2016

Differential Response of Barrier Island Dune Grasses to Species Interactions and Burial

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DIFFERENTIAL RESPONSE OF BARRIER ISLAND DUNE GRASSES TO SPECIES

INTERACTIONS AND BURIAL

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

by

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March 2016

Acknowledgements

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ABSTRACT

Dune grasses are integral to biogeomorphic feedbacks that create and alter foredunes and barrier island stability. In a glasshouse study, *Ammophila breviligulata* Fern. and *Uniola paniculata* L. were planted together and subjected to sand burial to quantify morphological and physiological response. *Ammophila breviligulata* physiological and morphological performance declined when planted with *U. paniculata* but *U. paniculata* was not affected when planted with *A. breviligulata*. Burial had a positive effect on *A. breviligulata* and *U. paniculata* as indicated by electron transport rate and total biomass at the end of the experiment. Due to their different growth strategies, *A. breviligulata and U. paniculata* form continuous versus hummocky dunes, respectively. As global temperatures rise and *U. paniculata* migrates into *A. breviligulata* dominated habitat, *A. breviligulata* performance may diminish, and changes in dune form could result in altered island stability via increased overwash. Foredune community structure could also change due to the shift in dominant species which could alter dune succession.

CHAPTER 1

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 on the front lines of climate change

from the effects of storms and sea-level rise (Miller 2015). They are sensitive and

dynamic systems due to high disturbance frequency, sediment mobility, and

biogeomorphic feedbacks, making them sentinels of climate change (Stallins and

Parker 2003; Brantley et al. 2014; Zinnert et al. 2016).Climate change effects could be

further exacerbated on barrier islands by species migrations and biotic feedbacks

(Durán and Moore 2013).

In addition to increased storm impacts and sea-level rise, climate change has the

potential to alter these systems through increased global temperature (Wang et al.

2014), an overlooked driver in coastal research. Increasing temperature could indirectly

alter the islands through shifts in flora distribution patterns. Semitropical plant species

may experience a latitudinal expansion due to the ameliorated conditions, which would

shift plant community compositions on these islands (Gonzalez et al. 2010). On the

Atlantic coast of North America, specifically on the barrier islands of Virginia, the

semitropical dune grass *Uniola paniculata* L. (Poaceae) has the potential to expand its

range northward into the habitat of *Ammophila breviligulata* Fern., the dominant dune grass species of mid-Atlantic coastlines. These two species currently co-occur on the Outer Banks, NC (Emery and Rudgers 2013; Hodel and Gonzalez 2013) (Figure 1) 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 (Figure 1) (Dolan 1972).

Foredunes established by *A. breviligulata*, a C_3 or cool season species, form long and continuous dune ridges along the shoreline (Brantley et al. 2014). *Ammophila breviligulata* is clonal and has "guerrilla root" morphology (Brantley et al. 2014). Connections between ramets are separated by long internodes resulting in widely spaced ramets that affect 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 *Uniola 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).

Because the photosynthetic pathway is C_4 based, warmer temperatures associated with climate change enhance the northern expansion of *U. paniculata* further into the Virginia barrier island system (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 overwash fans, propagules of *U. paniculata* and *A. breviligulata* could establish alongside one another. It is unlikely that *U. paniculata* would expand on already established *A. breviligulata* foredunes as *U. paniculata* propagules cannot compete with well-established *A. breviligulata*. Expansion through overwash could lead *U. paniculata* to directly compete for habitat with *A. breviligulata*. While 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 toleration for higher temperatures and higher water use efficiency (WUE) (Way et al. 2014). Under climate change scenarios, the benefits of the C_4 photosynthetic pathway could give *U. paniculata* the competitive advantage to displace *A. breviligulata* as the dominant species when they co-occur, for example, on the Virginia barrier islands.

Vegetation change on foredune habitats of barrier islands resulting from range expansion of a species can alter dune morphology and overwash frequency through differential responses to burial and species interactions (Durán and Moore 2013).

Foredune vegetation has a strong impact on dune morphology through influences on sediment deposition and mobility (Stallins and Parker 2003; Miller 2015). 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).

How dune grasses differentially respond to burial and species interactions (both morphologically and physiologically) is essential for predicting dune morphological changes (Feagin et al. 2015). Examining species interactions along with environmental stressors is essential to predicting plant response as both can act together to influence response (Zarnetske et al. 2013; He and Bertness 2014). The objective of our study was to determine how growth of the dominant dune grasses *Ammophila breviligulata* and *Uniola paniculata* respond when grown in monoculture or mixture planting. It was also of interest to determine how overwash induced burial influenced plant morphological and physiological responses. 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 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 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* seedlings (~25cm and 30cm respectively) were obtained from Cape Coastal Nursery, South Dennis, MA and Coastal Transplants, Bolivia, NC respectively. 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) (Figure 2). A total of 6 individual stems were planted per 15 X 15 cm pot containing 1.8 kg of sand. The experiment was conducted from late May 2015 to early July 2015 (9 weeks). Glasshouse photosynthetic photon flux density was ~1300 µmol m-1 s-1 with a mean temperature of 31.3 °C and a mean daily high of 40 °C (Thermodata ibutton data logger).

