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Planting Density Effects on the Growth of Dune Grasses.

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

By

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December 2019

Acknowledgements

I would like to thank my advisor, Julie Zinnert, for her assistance with this project and her overall support during my time in grad school. She has been a great advisor to me not only during grad school, but also as an undergraduate. I would also like to thank the Coastal Plant Ecology lab for their humor and conversation, as well as field work assistance. Thank you to my committee members; Dr. McCallister, Dr. Hulshof, and Dr. Jennings for their suggestions and help through this process. Thank you to Lauren Mowbray at Back Bay National Wildlife Refuge for working with me to organize field work. Lastly, I would like to thank my parents Lisa Thompson and William Kirschner for their support and encouragement throughout my years of education.

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Abstract

PLANTING DENSITY EFFECTS ON GROWTH OF DUNE GRASSES.

By Audrey Serena Kirschner, M.S.

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

Virginia Commonwealth University, 2019.

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

Coastal dune vegetation plays a key role in dune formation and stabilization through sediment trapping and erosion control. To restore degraded dunes, revegetation of dune building species is critical. Planting density has been found to effect growth of marsh species, with closer plantings alleviating stress through facilitation. As coastal dunes are high stress environments, it is expected that dune species may also exhibit facilitative interactions based on the Stress Gradient Hypothesis. Therefore, planting grasses in clumped configurations may lead to more successful dune revegetation. The objective of this research was to determine how planting density affects the growth of two dominant dune grasses along the US Atlantic coast, *Ammophila breviligulata* and *Uniola paniculata*, through field surveys of natural distribution, density, and a manipulation study of planting densities. Natural distribution differed between the two species with *A. breviligulata* occurring at lower dunes and *U. paniculata* occurring at higher dunes. *Ammophila breviligulata* occurred more densely than *U. paniculata*. Planting density of *U. paniculata* had an effect on growth parameters (shoot length, stem number, and ramet number) but not survival with dispersed plantings (50 cm apart) having higher growth than clumped plantings. The effect of density planting on growth parameters may impact dune building

processes. Sparsely planted *U. paniculata* may have greater sediment capture compared to densely planted *U. paniculata* due to greater stem number and biomass resulting in taller, steeper dunes.

Introduction

Coastal dunes are an understudied system that provide a number of ecosystem services including; habitat biodiversity, coastal protection, and sediment stabilization (Barbier et al., 2011). Despite their value, dunes are vulnerable and degraded due to human activity, changing climate, and species invasion (Barbier et al., 2011; Muñoz-Vallés et al., 2015). Coastal systems are heavily developed, with over 41.5 million people living along the Atlantic Coast, and recreational use of beaches impacts dune vegetation (Wilson and Fischetti 2010; Barbier et al., 2011). Along with human activity, species invasion is a major contributor to habitat degradation in coastal ecosystems (Lithgow et al., 2013; Muñoz-Vallés et al., 2015). Within coastal dune habitats, anthropogenic and abiotic (i.e. wind, salinity, storm disturbance) stressors affect dune vegetation, and therefore dune morphology and ecosystem functioning. Restoration efforts are critical in maintaining ecosystem functioning in degraded dune systems.

Maintaining dune systems by restoring vegetation is critical to protecting coastal areas, as coastal vegetation plays a key role in dune formation and stabilization (Durán and Moore 2013; Charbonneau et al., 2016). Dune vegetation affects sediment deposition and mobility, which influences dune morphology, and is considered ecosystem engineers of coastal systems (Woodhouse 1978; Stallins and Parker 2003; Durán and Moore 2013; Miller 2015; Charbonneau et al., 2016). Foredune vegetation influence dune formation through sand trapping by aboveground biomass and structural support from belowground biomass (Brantley et al., 2014; Feagin et al., 2015; Silva et al., 2016). Vegetation reduces dune erosion through wave attenuation by aboveground and belowground biomass (Feagin et al., 2019). Dune grass functional traits (i.e., growth rate, root structure, lateral expansion of propagation) can affect the morphology and functioning of the resulting dune (Zarnetske et al., 2012; Brantley et al., 2014;

Brown et al., 2017). The spatial arrangement of species within dune systems influence species interaction, erosion control, and water availability (McCallum et al., 2018) and, thus, dune morphology. Coastal dunes are comprised of a diverse range of species with unique and specific adaptations; including dune building and dune-stabilizing grasses (Wagner 1964; Durán and Moore 2013; Muñoz-Vallés et al., 2015). These plant adaptations enhance dune systems, create new habitats, allow for greater species diversity, and affect species interactions (Brantley et al., 2014; Miller 2015; Monge and Gornish 2014).

There has long been an interest in plant-plant interactions, however, many studies have focused on negative plant-plant interactions (i.e. competition). Over the last two decades, studies have shifted towards understanding positive plant-plant interactions (i.e. facilitation) (Montesinos 2015). The Stress Gradient Hypothesis (SGH) theorizes that facilitation outweighs competition in higher stress environments, and that competition prevails when conditions are mild (Bertness and Callaway 1994). A modified version of the SGH theorizes that facilitation is highest in moderate stress conditions, and in extreme stress conditions, competition prevails (Castanho et al., 2015). Plant facilitation studies have focused on community level interspecific interactions, often from different functional groups (i.e. nurse plant theory), while intraspecific interaction studies are minimal (Franks 2003; Zhang and Tielbörger 2019). More studies are needed to analyze intraspecific facilitation, due to limited experimental tests of interactions in these systems.

Along the mid-Atlantic coast, the dominant dune building grasses are *Ammophila breviligulata* (Poaceae), common name American beachgrass, and *Uniola paniculata* (Poaceae), common name sea oats (Hodel and Gonzalez 2013). *Ammophila breviligulata* is a C₃, cool-season grass, and *Uniola paniculata* is a C₄, warm-season grass. *Uniola paniculata* has been

expanding its range northward into the habitat of *A. breviligulata* and they now coexist in southeastern Virginia (Goldstein et al., 2018). Both species exhibit high tolerance to burial and therefore are likely to play a role in the formation and stabilization of dunes (Wagner 1964; Maun and Lapierre 1984). These two species are often planted to restore dunes due to their role in dune stabilization. As coastal ecosystems are continually degraded, restoration efforts have become more prevalent (Silliman et al., 2015). Coastal dune restoration is important, as dune systems provide many ecosystem services including protection from damaging storms. Planting designs for dune restoration should mimic natural spatial arrangement (McCallum et al., 2018).

