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Emergent interactions influence functional traits and success of dune building ecosystem engineers

Joseph K. Brown, Julie C. Zinnert and Donald R. Young*

Department of Biology, Virginia Commonwealth University, 1000 West Cary Street Richmond, VA 23284, USA
*Correspondence address. Department of Biology, Virginia Commonwealth University, 1000 West Cary Street Richmond, VA 23284, USA. Tel: +804-828-1562; Fax: +804-828-0503; E-mail: jczinnert@vcu.edu

Abstract

Aims
Dune building processes are affected by interactions between the growth of ecosystem engineering dune grasses and environmental factors associated with disturbance such as sand burial and sea spray. Research investigating how species interactions influence dune community structure and functional trait responses in high abiotic stress environments is minimal. We investigated how species interactions influence the functional trait responses of three dominant dune grasses to common abiotic stressors.

Methods
We performed a multi-factorial greenhouse experiment by planting three common dune grasses (*Ammophila breviligulata* Fern., *Uniola paniculata* L. and *Spartina patens* Muhl.) in different interspecific combinations, using sand burial and sea spray as abiotic stressors. Sand burial was applied once at the beginning of the study. Sea spray was applied three times per week using a calibrated spray bottle. Morphological functional trait measurements (leaf elongation, maximum root length, aboveground biomass and belowground biomass) were collected at the end of the study. The experiment continued from May 2015 to August 2015.

Important Findings
Species interactions between *A. breviligulata* and *U. paniculata* negatively affected dune building function traits of *A. breviligulata*, indicating that interactions with *U. paniculata* could alter dune community structure. Furthermore, *A. breviligulata* had a negative interaction with *S. patens,* which decreased *S. patens* functional trait responses to abiotic stress. When all species occurred together, the interactions among species brought about coexistence of all three species. Our data suggest that species interactions can change traditional functional trait responses of dominant species to abiotic stress.

Keywords: competition, coastal dunes, facilitation, intransitivity

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INTRODUCTION

Barrier islands provide the first line of defense against coastal disturbances (Feagin *et al.* 2015). These ecosystems are significantly affected by sea level rise and high intensity storms, both increasing with climate change (Brantley *et al.* 2014; Duran and Moore 2013; Prisco *et al.* 2013). Dunes are important geomorphological formations of barrier islands that protect inner island processes and associated wetlands (Duran and Moore 2013; Stallins 2003, 2005). Coastal dune formations rely on interactions between sediment movement, plant presence and plant physiological response to sand burial (Brantley *et al.* 2014; Duran and Moore 2013; Stallins 2003, 2006). Given the importance of dune formations to coastal protection, it is critical to understand how biotic and abiotic interactions influence dune engineering species.

While dune morphology is a function of grass species present, dunes themselves influence abiotic stressors that filter plant colonization. These include water limitation, nutrient limitation, sea-spray exposure and burial (Dilustro and Day 1997; Emery and Rudgers 2014; Gornish and Miller 2010; Maun 1998; Oosting and Billings 1942; Seliskar 1993; Stallins 2006). These constant plant–environment interactions influence dune grass establishment (Gornish and Miller 2010; Miller 2015; Stallins 2006). Many studies have focused on effects of sediment-plant interactions on dune formation (Brantley *et al.* 2014; Duran and Moore 2013; Disraeli 1984; Maun 1984; Seliskar 1993; Stallins 2006; Zarnetske *et al.* 2013), however, research investigating the influence of biotic interactions on functional trait responses of dune grasses to abiotic stressors has been investigated in few studies

(Zarnetske *et al.* 2013). Here we define functional traits as any morphological or physiological characteristic that indicates ecological strategies of growth relative to environmental conditions across spatial and temporal scales (Kraft and Ackerly 2010; Westoby and Wright 2006).

Ammophila breviligulata Fern. (Poaceae), is a common dune grass found in northern latitudes from North Carolina to Canada (Gleason and Cronquist 1963). *Ammophila breviligulata* builds large continuous ridges and has functional traits that allow for success in dune habitats. These include deep roots, increased leaf elongation response to burial, and adventitious root production (Disraeli 1984; Maun 1994; Seliskar 1993). On the mid-Atlantic coast, *A. breviligulata* and *Spartina patens* commonly occur together (Day *et al.* 2001), however, interactions between these species are not well documented. *Spartina patens* Muhl. (Poaceae), is a generalist species found across moisture gradients of barrier islands and exists along the Atlantic coast from Canada to Florida (Stalter 1993). *Spartina patens* has been suggested to maintain flatter areas on islands allowing for more frequent overwash and salt water inundation to occur (Brantley *et al.* 2014).