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 (Figure 2). 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 · L_2 - ln · 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.

$\delta^{13}C$, %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 72h and ground into a fine powder with a hand held 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

Before statistical analysis, data were found to be evenly distributed and had equal variance. 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. Principal components analysis (PCA, PC-ORD software v. 5.10) of measurement variables were used to separate species and treatments and determine which traits were most important for influencing separation. Resulting groups were then compared using multiple response permutation procedures (MRPP).

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) ($p > 0.05$) (Table 1). There were no interactions for electron transport rate (ETR) but there was an effect of species ($F = 7.9$, $p = 0.008$) and burial ($F = 19.1$, $p = 0.0001$); ETR was enhanced for both species with burial. *Uniola paniculata* had a higher mean ETR (51.0 ± 2.3 µmol m^{-2} s^{-1}) than *Ammophila breviligulata* (42.1 ± 3.2 µmol m^{-2} s^{-1}) under both burial regimes (Table 2). While not significant, there was a trend of *A. breviligulata* monoculture planting mean ETR (46.7 ± 4.8 µmol m^{-2} s^{-1}) being higher when compared to being grown in mixture with *U. paniculata* (37.5 ± 3.8 µmol m^{-2} s^{-1}) (Table 2).

All other physiological measurements (g_s, $\delta^{13}C$, %N, C:N) had a significant species x planting type interaction ($p < 0.05$) (Table 1). Stomatal conductance was

significant among planting type (F = 5.2, p = 0.029). 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 (285 ± 32 mmol m^{-2} s^{-1}) was higher than mixture plantings (163 ± 27 mmol m^{-2} s^{-1}) (Table 2). δ^{13}C was higher for *U. paniculata* than *A. breviligulata* (F = 7587.5, p = <0.0001). Percent nitrogen was higher for *A. breviligulata* than *U. paniculata* (F = 39.8, p < 0.0001) and burial was higher than controls (F = 9.2, p = 0.0001) (Table 1; Figure 3). 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 (Figure 3). C:N was higher (F = 38.0, p = <0.0001) for *U. paniculata* (28.1 ± 1.8) than *A. breviligulata* (19.5 ± 3.2) and buried plants had an 18.1% lower C:N than controls (F = 11.4, p = 0.0002) (Table 2).

Morphology

Aboveground biomass and belowground biomass had a significant species x planting type x burial interaction (F = 4.8, p = 0.034; F = 7.0, p = 0.013 respectively). Belowground biomass had a significant species x planting type interaction (F = 38.7, p <0.0001) and species x burial interaction (F = 9.5, p = 0.0004).Total biomass only had a significant species x planting type interaction (F = 8.7, p = 0.006). Belowground biomass was higher for both species when in monoculture versus mixture planting (F = 144.6, p = <0.0001) (Figure 4). *Ammophila breviligulata* had higher belowground biomass (0.7 ± 0.1) than *U. paniculata* (0.4 ± 0.04). Burial increased belowground biomass for *A.*

breviligulata but not *U. paniculata* (F = 72.9, p <0.001). Total biomass for monoculture plantings for both species was higher than for mixture plantings (F = 17.7, p = 0.0002) and burial yielded higher biomass than controls (F = 4.2, p = 0.048) (Figure 4). *Ammophila breviligulata* total biomass was higher than *U. paniculata* (F = 4.4, p = 0.044) (Figure 4).

Relative growth rate (RGR) exhibited significant species x planting type x burial interaction (F = 6.4, p = 0.016). *Ammophila breviligulata* monoculture planting RGR was higher (F = 13.8, p = 0.002) than mixture planting; however, burial had no effect (F = 2.2, p = 0.161) (Figure 5). *Uniola paniculata* displayed an opposite pattern where RGR was higher for buried treatment (F = 37.4, p = <0.0001) but planting type had no effect (F = 0.6, p = 0.446) (Figure 5). Number of alive leaves exhibited a significant species x planting type (F = 25.0, p < 0.0001) interaction. *Uniola paniculata* mixture planting had more leaves than monoculture planting and *A. breviligulata* monoculture planting had more leaves than mixture plantings (Figure 5). It also exhibited a significant species x burial (F = 17.5 p = 0.0002) interaction, where burial increased leaves of *U. paniculata* (Figure 5), and planting type x burial interaction (F = 8.1, p = 0.008). *Uniola paniculata* was higher than *A. breviligulata* with the exception of *A. breviligulata* control monoculture (F = 52.9, p < 0.0001) (Figure 5).