In coastal marshes, planting designs affected efforts to restore ecosystem functioning with closer plantings being more successful (Silliman et al., 2015). This has not been tested in the coastal dune system. In dune restoration, most planting-based efforts attempt to minimize competition through widely dispersed plantings (Halpern et al., 2007; Broome 2015). Although this approach limits possible negative effects, it reduces the possibility for positive interactions between plants, i.e. mutualism and facilitation. Coastal dunes are subjected to a variety of stressors including high temperatures, drought, salt spray, salt stress, burial, nutrient deficiency, and wave impact (Oosting and Billings 1942; Franks and Peterson 2003; Maun 2009). In this high stress coastal system, it is possible that dune plant communities will exhibit facilitative rather than competitive interactions.

The objective of this research was to determine how planting density affects the growth of two dominant dune grasses along the US Atlantic coast, *A. breviligulata* and *U. paniculata*. An assessment of the natural density and distribution of both species at our study site was included in our study. We hypothesized that *U. paniculata* and *A. breviligulata* would have the highest growth response under clumped planting conditions due to facilitation.

Methods

Field Site

Our experiment was performed at Back Bay National Wildlife Refuge (36° 69' N; 75° 92' W); a barrier spit in Southeastern Virginia. The refuge consists of a diverse range of habitats including grass covered dunes, shrub thickets, woodlands, and wetlands. Soils are composed of sand and have low nutrient levels. The foredune system is dominated by two grass species, *A. breviligulata* and *U. paniculata*. In North Carolina, the species colonize different areas of the dunes with *A. breviligulata* more abundant in the foredune, and *U. paniculata* most abundant on the top dune (Hacker et al., 2019). *Ammophila breviligulata* grows laterally 2-3m per year compared to *U. paniculata* which grows laterally at a slower rate of 0.6 m per year (Woodhouse et al., 1978). Although *A. breviligulata* spreads more rapidly, *U. paniculata* has been found to invade areas with *A. breviligulata* (Woodhouse et al., 1978). Recent laboratory studies have documented negative effects on *A. breviligulata* when grown with *U. paniculata* (Brown et al., 2017; Harris et al., 2017). However, no field studies have been conducted in the zone of overlap (i.e, southern Virginia) on the growth and interaction of these two species.

Carex kobomugi (cyperacea) is a United States ornamental dune grass well adapted to foredune systems with mobile sands, and its range extends from Massachusetts to North Carolina (Small 1954; Standley 1983). The presence of *C. kobomugi* has led to a reduction in the abundance and density of *Ammophila breviligulata* (Poaceae), (Small 1954; Wootton et al., 2005). Invasive species can alter plant communities, reduce species diversity, and affect dune functionality (Muñoz-Vallés et al., 2015). Restoration efforts have been implemented to remove *C. kobomugi* and restore the dune system (Wootton et al., 2005). Back Bay National Wildlife

Reserve in southeastern Virginia is currently implementing a *C. kobomugi* removal effort and re-planting of native species to restoration coastal dunes.

Distribution and density

We documented the distribution of two dominant grass species (*A. breviligulata* and *U. paniculata*) by establishing 33 cross-shore transects in 15 m intervals. Each transect traversed from foredune (where dune vegetation began) to dune top, encompassing the toe, heel, and crest of the foredune. Plots (1 m²) were established every 5 m (n = 184). Within each 1 m² plot, we estimated percent cover, species composition, and dominant species. GPS points were recorded at each sampled plot. Elevation data were acquired from the Coastal National Elevation Database (CoNED). To measure density, we haphazardly selected twenty 0.25m² monocultural plots across dune elevation (n =10 per species). The number of shoots were recorded within each plot. Density was calculated as shoot number per area.

Field experiment

. Plots were chosen at the top of the dunes (~5m above sea level) that were affected by invasive *C. kobomugi* in coordination with refuge managers. Experimental plots were established by removing *C. kobomugi* and other existing vegetation by hand through the pulling of individual plants. 4x4 m blocks were established at equal elevation and distance from ocean (n=5) at an elevation where *A. breviligulata* and *U. paniculata* both occur. Each block was divided into four 2x2 m plots with two different treatments: species (A or U) and planting design (dispersed or clumped) (Fig 1). Six plugs of grasses were planted in each plot. Grasses were purchased by Back Bay NWR from local stock. Grasses in the dispersed plots were planted 50

cm apart to simulate typical restoration planting (Broome 2015). Grasses in clumped plots were planted in the center of the plots with the leaves nearly touching following the methods of Silliman et al. (2015). To reduce transplant shock, fertilizer (Osmocote, smart release fertilizer, 19-6-12) was added at the time of planting, and plants were regularly watered for the first few weeks. Throughout the experiment, any plants other than experimental plants that occurred within the experimental plots were removed.

At the time of planting, leaf length was cut to 30cm, and 10 additional plugs of *A. breviligulata* and *U. paniculata* were dried and weighed to obtain starting aboveground and belowground biomass. The initial aboveground biomass of the plugs was 0.51 ± 0.05 g for *U. paniculata*, and 1.17 ± 0.07 g for *A. breviligulata*. The initial belowground biomass of the plugs was 0.27 ± 0.03 g for *U. paniculata* and 1.63 ± 0.11 g for *A. breviligulata*. Daily fluctuations of air temperature and precipitation were acquired from a meteorological station at Back Bay, Virginia during two growing seasons (May 2018 – Aug. 2018, and May 2019 – Aug. 2019).

Non-destructive measurements were taken at the end of each growing seasons (2018 and 2019) to assess plant growth. Measurements were taken on 3 plants in each plot (n=15). Growth parameters include shoot length, number of stems, number of ramets, and ramet elongation (RE). Leaf length (cm) was measured from soil to longest leaf tip. Number of stems were counted on each plant. Number of ramets were counted as all stems that are greater than 5cm from the original parent plant. Ramet Elongation (cm) was measured as the distance from the parent plant to the furthest ramet of each plant.