In its southern distribution, *S. patens* coexists with *Uniola paniculata* L. (Poaceae); interactions between these species are also not well documented (Stallins 2002). *Uniola paniculata* is a semi-tropical dune grass that grows on the southern Atlantic coast from southern Virginia into the Gulf Coast (Wagner 1964). This species exhibits a phalanx growth strategy resulting in hummock dunes and recolonizes newly disturbed areas slowly (Mendelssohn *et al.* 1991; Stallins 2006; Wagner 1964). Since the last glacial maximum *U. paniculata* has continued to migrate north, a pattern that is expected to continue as climate change persists and global temperatures rise (Hodel and Gonzalez 2013). This suggests that novel interactions could arise between *U. paniculata*, *A. breviligulata* and *S. patens* resulting in shifts of species specific functional traits. It is important to understand how interactions cause functional trait shifts because resulting plant communities will influence dune topography, dune building processes, and ultimate island formation (Stallins 2006).

Habitats where these species occur are dominated by high environmental stress due to increased sediment deposition (via aeolian sand transport), overwash events, high wind events and high sea-spray exposure (Brantley *et al.* 2014; Emery and Rudgers 2014; Maun 1998; Miller 2015; Oosting and Billings 1942; Stallins 2002; Seliskar 1993). These harsh environmental factors could possibly be mitigated through positive species interactions (Bertness and Callaway 1994; Callaway *et al.* 2002; Zarnetske *et al.* 2013), but competitive interactions that emerge as a result of climate change could increase plant vulnerability to abiotic stress (Alpert *et al.* 2000; Paz Esquivias *et al.* 2015; Going *et al.* 2009). Although facilitation and competition differ in result, they are similar in mechanism and can be drivers of ecological change and are of importance in environments sensitive to rapid ecological change (Bertness *et al.* 2015; Bruno 2000; Paz Esquivias *et al.* 2015; van de Koppel *et al.* 2006, Zarnetske *et al.* 2013; Zinnert *et al.* 2016).

Changes in plant functional traits as outcomes of species interactions can cause variable feedbacks with physical processes like burial and sea-spray, thereby changing dune morphology (Hayden *et al.* 1995; Stallins 2006). Our objective was to investigate the net effect of novel and current dune grass species interactions using morphological functional trait responses. We tested the hypothesis that current and novel species interactions cause functional trait modifications that either promote or hamper plant response to abiotic factors.

METHODS

A multi-factorial greenhouse experiment was designed to measure *A. breviligulata* (A), *U. paniculata* (U) and *S. patens* (S) response to varying interspecific mixtures and a combination of abiotic treatments (supplementary Fig. S1). Four different plant species mixture levels (AU, AS, US, USA), as well as monoculture levels (A, S, U), were planted in 15 × 15 cm plastic pots to induce competition. Each pot was planted with an even density of six stems and even species density in each mixture (i.e. when two species were present there were three individuals of each species, and when three species were present there were two individuals of each species). Each species mixture was treated with abiotic treatments common to barrier islands: control (no treatment), sea spray with no burial, burial with no sea spray and burial + sea spray. Sample size was even across all species × species mixture × treatment combinations ($n = 5$).

All plants were purchased in plugs from nurseries (*A. breviligulata* from Cape Coastal Nursery in South Dennis, MA, *S. patens* from Green Seasons Nursery in Parrish, FL and *U. paniculata* from Coastal Transplants in Bolivia, NC). Upon arrival, plants were potted and a 2-week growth period was permitted for plant establishment. All plants were trimmed to a 35 cm height. Burial collars made from PVC piping, 10 cm in diameter, were placed around each group of plants and inserted 1 cm into the soil. Plants being buried received collars 25 cm in length, while unburied groups received collars of 5 cm in length. Burial and burial + sea-spray pots were treated with 25 cm of sand burial through one application at the beginning of the study to simulate large sand deposition events found in natural systems.

A mixture of water and Instant Ocean (Aquarium Systems) was used to create a 20 ppt sea-spray solution to be applied to designated groups. In order to retain consistency during the experiment, a spray bottle was calibrated before each sea-spray treatment to administer as close to a fixed amount of salt solution as possible. Five sprays, ~4 ml per pot, were applied three times per week, two sprays on the front and back of each pot and one spray from the top. When watering plants, salt buildup on the leaf surface was rinsed into the sand of each pot. Plants were watered as needed with fresh water. All pots were treated once during the study with a 25 ml Hoagland's solution (Hoagland and Arnon 1950) diluted to 50 ml with tap water. The experiment continued from May of 2015 to August of 2015.

