift due to climate change, the role of biotic interactions in response to abiotic drivers such as burial must be understood. Our study is unique because it examined both species interactions and burial jointly, while measuring both plant morphological and physiological responses. The most noteworthy result of this study is that *A. breviligulata* performance decreased in the presence of *U. paniculata*. This response has implications for coastal dune morphology due to species differences in rooting strategy and dune-building. Overall, this demonstrates the importance of studying species interactions along with environmental drivers, as this could shift individual species response.

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