Combined traits

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 axis 1 explained 42.2% of the variation with height (r = 0.94) and $\delta^{13}C$ (r = 0.90) being most influential in providing separation (Table 3). Axis 2 explained 26.6% of data variation, and below ground biomass (r = 0.64) and stomatal conductance (r = 0.79) were most influential in providing separation (Table 3). Using MRPP, three significantly different groupings were observed (t = -7.9, p < 0.0001; Figure 6). *Uniola paniculata* separated completely from *A. breviligulata* into a distinct group. Ammophila *breviligulata* grouping further divided into monoculture plantings versus mixture plantings. While not significant from the MRPP, *U. paniculata* had a trend of controls clustering at the bottom of the group and burial treatment clustering at the top (Figure 6).

DISCUSSION

Overwash is essential for the natural landward migration of barrier islands in response to sea level rise (Walters et al. 2014). Overwash provides opportunities for species propagules to establish as ecological succession is reset within overwash fans (Brantley et al. 2014). As climate change alters abiotic conditions and range expansion of species occurs, it is crucial to understand expanding species interactions with present species. *Uniola paniculata* has the potential to expand northward along the Atlantic coast into *A. breviligulata* dominated habitat and has been observed on the Virginia Barrier Islands (Young, personal observation). The relationship between *A. breviligulata* and *U. paniculata,* and how they respond both morphologically and physiologically to environmental factors such as burial, will eventually influence dune morphology (Stallins and Parker 2003). Understanding interactions between these two dune grasses and response to burial is the first step in predicting shifts in dune morphology after storm

induced burial events (Brantley et al. 2014). Our study demonstrates that *A. breviligulata* and *U. paniculata*, species that are both adapted to withstand foredune conditions, differentially respond to varying conditions such as being planted in a mixture or being buried.

Our results indicate *A. breviligulata* physiological and morphological performance declined when planted with *U. paniculata*, while *U. paniculata* did not appear to be affected when planted with *A. breviligulata*. Burial had a positive effect on *U. paniculata* and *A. breviligulata*. This can be seen at a physiological level which underpins whole plant responses to stressors. Electron transport rate (ETR) was higher for *U. paniculata* than *A. breviligulata*. *Uniola paniculata* having a higher ETR is not unusual given the C_4 photosynthetic pathway (Taylor et al. 2010). Relative to monoculture plantings, ETR and relative growth rate (RGR) for *A. breviligulata* mixture plantings were reduced. This directly contributed to *A. breviligulata* mixture plantings having a lower total biomass than monoculture plantings. 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*. Buried plants of both species had higher ETR and total biomass than controls. *Ammophila breviligulata* (Disraeli 1984; Maun and Lapierre 1984) and *U. paniculata* (Wagner 1964) morphology has been reported to respond positively to burial. Yaun et al. (1993) reports *A. breviligulata* physiology responds positively to burial with increased net photosynthetic rate and CO_2 assimilation rate. Our results of higher *A. breviligulata* ETR with burial agree with these findings. *Uniola paniculata* physiological response to burial is less documented. We report *U. paniculata* having higher ETR and RGR when buried. Positive responses, both physiologically and

morphologically, are needed in foredune environments in order to recover from frequent burial by overwash events.

How dune grasses utilize fresh water and nutrients is important due to limited availability of both within the strand environment (Frosini et al. 2012). High water use efficiency (WUE; carbon gain per water use) is important due to low water holding capacity of sandy soils (Uzoma et al. 2011). 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). 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). *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*. This 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.

For both species, burial enhanced percent nitrogen. Brown (1997) also showed this effect for two coastal dune shrub species *Chrysothamnus nauseous* and *Sarcobatus vermiculatus*. Enhanced percent nitrogen in remaining leaves could come

from re-allocated buried portions of the plant (Frosini et al. 2012). Gilbert and Ripley (2008) reported that 52-80% of nitrogen could be remobilized from buried leaves with other nitrogen from decaying leaves being absorbed by roots. This nutrient influx could be used to help stimulate growth of buried plants.

When all measures were integrated together it was clear that *A. breviligulata* was more affected by planting type than burial. *Uniola paniculata* responded inversely, with burial contributing more to grouping than planting type. These alterations of responses indicate that *A. breviligulata* has a diminished capacity of performance 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 the northern most site, out of 5 total sites, had a greater *A. breviligulata* absolute species cover that *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.

Interactions between *A. breviligulata* and *U. paniculata* could have impacts on dune morphology, community structure, and succession. As *A. breviligulata* performance diminishes in the presence of *U. paniculata*, changes in dune form could result in altered island stability via increased overwash leading to landward migration (Walters et al. 2014). Foredune community structure could also change due to the shift in dominant species. *Uniola paniculata* is associated with several other plant species within dune communities when compared with *A. breviligulata* (Dilustro and Day 1997;

Leonard et al. 2011). Stallins (2002) shows that sites at Core Banks, North Carolina, which have higher percent cover of *U. paniculata*, also have higher species richness than those with greater percent cover of *A. breviligulata*. These differences in community associations could impact future trajectories of dune succession. On Virginia barrier islands, increases in *U. paniculata* may shift community structure and island stability into a new realm previously unexperienced by northern Atlantic barrier islands.