Functional trait measurements

Morphological measurements were selected based on relevance to field studies of plant communities and individual plant success (Lavorel and Garnier 2002). All traits were collected on all experimental units at the conclusion of the study. Leaf elongation was calculated by taking a final height measurement (to the nearest ± 1 mm) of each plant and subtracting the original height of each plant (35 cm), providing a metric that quantifies the amount of vertical growth of each species over the duration of our study. Aboveground biomass was defined as any biomass not buried by sand addition treatments. Aboveground biomass was clipped away from belowground biomass during deconstruction of pots and maximum root length (MRL) was gathered by extending the longest root of each species and using a ruler to measure length (to the nearest ± 1 mm) from the plant base to the root tip. MRL provides evidence of belowground functional trait strategies of water and nutrient capture as well as sediment stabilization (Lou *et al.* 2014; Qu *et al* 2014). Biomass samples were put in paper bags, dried at 65° C for 72 h and weighed. We calculated a relative yield (RY) index to quantify interspecific interactions given our replacement series experimental design (De Wit 1960; Fowler 1982; Williams and McCarthy 2001). The RY index was calculated as the biomass yield of a species when grown in a species mixture relative to when grown in monoculture.

Statistical analyses

All analyses were performed with JMP statistical software (JMP Pro 11, SAS Institute Inc. Cary, NC, 1989). A three-way ANOVA was used to determine any interactions among species, abiotic treatment and species mixture. Models were simplified to consist of a single abiotic factor with four levels. There were no species × abiotic treatment × species mixture interactions for any measurements, but there was a significant effect of species on elongation, MRL, aboveground and belowground biomass (supplementary Tables S1 and S2). Therefore, all data were analyzed by two-way ANOVA ($\alpha = 0.05$) to test abiotic treatment × species mixture for individual species. When two-way interactions were present, Tukey HSD was performed to determine which abiotic treatment levels and biotic competition levels differed. Student's *t*-test was performed to determine whether RY of species grown in mixtures were different from 1 ($\alpha = 0.05$). We performed the same analysis on the RY of species based on species richness.

RESULTS

Biomass

Ammophila breviligulata

There was a significant abiotic treatment × species mixture interaction on *A. breviligulata* aboveground biomass (Table 1). Burial and burial + sea-spray treatments decreased aboveground biomass regardless of species mixture ($F_{3,64} = 177.68$, $P < 0.0001$, Fig. 1). In control treatments, *A. breviligulata* aboveground biomass was 32% higher when grown with

Table 1: *F* statistics and *P* value results of two-way ANOVA for all species between abiotic treatment and species mixture

	Abiotic treatment		Species mixture		Abiotic treatment × species mixture	
Species	$F_{3,64}$	P	$F_{3,64}$	P	$F_{9,64}$	P
Ammophila breviligulata						
Aboveground biomass	177.68	**<0.0001**	19.92	**<0.0001**	2.39	**0.0209**
Belowground biomass	32.76	**<0.0001**	3.74	**0.0153**	0.32	0.9657
Leaf elongation	1.19	0.3191	15.85	**<0.0001**	1.41	0.2012
Maximum root length	4.20	**0.0090**	10.95	**<0.0001**	1.37	0.2193
Spartina patens						
Aboveground biomass	26.30	**<0.0001**	6.78	**0.0005**	1.02	0.4334
Belowground biomass	11.06	**<0.0001**	6.26	**0.0009**	0.59	0.8023
Leaf elongation	16.07	**<0.0001**	0.16	0.9260	2.05	**0.0479**
Maximum root length	1.02	0.3881	4.33	**0.0077**	3.95	**0.0005**
Uniola paniculata						
Aboveground biomass	9.81	**<0.0001**	6.62	**0.0006**	1.07	0.4002
Belowground biomass	7.41	**0.0002**	0.45	0.7201	2.01	0.0530
Leaf elongation	6.53	**0.0006**	9.06	**<0.0001**	2.03	**0.0499**
Maximum root length	0.48	0.6947	0.71	0.5500	1.05	0.4139

Bold indicates $P \leq 0.05$.

S. patens than when grown with *U. paniculata*, but was not significantly different from any other species mixture (Fig. 1). In sea-spray treatments, *A. breviligulata* aboveground biomass was significantly hindered when grown with just *U. paniculata*, causing a >34% decrease in aboveground growth compared to USA (all species grown together) mixture, 38% compared to *A. breviligulata* monoculture, and 49% when compared to AS (*A. breviligulata* and *S. patens*) mixture (Fig. 1). While not significant, under the burial treatment *A. breviligulata* aboveground biomass was higher when grown with *S. patens* compared to when grown with *U. paniculata*, when grown in USA mixture, or when grown in monoculture (Fig. 1). Species mixture within burial + sea-spray treatment also produced no significant results but exhibited a similar pattern as seen in burial treatments (Fig. 1).