At the end of the second growing (2019) season above - and belowground biomass of 1 original plants from each plot were quantified. Root traits were analyzed using winRHIZO. Root traits included; Specific root length (root length / root dry mass), root diameter, and Root tissue

density (root dry mass / root volume). Aboveground and belowground biomass (including scanned roots) were oven dried at 70°C for 72 hours and weighed.

Statistical analysis

Kolmogorov-Smirnov (K-S) test was run to analyze differences in the distribution of *U. paniculata* and *A. breviligulata*. A t-test was run to analyze the natural density between species. A Chi-square test was used to assess the survival of species across treatments. Due to no survival in season two, an ANOVA with subsampling was run to analyze growth (shoot length, stem #, ramet #, and RE) between clumped and dispersed of *A. breviligulata* during season one. A two-way ANOVA with subsampling was run to analyze the effect of spacing (dispersed or clumped) and season, on growth (shoot length, stem #, ramet #, and RE) for *U. paniculata*. If significant interactions or differences were found, Tukey's test were used as post-hoc analysis. T-tests were run to assess aboveground and belowground biomass of *U. paniculata*. Statistical analyses were performed using JMP statistical software (JMP Pro 13; SAS Institute, Cary, North Carolina, USA).

Results

Meteorological data

Temperatures were similar between 2018 and 2019 growing seasons (May – Sept) but precipitation varied. Average maximum and minimum temperatures for 2018 were 28.6 °C and 21.5°C, respectively. For 2019, average maximum and minimum temperatures were 28.9 °C and 21.5°C, respectively. Total precipitation was lower in 2018 growing season (261.4 mm) compared to 2019 growing season (351.3 mm) (Fig 3).

Natural distribution and density

The two species differed significantly in their distribution and density. Elevational distributions were significantly different between species ($\chi^2 = 3.05$, $p < 0.0001$) (Fig 4). At 2 m above sea level, *A. breviligulata* was the dominant species 85% more than *U. paniculata*. Whereas, at 5 m above sea level, *U. paniculata* dominated 72% more than *A. breviligulata*. *Ammophila breviligulata* exhibited higher density compared to *U. paniculata* ($t = 10.72$, $p < 0.0001$) (Fig 5). Density in *A. breviligulata* was 85% higher than *U. paniculata*.

Field experiment

Survival was significantly higher in *U. paniculata* compared to *A. breviligulata* for both seasons ($\chi^2 = 27.58$, $p < 0.0001$) (fig 6). There was not a significant difference in survival between treatments ($\chi^2 = 0.002$, $p = 0.97$). There was a 0% survival of *A. breviligulata* in season two. During season one, there were no significant differences in shoot length ($F = 2.6$, $p = 0.06$), stem # ($F = 1.1$, $p = 0.37$), or ramet # ($F = 1.78$, $p = 0.17$) between clumped and dispersed plantings of *A. breviligulata* (Table 1).

For *U. paniculata*, there was no significant difference in shoot length between planting densities (clumped and dispersed) ($F = 0.08$, $p = 0.78$), but it was significantly greater in season two ($F = 446.41$, $p < 0.0001$) (Table 1). There was a significant season x density interaction for stem # ($F = 8.76$, $p = 0.005$) (Table 1). Season two dispersed plantings had the highest stem number (mean and se), and season one clumped had the lowest (mean and se) (Table 1). Dispersed plantings had a significantly larger stem # than clumped plantings ($F = 28.08$, $p < 0.001$). Stem # was significantly greater in season two compared to season one ($F = 54.23$, $p < 0.0001$). Planting density ($F = 64.68$, $p < 0.0001$) and season ($F = 16.32$, $p < 0.0002$) had an effect on ramet number with dispersed plantings and season two having higher ramet numbers (Table 1). Ramet

elongation (RE) differed significantly between planting densities ($F=8.36$, $p=0.026$) with dispersed planting having higher RE than clumped plantings. There was a significant difference in RE between seasons ($F=46.00$, $p<0.0001$) (Table 1)

Due to no survival, biomass was not assessed for *A. breviligulata*. For *U. paniculata*, aboveground biomass was 33.8% greater in dispersed plantings ($t=2.66$, $p=0.02$). Belowground biomass was 44.9% greater in dispersed plantings ($t=3.78$, $p=0.01$) (Fig 7). There were no significant differences found in any measured root traits ($p > 0.05$ for specific root length, root diameter, and specific root density) (Table 2).

Discussion

Coastal dune vegetation plays an important role in dune building and stabilization (Cowles 1899; Olson 1958; Wagner 1964; Durán and Moore 2013; Charbonneau et al., 2016) and revegetation is critical for restoring degraded dune systems, especially with increasing sea-level rise and storm surge. Successful dune revegetation should replicate the natural distribution of species (McCallum et al., 2018). The purpose of our experiment was to measure the natural distribution and density of *U. paniculata* and *A. breviligulata* at Back Bay National Wildlife Refuge, and to experimentally examine the response of these species to clumped and dispersed plantings.

Our results suggest that *A. breviligulata* dominates dune systems at Back Bay National Wildlife Refuge compared to *U. paniculata*. Our findings correspond with those of Hacker et al. (2019), with lower relative proportions of *U. paniculata* found at False Cape State Park, VA (adjacent to Back Bay NWR). Lower abundance of *U. paniculata* is likely due to the species distribution range. The upper range of *U. paniculata* is Assateague Island (~100 miles from Back

Bay), whereas the Southern range of *A. breviligulata* is cape Fear, NC (~200 miles from Back Bay) (Goldstein et al., 2018, Hacker et al., 2019). Moving south, abundance of the two species switches, with *U. paniculata* dominating dunes in southern North Carolina.

Higher density of *A. breviligulata* leads to greater sand accumulation (Hacker 2019). Sparse growth form, and slow lateral spread of *U. paniculata* (Woodhouse et al., 1978; Goldstein et al., 2017) leads to steep, narrow, hummocky dunes. Density of *U. paniculata* at our site is similar to those reported by Nabukalu (2013; 24 shoots m² in VA and NC) but higher than those reported elsewhere dunes along the US Atlantic and Gulf coasts (3-8 shoots m⁻² in LA, and 9.5 shoots m² on dune slope, 1.5 shoots m² on dune crest in NC; Wagner 1964; Hacker 2019). As relative abundance of *U. paniculata* decreases at higher latitudes, density increases which may enable expansion into northern latitudes.