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 stresses, as species interactions could shift with stress (Zarnetske et al. 2013; He and Bertness 2014). Plant communities on barrier island systems, which cope with multiple stressors simultaneously such as sea spray, burial, high radiation, salt water intrusion, and limited access to nutrients, demonstrate the need for species interactions and environmental stressors to be studied together. It is through differential dune grass interactions that feedbacks with foredune topography could be altered, shifting the future of barrier island stability and community composition.

ACKNOWLEDGEMENTS

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Table 1. Three-way ANOVA results (f,p) of electron transport rate (ETR), stomatal conductance (g_s), $\delta^{13}C$, %N, %C, C:N, aboveground biomass (AGB), belowground biomass (BGB), total biomass, relative growth rate (RGR) and number of alive leaves for the independent variables species (S), planting (P) and Burial (B). Bold indicates significance at $\alpha = 0.05$.

	S	P	B	S x P	S x B	P x B	S x P x 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
AGB	2.5, 0.125	0.2, 0.664	1.9, 0.175	0.7, 0.396	6.3, **0.017**	1.7, 0.198	4.8, **0.034**
BGB	72.9, **<0.0001**	144.6, **<0.0001**	8.1, **0.007**	38.7, **<0.0001**	9.5, **0.004**	3.1, 0.867	7.0, **0.013**
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
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

Table 2. Electron transport rate (ETR), stomatal conductance (g_s), $\delta^{13}C$, %N, %C, C:N, mean± standard error. *Ammophila breviligulata* = A, *Uniola paniculata* = U, Mixture planting = MX, Monoculture planting = MO, Burial = B, Not buried = NB.

	A-MX-NB	A-MX-B	A-MO-NB	A-MO-B	U-MX-NB	U-MX-B	U-MO-NB	U-MO-B
ETR	34.4 ± 3.2	40.6 ± 7.1	38.5 ± 5.3	54.9 ± 6.4	44.0 ± 2.0	58.3 ± 2.7	41.6 ± 3.8	60.0 ± 3.0
g_s	159 ± 33	168 ± 46	280 ± 21	289 ± 64	158 ± 12	243 ± 24	168 ± 18	206 ± 25
$\delta^{13}C$	-27.0 ± 0.3	-26.5 ± 0.8	-27.2 ± 0.1	-27.3 ± 0.1	-16.6 ± 0.1	-16.5 ± 0.1	-16.3 ± 0.1	-16.2 ± 0.1
%N	2.13 ± 0.19	2.39 ± 0.19	2.50 ± 0.12	2.67 ± 0.13	1.93 ± 0.07	2.18 ± 0.16	1.27 ± 0.12	1.80 ± 0.12
%C	43.32 ± 0.31	45.98 ± 0.30	46.59 ± 0.50	45.52 ± 0.40	45.53 ± 0.28	45.78 ± 0.43	46.85 ± 0.47	45.91 ± 0.14
C:N	22.28 ± 1.63	19.76 ± 1.57	18.78 ± 0.79	17.19 ± 0.80	23.68 ± 0.70	21.47 ± 1.85	38.40 ± 3.23	26.93 ± 1.78

Table 3. Pearson correlation of measurement variables with Principal Component Axes 1 and 2. Electron transport rate (ETR), stomatal conductance (g_s), aboveground biomass (AGB), belowground biomass (BGB), height, and number of alive leaves were used as input variables.

Variables	PCA 1	PCA 2
ETR	0.48	0.60
g_s	-0.09	0.79
% N	-0.54	0.58
$\delta^{13}C$	0.90	-0.26
AGB	0.55	0.42
BGB	-0.42	0.64
Height	0.94	0.07
# Alive Leaves	0.82	0.31

Figure Legends

Figure 1. Naturally occurring habitat range of *Ammophila breviligulata* Fern. (red) and *Uniola paniculata* L. (purple) on the east coast of the United States.

Figure 2. Multifactorial design consisting of two dune building grasses, two planting types, and burial treatment (20 cm) or control (0 cm).

Figure 3. *Ammophila breviligulata* Fern. and *Uniola paniculata* L. electron transport rate, stomatal conductance and % nitrogen for control/buried treatment and monoculture/mixture planting type. Values are means ± 1 standard error.

Figure 4. *Ammophila breviligulata* Fern. and *Uniola paniculata* L. aboveground biomass, belowground biomass, and total biomass for control/buried treatment and monoculture/mixture planting type. Values are means ± 1 standard error.

Figure 5. *Ammophila breviligulata* Fern. and *Uniola paniculata* L. relative growth rate and number of alive leaves for control/buried treatment and monoculture/mixture planting type. Values are means ± 1 standard error.