There was no abiotic treatment × species mixture interaction on belowground biomass of *A. breviligulata* (Table 1). Abiotic treatment and species mixture were both significant main effects on belowground biomass of *A. breviligulata* (Table 1). Belowground growth was 29% higher in *A. breviligulata* when it was grown with *S. patens* (0.52 ± 0.06 g) than when competing with *U. paniculata* (0.37 ± 0.04 g). Belowground biomass also significantly decreased when *A. breviligulata* was grown in USA mixture (0.37 ± 0.05 g) compared to AS mixture (0.52 ± 0.06 g). Plants experiencing burial had a significantly higher belowground biomass than non-buried plants.

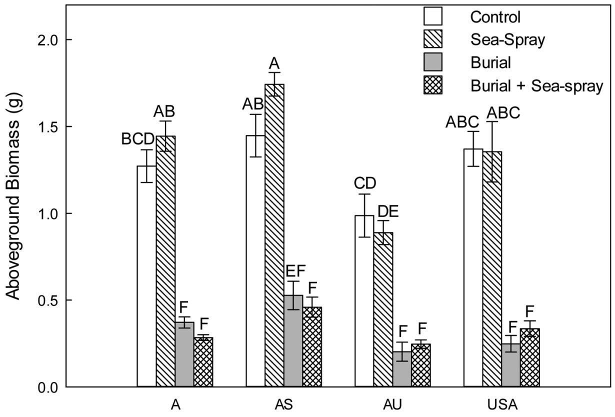

Figure 1: aboveground biomass of *A. breviligulata* in all abiotic treatments and in all species mixtures. A = *A. breviligulata*, AS = *A. breviligulata* + *S. patens*, AU = *A. breviligulata* + *U. paniculata*, and USA = *U. paniculata* + *A. breviligulata* + *S. patens*. All bars show mean ± SE. Results of Tukey's test for significant difference are indicated by letters ($P \le 0.05$).

Uniola paniculata

There was no abiotic treatment × species mixture interaction for above- or belowground biomass of *U. paniculata* (Table 1). Both species mixture and abiotic treatment were significant main effects on aboveground biomass of *U. paniculata* (Table 1). *Uniola paniculata* aboveground biomass was 26% higher when grown with *A. breviligulata* (0.76 ± 0.05 g) compared to any other species mixture (Fig. 2a). Burial and sea-spray + burial treatments caused a significant decrease in aboveground biomass compared to non-buried plants (Table 2). In comparison, abiotic treatment also had a significant effect on belowground biomass of *U. paniculata* (Table 1). Burial and burial + sea-spray treatments caused a significant increase in belowground biomass compared to belowground biomass production of non-buried plants (Table 2).

Spartina patens

No significant abiotic treatment × species mixture interaction was found for above- or belowground biomass of *S. patens* (Table 1). Aboveground biomass was affected by growing in mixture (Table 1). When *S. patens* was grown with *A. breviligulata* and *U. paniculata* together (USA mixture) it produced aboveground biomass >30% higher than when grown with *A. breviligulata* or when grown in a monoculture (Fig. 2b). Aboveground biomass was also affected by abiotic treatment (Table 1); burial (0.41 ± 0.04 g) and burial + sea-spray (0.35 ± 0.03 g) treatments produced less aboveground biomass when compared to control (0.77 ± 0.06 g) and sea-spray treatments (0.71 ± 0.06 g). *Spartina patens* belowground biomass was also affected when grown in species mixtures (Table 1). Belowground growth decreased by 33% when *S. patens* was grown with *A. breviligulata* than when grown with *U. paniculata* (Fig. 2b). Belowground biomass of *S. patens* was also 35% higher when all species were present compared to when

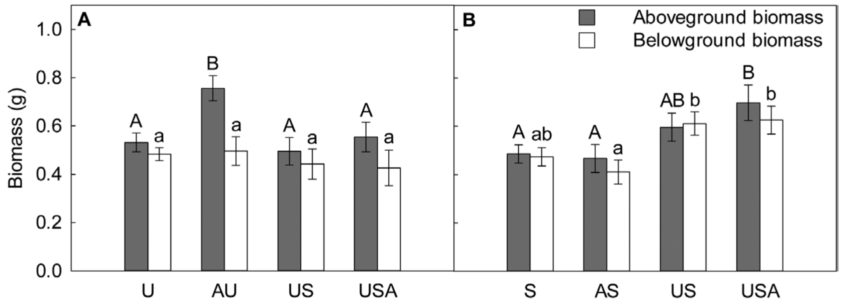

Figure 2: aboveground and belowground biomass of *U. paniculata* (**A**) and *S. patens* (**B**) in all species mixtures. S = *S. patens*, U = *U. paniculata*, US = *U. paniculata* + *S. patens*, AS = *A. breviligulata* + *S. patens*, AU = *A. breviligulata* + *U. paniculata*, and USA = *U. paniculata* + *A. breviligulata* + *S. patens*. All bars show mean ± SE. Results of Tukey's test for significant difference are indicated by letters ($P \le 0.05$).

grown with *A. breviligulata* (Fig. 2b). Abiotic treatment also significantly affected belowground biomass (Table 1). There was an increase in belowground biomass when *S. patens* was treated with burial (0.70 ± 0.03 g) as well as burial + sea-spray (0.60 ± 0.06 g) compared to control (0.39 ± 0.03 g) and sea-spray (0.44 ± 0.03 g) treatments.