There was a significant difference in the frequency distribution of both species with regards to elevation. *Ammophila breviligulata* was greater in lower dunes (2-3 m) while *U. paniculata* exhibited greater frequency at higher elevations (5-6 m). This corresponds with Hacker et al. (2019), and is likely due to distance from the water table (Oosting and Billings 1942; Hester and Mendelssohn 1989). *Uniola paniculata* thrives at ~1.3 m above the water table or greater, and is limited by prolonged inundation (Oosting and billings, 1942; Hester and Mendelssohn, 1989). Possible competitive interactions may also account for elevation variations in distribution. *Ammophila breviligulata* is negatively affected by *U. paniculata*, with *U. paniculata* found to invade *A. breviligulata* dominated foredunes (Woodhouse et al., 1978; Brown et al., 2017; Harris and Zinnert 2017). Negative interactions with *U. paniculata* could limit *A. breviligulata* abundance at higher elevations where the two species co-occur (VA and NC).

The natural distribution of *A. breviligulata* and *U. paniculata* indicates that the two species should be planted separately, with *A. breviligulata* planted at lower foredunes and *U. paniculata* planted in upper foredunes. Differing natural densities between the two species also indicates the need for different planting densities. *Ammophila breviligulata* occurs at high densities indicating that clumped planting designs may be beneficial. *Uniola paniculata* occurs more sparsely, and may benefit from spaced plantings. Our experimental results validate dispersed planting for *U. paniculata*, but due to low survival, further research is needed to look at the response of *A. breviligulata* to clumped plantings.

Ammophila breviligulata had low survival by the end of season one and complete loss of all plantings by the end of season two. The survival results were surprising due to the natural range of the species and large initial biomass of *A. breviligulata* relative to *U. paniculata*. High temperatures and lower precipitation during the planting timeframe may have contributed to survival. Average temperature in May 2018 was 26.1°C and growing season maximum temperatures were ~28°C. *Ammophila breviligulata* exhibits temperature sensitivity with a reduction in biomass as temperatures exceed 26°C (Seneca and Cooper 1971). *Ammophila breviligulata* plantings may be more sensitive due to lower root development. During season one, there were no significant differences in any growth parameters of surviving plants based on planting design.

Growth parameters differed with density in *U. paniculata* which may affect the dune building process. Our experimental results suggest that *Uniola paniculata* exhibits more competitive intraspecific interactions in clumped plantings. Negative intraspecific interactions were seen in growth parameters but not survival. Stem number, which is a good indicator of sediment capture (Zarnetske et al., 2015; Hacker et al., 2019), was greater in the dispersed

plantings. Greater ramet number in *U. paniculata* dispersed plantings indicates more rapid lateral growth compared to the clumped plantings, leading to faster growing dune systems with greater area (Cowles 1899). Higher ramet number allows access to water and nutrients from a greater range, allowing species to inhabit stressful areas (Evans 1992). Biomass allocation (i.e. the proportion above vs. belowground) was not influenced by planting design, but above and belowground biomass was reduced by >30% in clumped plantings. Sparsely planted *U. paniculata* may have greater sediment capture compared to densely planted *U. paniculata* due to greater stem number and biomass resulting in taller, steeper dunes (Zarnetske et al., 2015; Charbonneau and Castper, 2018).

Facilitation has been found to increase in high stress environments such as marshes (Silliman et al., 2015), therefore facilitation was assumed to be more common in high stress coastal dune systems. Our findings of reduced performance in *U. paniculata* when planted at higher densities are counter to those of marsh grasses indicating ecosystem-specific or species-specific responses to density planting (Silliman et al., 2015; Harpenslager et al., 2016). Dune plants exhibit high variability in interaction response including competitive, neutral, or facilitative interactions (Franks 2003; Brown et al., 2017). *U. paniculata* is tolerant of coastal dune stressors making it less likely to be positively affected by interaction (Liancourt et al., 2005). Lower biomass of clumped *U. paniculata* may be due to competition for soil resources (Franks 2003). In marsh grasses, elevation was found to influence facilitation (Silliman et al., 2015). Based on the natural distribution of dune grasses, elevation and latitude may play a critical role in density planting success, with differences for varying dune species. Therefore, revegetation efforts should individualize species planting designs, with natural species distribution as an indicator of optimal planting density.

Restoration efforts, specifically revegetation, are critical to dune development and stabilization (Charbonneau and Casper, 2018). *Ammophila breviligulata* and *U. paniculata* are commonly used in dune restoration as they are ecosystem engineers of coastal foredunes (Wagner 1964; Woodhouse 1978). Dune building and stabilizing traits of these species makes them ideal for dune restoration. Proper planting configurations of dune vegetation could have implication for dune morphology. Dispersed plantings of *U. paniculata* could encourage sediment capture and lateral growth due to increased stem and ramet number, forming of taller and larger area dune ridges (Cowles 1899; Zarnetske et al., 2015). Based on natural distribution, *A. breviligulata* may exhibit higher performance when planted in clumped configurations, but this remains to be tested. Although our results indicate negative interactions within clumped *U. paniculata*, facilitation theory should still be incorporated into restoration practices (Silliman et al., 2015). Future studies should measure the density and interaction (intra- and inter- specific) effect of dominant restoration species to incorporate into productive restoration practices.

Table 1. Averages \pm SE of shoot length (SL), stem number, ramet number, and ramet elongation (RE) for clumped and dispersed plantings of *Ammophila breviligulata* and *Uniola paniculata* during two growing seasons. Results of Tukey’s test for significant difference are indicated by letters ($P \leq 0.05$). Significant season effect is indicated by a blue asterisk, and significant treatment effect is indicated by a red asterisk. There were no significant differences in season one for *A. breviligulata*.