Figure 6. Principal Component Analysis (PCA) ordination for species, planting type and burial. PCA axis 1 and 2 are shown. Circles are buried *Ammophila breviligulata* Fern., triangles are control *A. breviligulata*, squares are buried *Uniola paniculata* L., and diamonds are control *U. paniculata*. Open symbols indicate mixture planting and solid symbols indicate monoculture planting. Three significantly different groups were observed (MRPP; t = -7.9, p < 0.0001). Dotted line in *U. paniculata* group represents the transition from control to burial treatment.
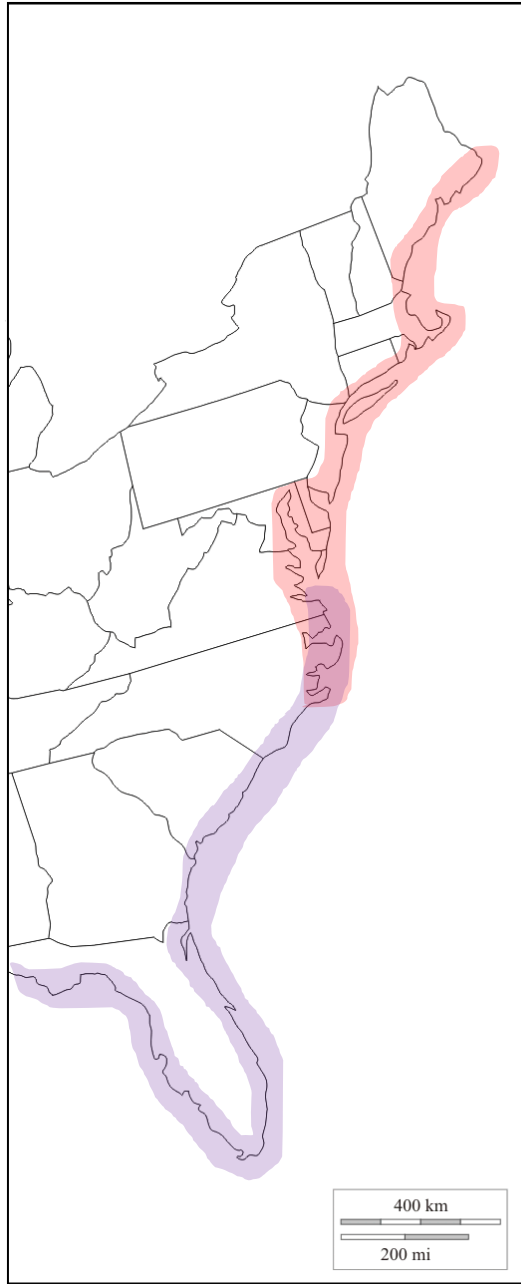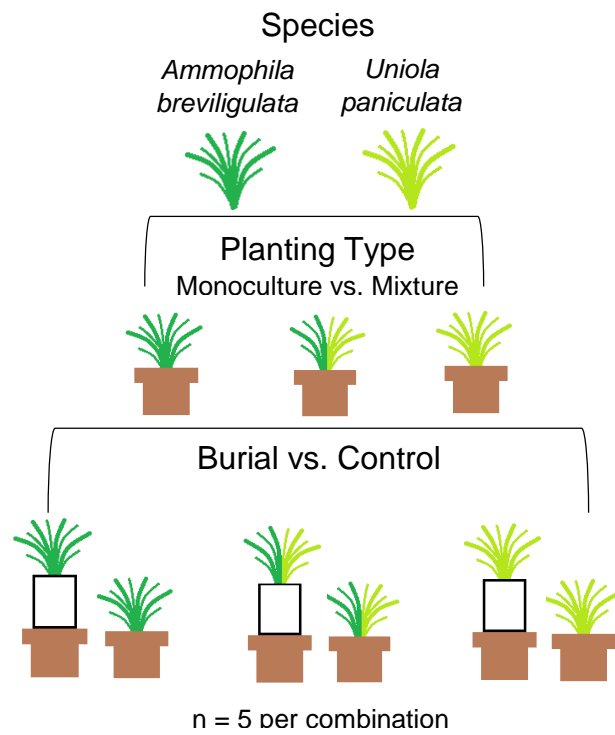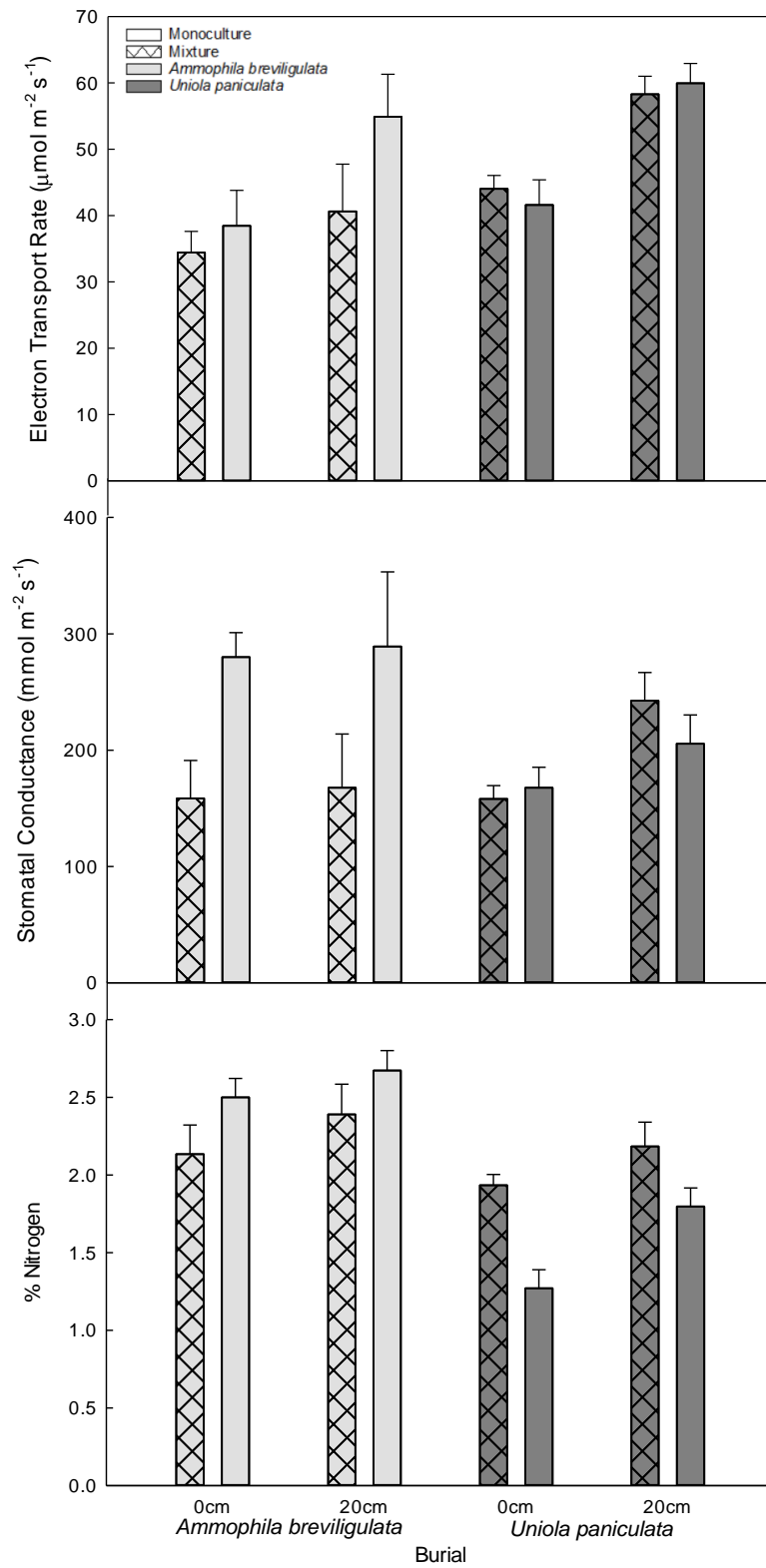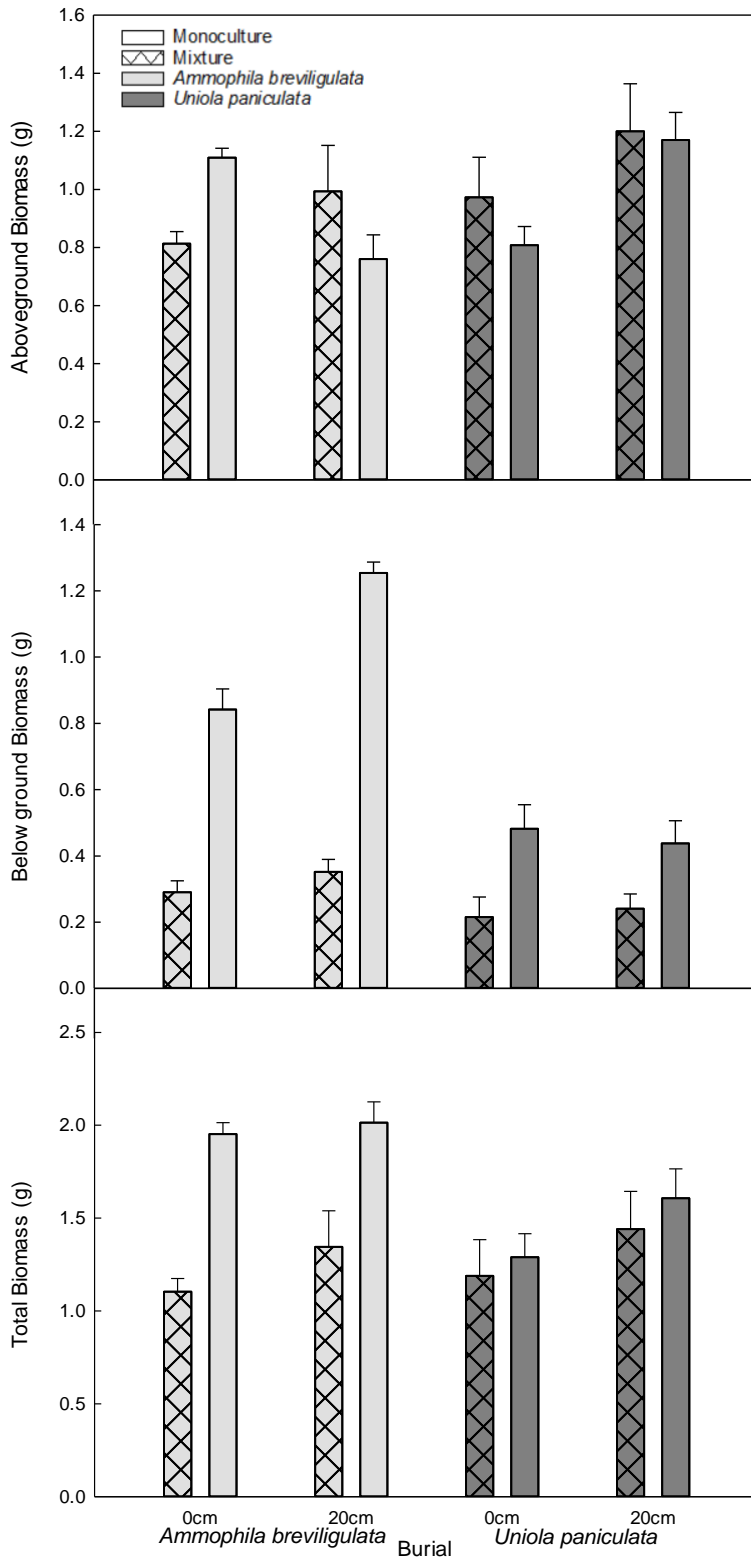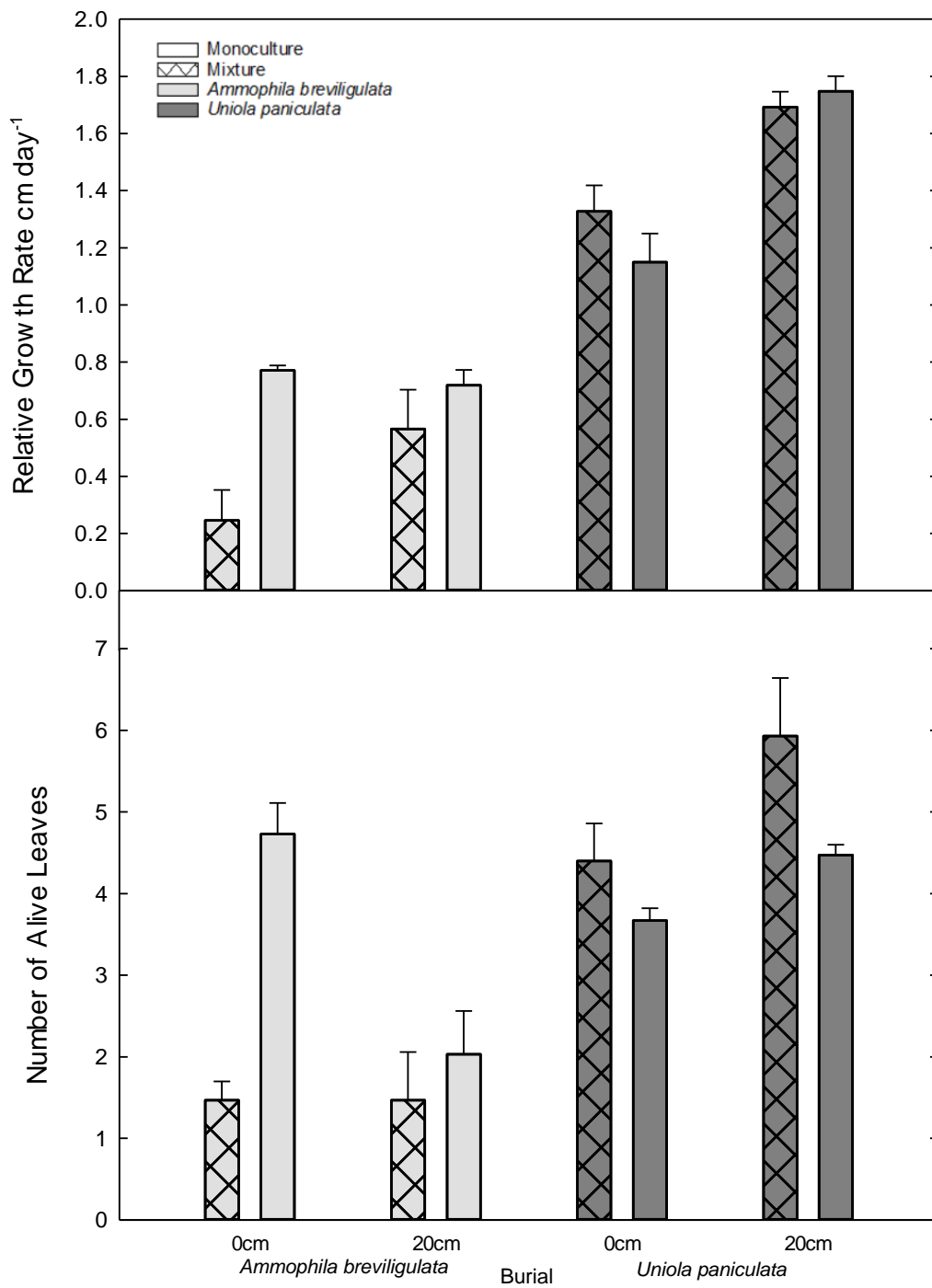
Figure 1.