Leaf elongation and MRL

Ammophila breviligulata

There were no interactions between species mixture and abiotic treatment for leaf elongation or MRL of *A. breviligulata* (Table 1). Abiotic treatment had no effect on leaf elongation of *A. breviligulata* but did affect MRL (Table 1). Growing in mixture affected leaf elongation of *A. breviligulata* (Table 1). When grown with *U. paniculata*, leaf elongation of *A. breviligulata* significantly decreased by as much as 52% compared to all other species mixtures (Fig. 3a). Leaf elongation significantly decreased by >25% when *A. breviligulata* was grown in USA mixture than when grown in a monoculture or with *S. patens* (Fig. 3a). Growing in mixture also had a significant effect on MRL of *A. breviligulata* (Table 1); competition with *U. paniculata* inhibited MRL of *A. breviligulata* by 42%, more than any other species mixture (Fig. 3a). *Ammophila breviligulata* MRL was significantly lower in burial treatments (11.9 ± 0.9 cm) compared to sea-spray treatments (16.7 ± 1.2 cm).

Table 2: **Tukey multiple comparison test results for above- and belowground biomass of** *U. paniculata* **across abiotic treatments**

	Aboveground biomass		Belowground biomass	
Level	Difference	*P*	Difference	*P*
Control – Burial	0.272	**0.0004**	0.189	**0.0444**
Control – Sea-spray + burial	0.237	**0.0027**	0.227	**0.0104**
Control – Sea-spray	0.019	0.9911	0.046	0.9159
Sea-spray – Burial	0.254	**0.0011**	0.235	**0.0076**
Sea-spray – Sea-spray + burial	0.218	**0.0065**	0.273	**0.0014**
Burial – Sea-spray + burial	0.036	0.9449	0.038	0.9483

Bold indicates $P \leq 0.05$.

Uniola paniculata

An abiotic treatment × species mixture interaction was identified for leaf elongation but not for MRL (Table 1). MRL was not significantly affected by abiotic treatment or species mixture (Table 1). While a significant abiotic treatment × species mixture interaction was found for elongation, further analysis could not detect where those differences lie. However, as described below, abiotic treatment and species mixture were both significant main effects on leaf elongation of *U. paniculata* (Table 1). When *U. paniculata* was grown with *A. breviligulata*, leaf elongation was 33% higher than when grown in any other species mixture besides monoculture (Fig. 3b). *Uniola paniculata* leaf elongation was lower in control group (45.0 ± 4.0 cm) compared to burial (61.3 ± 6.6 cm) and burial + sea-spray (65.8 ± 4.8 cm) treatments. Sea-spray treatment (47.0 ± 3.4 cm) only caused significantly lower leaf elongation when compared to burial + sea spray.

Spartina patens

A significant abiotic treatment × species mixture interaction was found for *S. patens* leaf elongation and MRL (Table 1). Leaf elongation of *S. patens* significantly increased by >45% when burial was present compared to when burial was absent (Fig. 4a). While a significant abiotic treatment × species mixture interaction in *S. patens* MRL was found, further analysis could not indicate where differences lie. In burial treatments there was no difference in MRL across species mixture levels (Fig. 4b). However, when burial was added to sea-spray treatments (burial + sea spray), *S. patens* MRL was significantly longer (73%) when grown with *U. paniculata*, than when grown with *A. breviligulata* (Fig. 4b).

RY index

Ammophila breviligulata RY was significantly reduced when grown in three-species combinations and two-species combinations (supplementary Fig. S2). *Spartina patens* RY was

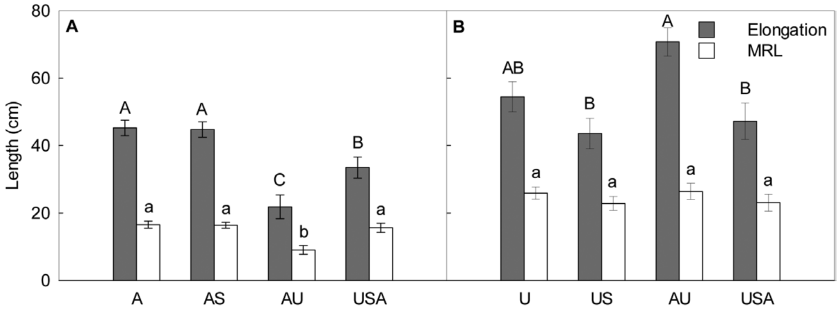

Figure 3: leaf elongation and maximum root length (MRL) of *A. breviligulata* (**A**) and *U. paniculata* (**B**) in all species mixtures. A = *A. breviligulata*, U = *U. paniculata*, US = *U. paniculata* + *S. patens*, AS = *A. breviligulata* + *S. patens*, AU = *A. breviligulata* + *U. paniculata*, and USA = *U. paniculata* + *A. breviligulata* + *S. patens*. All bars show mean ± SEM. Results of Tukey's test for significant difference are indicated by letters ($P \leq 0.05$).