	Season 1		Season 2	
	<i>Clumped</i>	<i>Dispersed</i>	<i>Clumped</i>	<i>Dispersed</i>
<u><i>A. breviligulata</i></u>				
SL	16.7 \pm 1.5	18.2 \pm 1.1	-	-
stem #	2 \pm 0.2	2.2 \pm 0.3	-	-
Ramet #	0.1 \pm 0.1	0.2 \pm 0.1	-	-
RE	2 \pm NA	5 \pm 3	-	-
<u><i>U. paniculata</i></u>				
SL *	30.8 \pm 1.0	33.1 \pm 1.3	89 \pm 4.8	84.3 \pm 2.8
stem #	7.7 \pm 0.7 ^C	11.8 \pm 1.0 ^{BC}	14 \pm 1.8 ^B	26.6 \pm 2.0 ^A
Ramet # **	2.7 \pm 0.5	5.1 \pm 0.7	5.1 \pm 1.1	10.9 \pm 1.3
RE **	4.1 \pm 0.3	8.5 \pm 0.7	34.5 \pm 6.0	52.2 \pm 10.7

Table 2. Averages \pm SE and t, p values of root traits in clumped and dispersed plantings of *Uniola paniculata*.

<i>Uniola paniculata</i>			
	clumped	dispersed	Sig.
Mean root diameter	1.05 \pm 0.03	1.14 \pm 0.05	t = -1.70, p = 0.14
Relative root length	464.01 \pm 32.10	428.55 \pm 22.60	t = 0.90, p = 0.40
Root tissue density	0.25 \pm 0.02	0.23 \pm 0.01	t = 1.06, p = 0.33

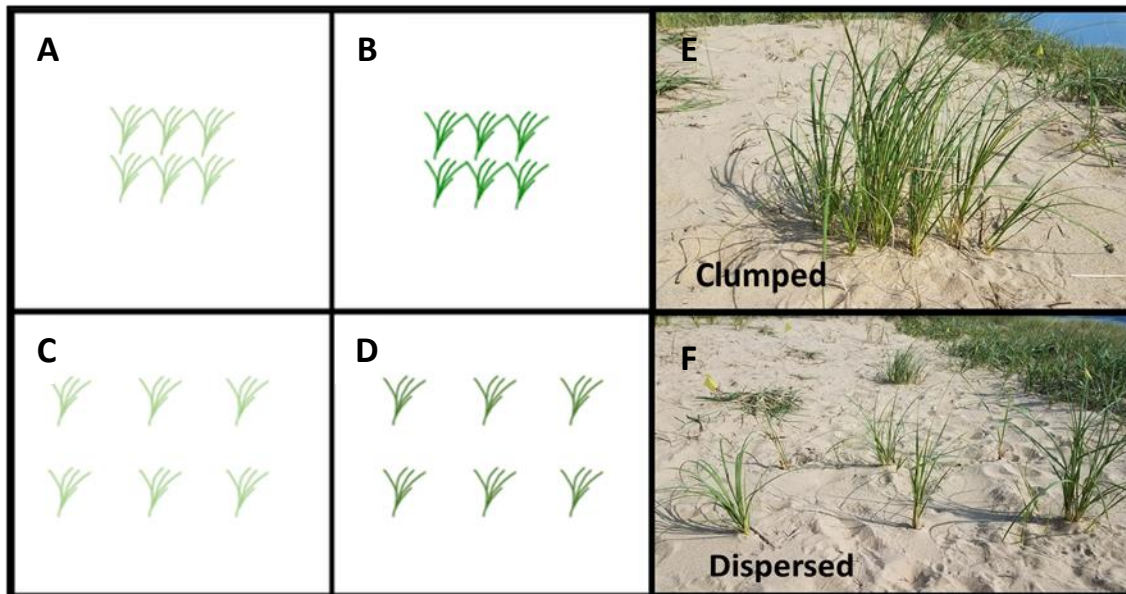


Figure 1. The experimental planting design included; clumped planting patterns for *Ammophila breviligulata* (A) and *Uniola paniculata* (B), and dispersed (50 cm apart) planting patterns for *Ammophila breviligulata* (C) and *Uniola paniculata* (D). Images show clumped (E) and dispersed (F) plantings.