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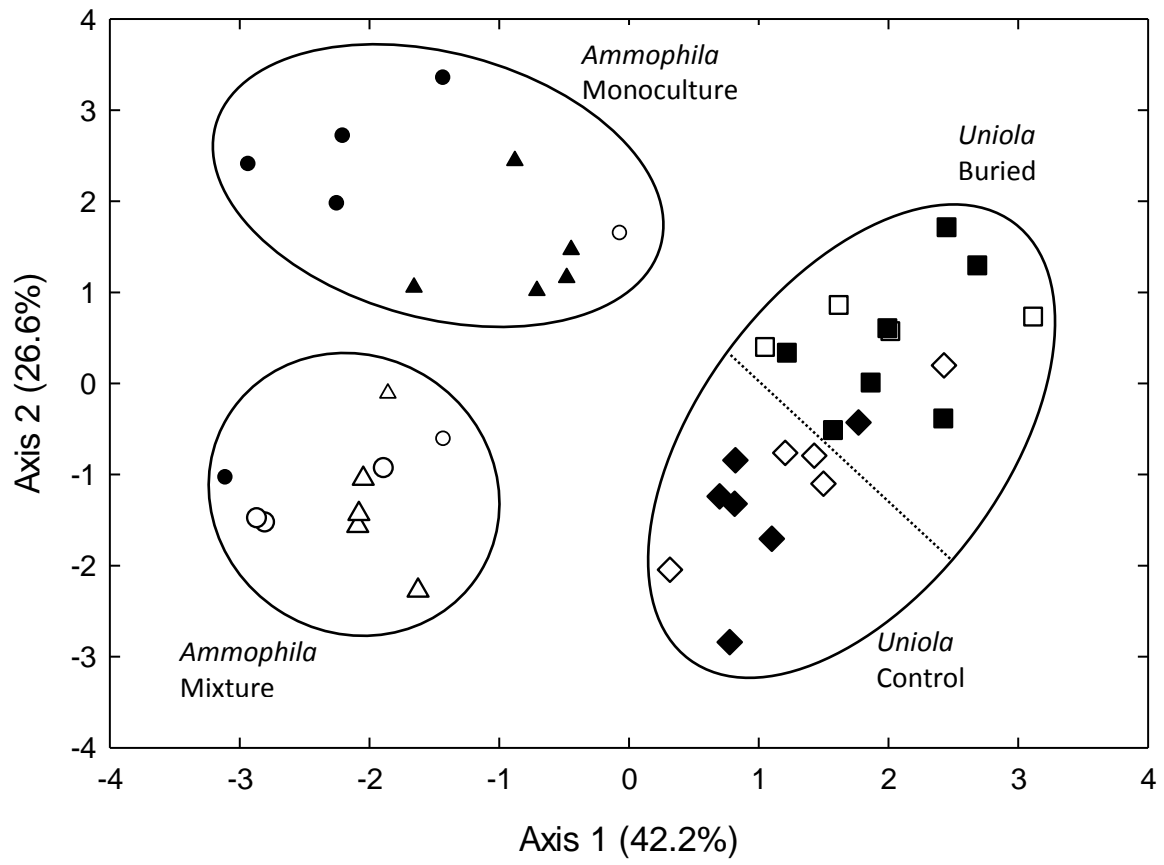
Figure 4.