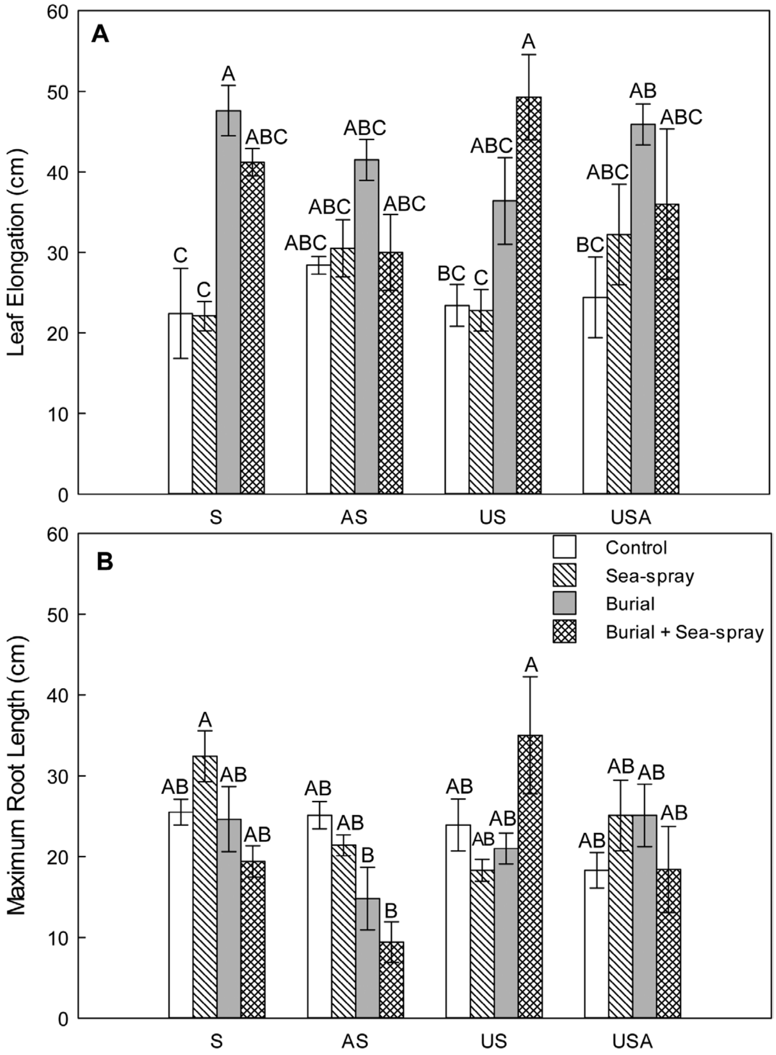

Figure 4: leaf elongation (**A**) and maximum root length (MRL) (**B**) of *S. patens* in all abiotic treatments and in all species mixtures. S = *S. patens*, US = *U. paniculata* + *S. patens*, AS = *A. breviligulata* + *S. patens* and USA = *U. paniculata* + *A. breviligulata* + *S. patens*. All bars show mean ± SEM. Results of Tukey's test for significant difference are indicated by letters ($P \leq 0.05$).

only significantly affected by the highest species richness level (supplementary Fig. S2), while *U. paniculata* RY was not affected by species richness (supplementary Fig. S2). Further analysis concluded that species identity in each mixture is more informative than specie richness alone. Specifically, the RY of each species was affected differentially depending on interspecific combination. *Ammophila breviligulata* RY significantly decreased by 41% and 28% when grown with *U. paniculata* and in the USA mixture, respectively (Fig. 5a). Biomass yield of *A. breviligulata* was not affected when grown with *S. patens* (Fig. 5a). Relative yield of *S. patens* was negatively affected when grown with *A. breviligulata* decreasing by 22%, but when grown with *U. paniculata* and in USA mixture RY increased by 17% and 29% respectively (Fig. 5b). *Uniola paniculata* RY was significantly reduced by 25% when grown with *S. patens* (Fig 5c).