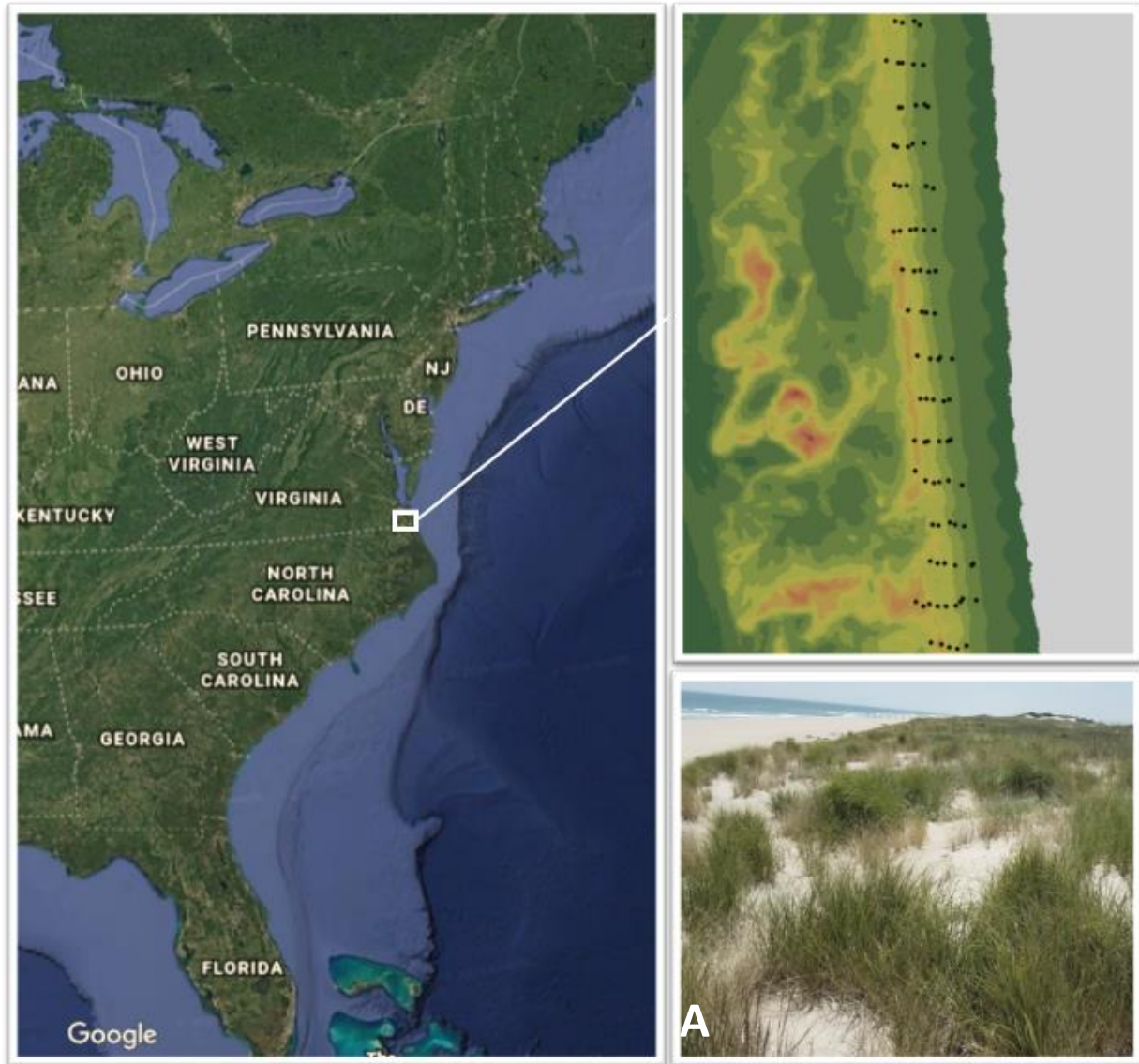


Figure 2. Map marking the location of Back Bay National Wildlife Refuge (A), the transect locations used to survey the distribution of *Ammophila breviligulata* and *Uniola paniculata* at Back Bay National Wildlife Refuge (B), and an image of *Ammophila breviligulata* on the dunes at Back Bay National Wildlife Refuge (C).

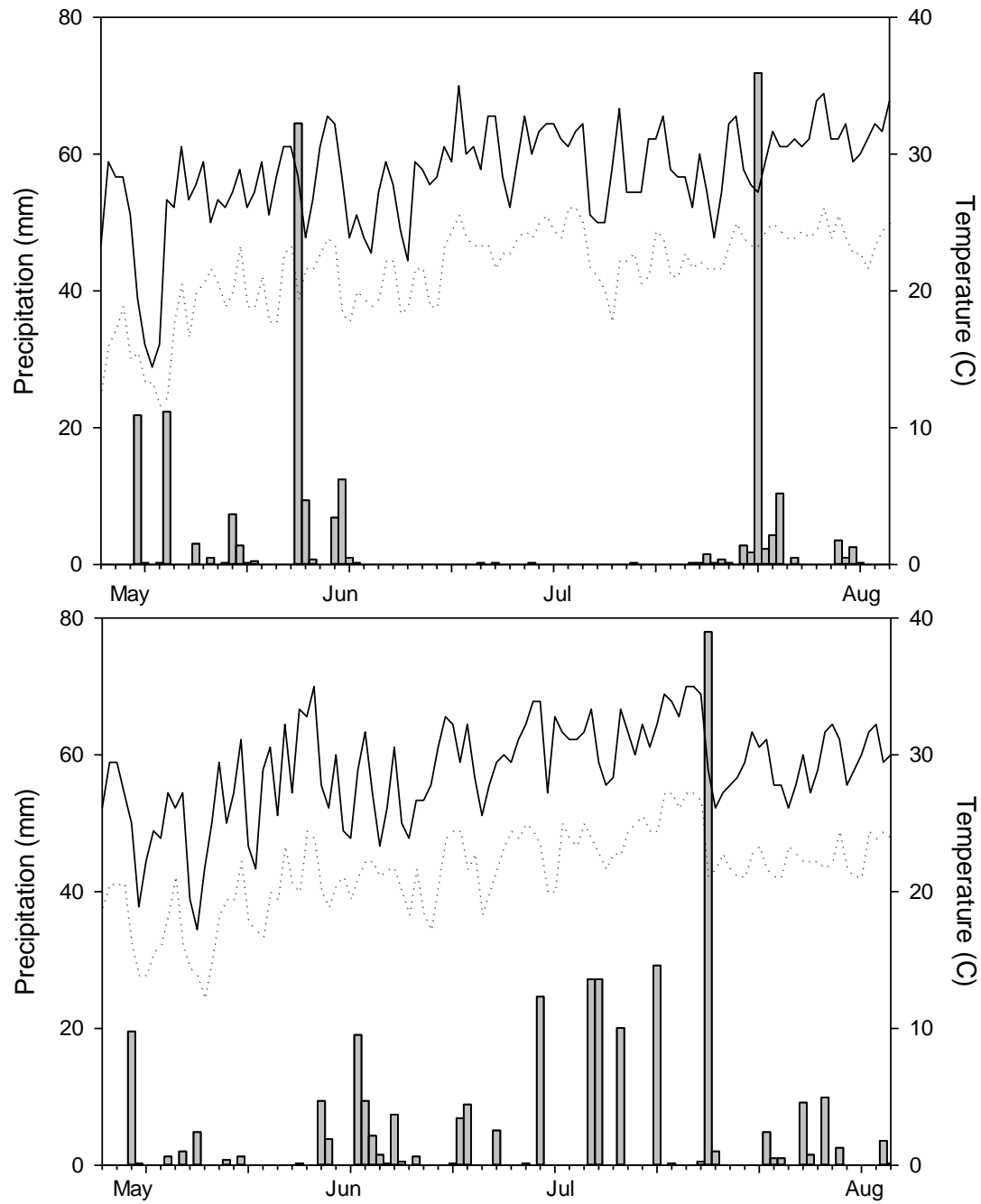


Figure 3. Meteorological data from the growing seasons of 2018 (A) and 2019 (B). Grey bars represent daily precipitation, solid line represents daily maximum temperature, and dotted line represents daily minimum temperature.