Figure 5.

Figure 6.

VITA

April Lynn Harris was born on December 1, 1991 in Petersburg, Virginia. She was raised in South Hill, Virginia where she enjoyed a childhood filled with trips to Lake Gaston, visits to her grandpa's farm, and time spent in the woods and creeks. April graduated from Park View High School in 2010 fully intending to pursue chemistry as her course of study. At Southside Virginia Community College (SVCC) however, she discovered that biology was her true passion through the exciting and interesting lectures of Mr. Wheeler. With the help and support of Mrs. Cline, April graduated from SVCC with highest honors in 2011, earning an Associate of Arts and Science degree. She then when on to transfer to Longwood University where she did undergraduate research with Dr. Lehman, studying how plant chemistry influenced the ovipositional behavior of cabbage white butterflies. It was in this lab, after many hours spent cleaning caterpillar poop out of urine specimen cups, that April learned she wanted to study plants. After graduating Longwood summa cum laude with her B.S. in Biology in 2013, she went on to pursue her M.S. degree in the Coastal Plant Ecology Lab at Virginia Commonwealth University. There she studied dune grasses and learned that water stress was not a joke to be taken lightly. She graduated with her M.S. in biology in May of 2016. April hopes to pursue scientific outreach education as a career, inspiring young minds to love science!