DISCUSSION

Our results suggest that dune grass functional trait response to abiotic factors common to coastal ecosystems are altered by positive and negative interactions among species. Plant response to interspecific interaction was dependent on the identity of the species involved, not just the number of species. Interestingly, we found competitive and facilitative interactions among species occurred depending on the species mixture and abiotic stress. When *A. breviligulata* was grown with *U. paniculata*, a negative species interaction (significantly decreased RY) ensued that caused a reduction in functional trait values of *A. breviligulata* and affected plant response to common abiotic factors of dune habitats (e.g. sea-spray and burial). Novel competition between *A. breviligulata* and *U. paniculata* inhibited aboveground biomass, leaf elongation and MRL of *A. breviligulata* across various abiotic treatments.

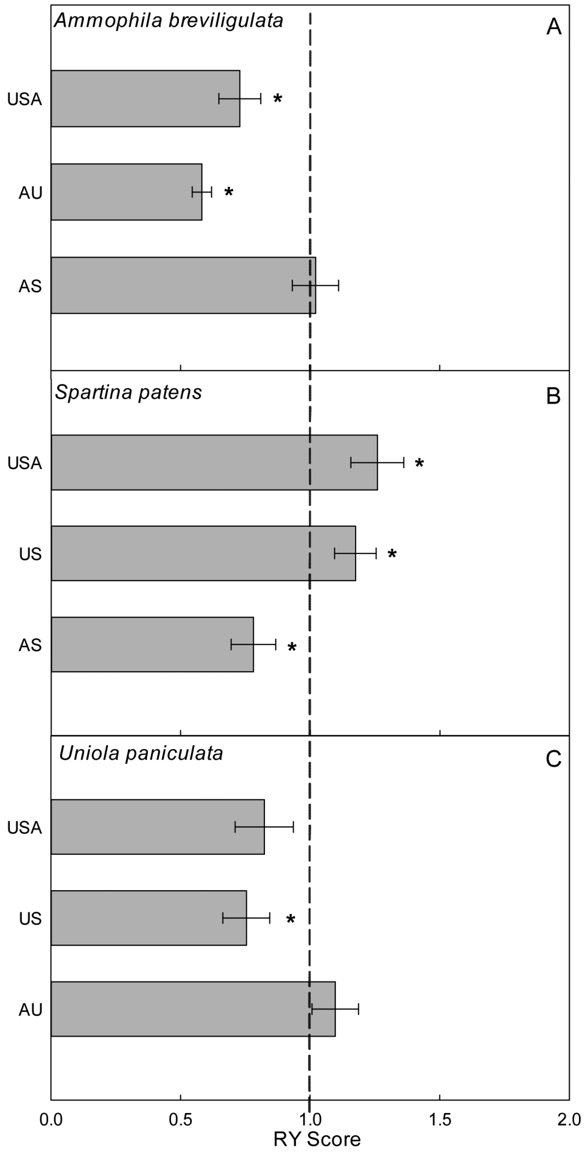

Figure 5: the average RY for *A. breviligulata* (**A**), *S. patens* (**B**) and *U. paniculata* (**C**) in each species mixture. Species interactions are present if the RY is significantly different than 1.0. An RY > 1.0 indicates that a species grew better in mixture than in monoculture. In contrast, an RY < 1.0 indicates that species grew better in a monoculture than in mixture. A = *A. breviligulata*, S = *S. patens*, U = *U. paniculata*, US = *U. paniculata* + *S. patens*, AS = *A. breviligulata* + *S. patens*, AU = *A. breviligulata* + *U. paniculata*, and USA = *U. paniculata* + *A. breviligulata* + *S. patens*. All bars show mean ± SE, **P* ≤ 0.05.

Uniola paniculata did not reduce MRL to increase leaf elongation, indicating no change in resource allocation, and was able to maintain high belowground biomass when in competition with *A. breviligulata*. The amount of nutrients acquired by a plant is related to spatial distribution of roots as well as belowground functional traits such as MRL, biomass and surface area of root mass (Lambers *et al.* 2008; Lou *et al.* 2014). By having high belowground biomass and MRL in burial treatments, *U. paniculata* presumably acquired nutrients faster and more efficiently, perpetuating fast leaf elongation and thus, theoretically, increasing photosynthetic efficiency (Lou *et al.* 2014). Not only could this strategy have increased growth quickly after burial in *U. paniculata* but it may have also caused decreased growth of competing species, in this case *A. breviligulata*, by impeding on rooting space while draining available nutrients and water (Luo *et al.* 2014).

Our data also show decreased success of *U. paniculata* and increased success of *S. patens* when grown in US mixture, evidenced by higher RY compared to growth in monocultures. The MRL of *S. patens* was significantly higher in burial + sea-spray treatments when grown in US mixture than when grown in AS mixture. This pattern is of interest because longer MRL is characteristic of dune builders, however *S. patens* is suggested to contribute to maintaining flat topography (Brantley *et al.* 2014; Wolner *et al.* 2013; Stallins 2005). This provides evidence that the positive competitive effect of *S. patens* over *U. paniculata* may cause a change in functional traits of *S. patens* that could potentially enable small dune building.