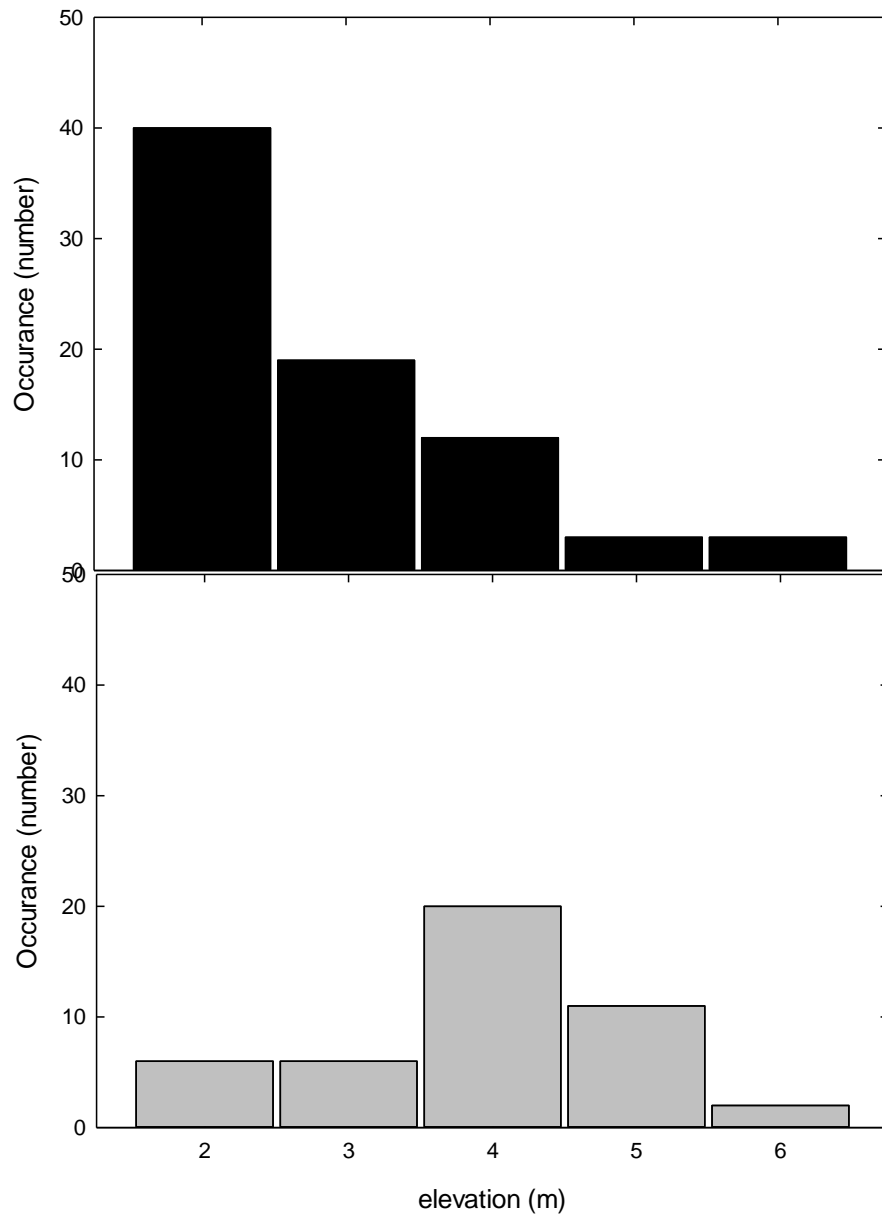


Figure 4. Distribution of *Ammophila breviligulata* (black) and *Uniola paniculata* (grey) within the front primary dune at Back Bay National Wildlife Refuge.

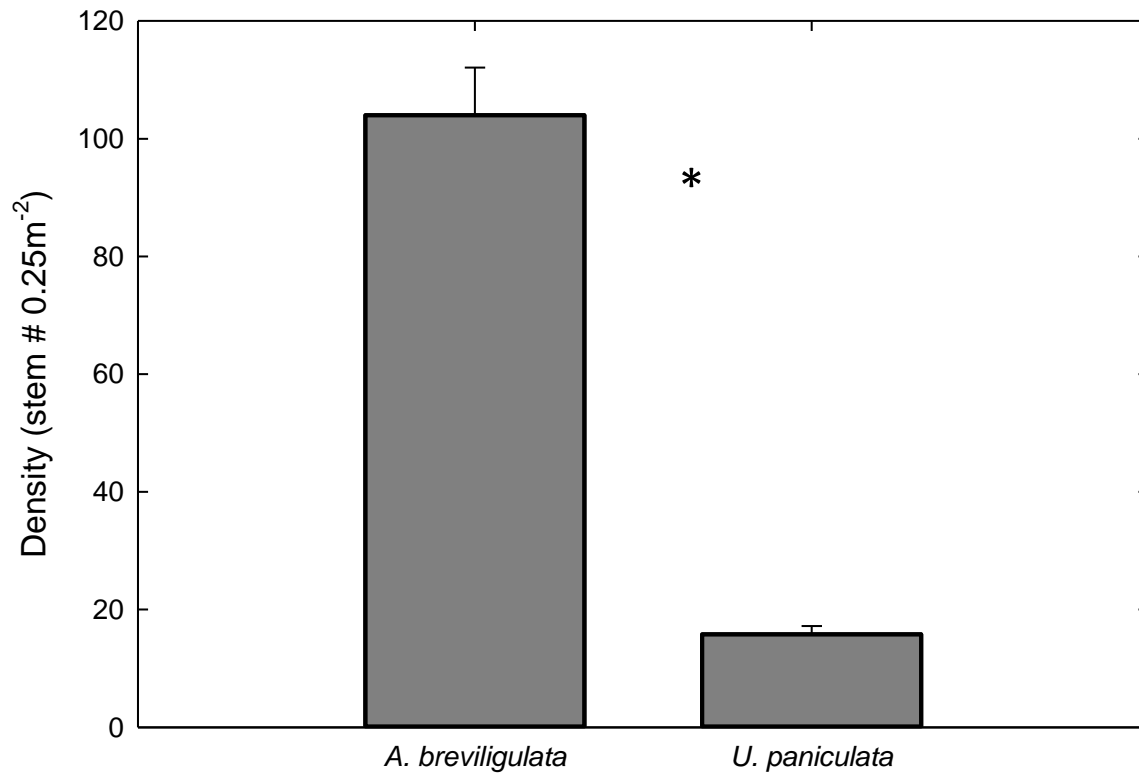


Figure 5. Natural density of *Ammophila breviligulata* and *Uniola paniculata* at Back Bay National Wildlife Refuge. All bars show mean \pm SE. Results of t-test are indicated by a star ($P \leq 0.05$).