Positive species interactions have been theorized to be driven by harsh abiotic environments, and some discussions propose that positive species interactions are also influenced by other factors, including plant traits (Bertness and Callaway 1994; Callaway *et al.* 2002; He *et al.* 2013). Our data support this by showing that facilitation caused by abiotic stress, drives functional trait shifts that enable success of certain species (Bertness and Callaway 1994; Olofsson *et al.* 1999; Zarnetske *et al.* 2013). A positive interaction was established between *A. breviligulata* and *S. patens* that explains the trends of increased aboveground biomass and higher RY values of *A. breviligulata* when treated with abiotic stress. This explains current coexistence of these two species in natural habitats (Dilustro and Day 1997; Day *et al.* 2001; Wolner *et al.* 2013). Facilitative interactions promoting the growth of *S. patens*, as indicated by RY, came indirectly, driven by the competitive interaction between *A. breviligulata* and *U. paniculata*. *Spartina patens* produced the highest RY values when grown in USA mixture, likely caused by reduced competitive ability of *A. breviligulata*, when interacting with *U. paniculata*. Here, positive interactions only occurred in certain species mixtures, indicating that species specific traits play a role in facilitation (Bruno 2000; Gomez-Aparicio 2004; He *et al.* 2013). Using our data to synthesize positive and negative interactions described above, we were able to infer presence of intransitivity among these three ecosystem engineering dune grasses.

Coexistence between these three species is possible via competitive intransitivity where varying species-to-species interactions create a rock-paper-scissors scenario in which competitive hierarchy no longer exists (Laird and Shamp 2006, 2008, 2015; Reichenbach *et al.* 2007; Allesina and Levine 2011; Soliveres *et al.* 2015). Within our species mixtures, intransitivity resulted in an indirect facilitative effect on *S. patens* rather than creating a balance of all species. When *S. patens* was grown together with *A. breviligulata* and *U. paniculata*, increases in above and belowground biomass were observed, as well as a significantly greater RY than when grown in monoculture. This is likely due to different functional trait responses between species pairs that determine intransitive stabilization (Allesina and Levine 2011). Current models suggest that within plant communities, intransitive interactions are most commonly found between dominant species, and are dependent on short disturbance intervals, along with other coexistence mechanisms such as high abiotic stress (Laird and Shamp 2008; Soliveres *et al*. 2015). Both short disturbance intervals and high abiotic stress are present in coastal areas including the Virginia barrier island system where these species are dominant (Brantley *et al.* 2014; Hayden *et al.* 1995; Stallins 2005), making these ideal environments to investigate intransitivity.

On a larger scale, our results suggest that as variable abiotic and biotic conditions emerge, different species will prevail, initiating changes in active synergisms among plant presence, sediment movement and functional trait response. Our data strongly suggest that changes in functional trait response to abiotic stressors, caused by any of the complex species interactions discussed above, can lead to changes in vegetation distribution, recovery rates and vulnerability of Virginia barrier islands (Brantley *et al.* 2014; Stallins 2006; Zinnert *et al.* 2016). For example, if competition emerges as *U. paniculata* experiences northward expansion (Hodel and Gonzalez 2013), *A. breviligulata* could experience damaging alterations to functional traits that specifically make it a good dune engineer (e.g. high aboveground biomass, high MRL and high leaf elongation).

Species interactions may also effectively cause alterations in functional form of species; for example, *A. breviligulata* functioning as a competitor when grown with *S. patens*, but as a competitive subordinate when grown with *U. paniculata*. It is this type of community composition dependent response that may bring about intransitive coexistence. Examining species interactions in high abiotic stress environments can inform our understanding of how plant-to-plant relationships influence functional traits of dominant species. Intransitivity, competition, and facilitation can all alter functional trait responses of dominant species to abiotic stress. Although *A. breviligulata* can have significant detrimental effects on dune building functional traits of *S. patens* at high abiotic stress, it is critical to consider the interactions among all species present. Our results indicate that interactions between two species (*A. breviligulata* and *S. patens*) can be modified by presence of a third species (*U. paniculata*), perhaps due to intransitive coexistence. This highlights the importance of multi-species studies in environments with harsh abiotic conditions. It is also becoming more evident to consider plant functional traits as both a driver and consequence of species interactions that can inform as to how plant communities shape the environment in which they are dominant (Bertness *et al.* 2015; Hacker and Bertness 1995; Paz Esquivias *et al*. 2015; Zarnetske *et al.* 2013).

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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