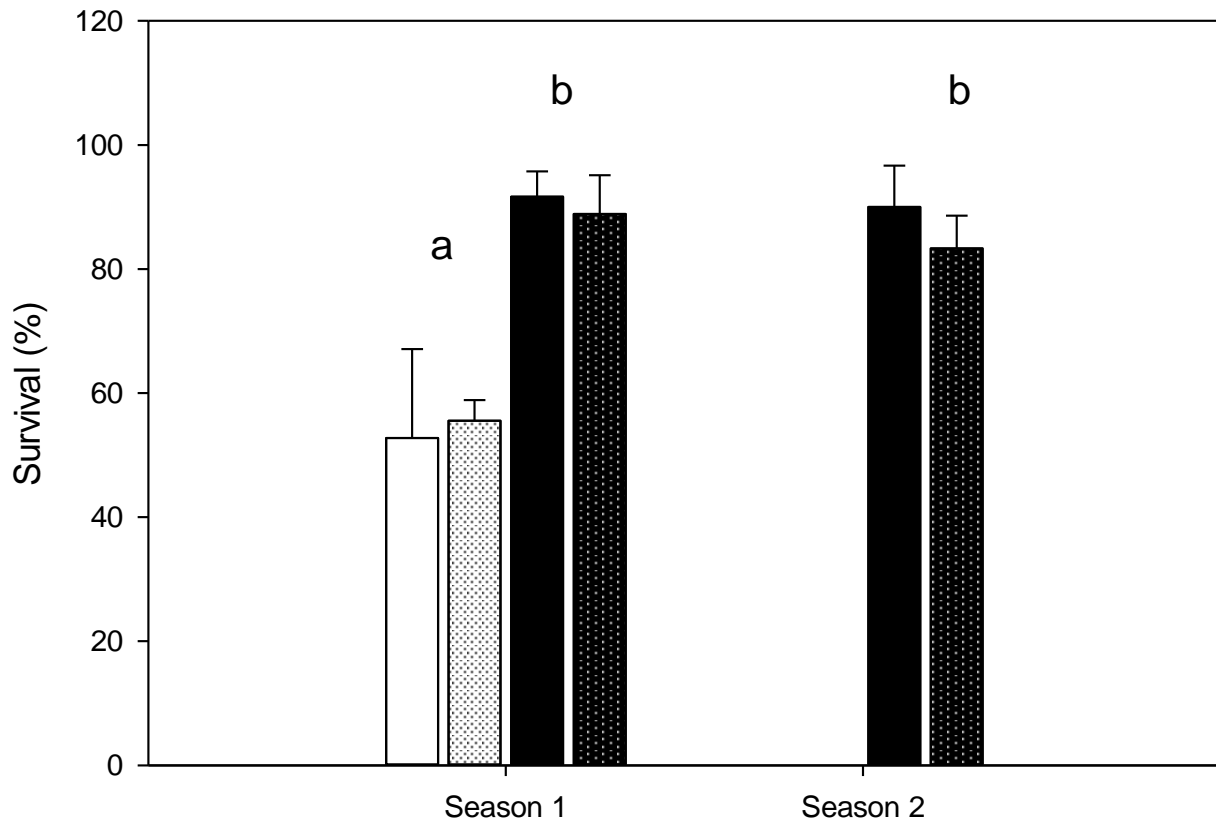


Figure 6. Percent survival of *Ammophila breviligulata* (white) and *Uniola paniculata* (black) in clumped (solid) and dispersed (dotted) plantings during seasons one (2018) and two (2019). All bars show mean \pm SE. Results of Tukey's test for significant difference are indicated by letters ($P \leq 0.05$).

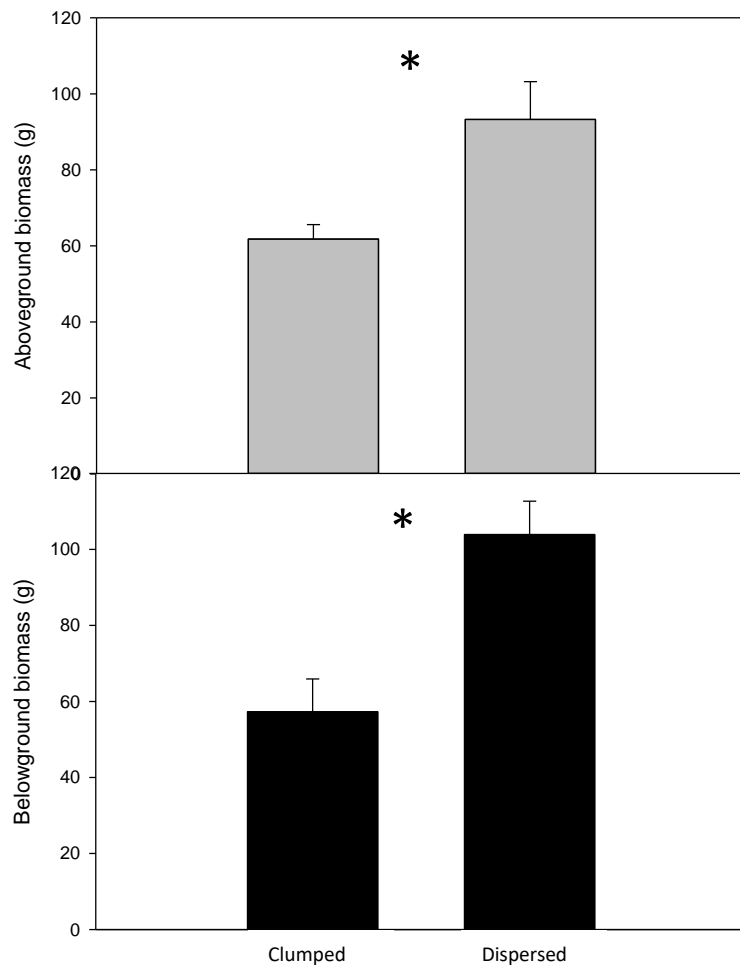


Figure 7. Aboveground (grey) and belowground (black) biomass of *U. paniculata* in clumped and dispersed plantings. All bars show mean \pm SE. Stars indicate significant difference between clumped and dispersed ($P \leq 0.05$).

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