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Stimulated growth response to sand burial of a coastal shrub

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

By

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Acknowledgements

I never would have made it across this finish line if it were not for the support, understanding, and help of so many people. The last two years have been difficult ones, nation-wide; no one will remember the years circa 2020 as an easy time to do anything. Obstacle after obstacle were thrown against Julie and I, including two major health crises. The journey I took over the course of my instruction required that I rely on others to a greater degree than I ever have in my life; truthfully, that was the hardest lesson of my master's education. No endeavor is truly made independently, though; no success is autonomous. None of us move forward without relying on those who went before, those who are travelling with us, and the privileges we have been afforded in life.

The utmost thanks and credit go to my adviser, Dr. Julie Zinnert, who was steadfast, honest, and generous in her mentorship. She modeled balance, vulnerability, and tenacity along with scientific prowess and fierce leadership. If she were a less capable mentor or less dedicated to the success of her students, I am not sure I would have made it.

Innumerable thanks also go to my labmates – all of the graduate students, undergraduate volunteers, and technicians of the Coastal Plant Ecology Lab who were generous with their advice, time, and labor when injury and illness threatened to derail us all.

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Abstract

STIMULATED GROWTH RESPONSE TO SAND BURIAL OF A COASTAL SHRUB

By Dawn Nicole Keller, M.S.

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

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Major Adviser: Dr. Julie Zinnert, Assistant Professor, Biology

Drivers of vegetation zonation on barrier islands are complex and interconnected. Sand burial is a strong driver in dynamic coastal systems, especially in the foredune community. However, it is not well understood how burial impacts the interdunal swales communities and it is especially difficult to separate the effects of burial from salinity. Climate change is altering the frequency of overwash events as well as expanding the range of the native shrub, *Morella cerifera*, on the Virginia barrier islands. To accurately forecast island response to climate change it is important to understand how the shrub responds to sand burial. Juvenile and mature shrubs were experimentally buried at 0, ¼, ½, and ¾ height in a glasshouse to observe the growth response to burial independent of other factors. *Morella cerifera* shrubs were largely unaffected at low burial levels (< ½ height) and were stimulated at high levels (≥ ½ height). Shrubs recovered biomass deficits at low levels and prioritized vertical growth at high levels of burial. Shrubs in both life stages also produced adventitious roots in response to burial, increasing production with burial severity. Adult shrubs sacrificed belowground root biomass to support adventitious root and vertical growth at ¾ burial. Young shrubs were able to have an elevated growth in all three zones without sacrifice at any burial level. *Morella cerifera* exhibits a neutral, then positive response to sand burial and is resilient at both juvenile and mature stages. Burial is therefore not a major driver of *M. cerifera* zonation on the Virginia barrier islands.

Vita

Dawn Nicole Keller, who goes by Nicole, is a native of West Virginia who has wanted to be a natural scientist of some kind since age three.

She graduated with an International Baccalaureate Degree from South Charleston High School, South Charleston, WV in 2008. She received a Bachelor of Arts in 2012 from Marietta College, Marietta, Ohio, where she majored in Environmental Studies and Political Science, minored in Spanish, and completed a Certificate in Leadership Studies from the McDonough School of Business and Leadership. She was awarded the David F. Young award for excellence environmental science studies and future potential. She went on to work in Washington, D.C. across the private and public environmental sectors, including interning at the Smithsonian Conservation Biology Institute and National Wildlife Federation (NWF). As an intern on the Climate and Wildlife Safeguards team at NWF, she worked primarily on climate-smart adaptation and natural hazard mitigation strategies. She co-authored the Natural Defenses in Action report, published by NWF in 2016. She moved to Richmond Virginia in 2016 and joined VCU as a lab technician in the Wetland Ecology Lab.

She is interested in pursuing a career in environmental policy or federal research using remote sensing and GIS technologies to examine ecosystem response to climate change and to plan adaptation and mitigation strategies.

Introduction

Drivers of vegetation zonation in coastal systems have been a major focus of coastal ecology as researchers aim to understand feedback mechanisms between vegetation and coastal morphology (Cowles, 1899; Ehrenfeld, 1990; Hayden et al., 1995; Oosting & Billings, 1942; Stallins & Parker, 2003). Sediment deposition and salinity are two major drivers of vegetation patterns in coastal systems (Barbour & DeJong, 1977; Maun, 2004; Valk, 1974; Wilson & Sykes, 1999). On barrier islands, sand and salt move across the landscape, interacting with vegetation to form a heterogeneous landscape. The disparate distribution of abiotic factors leads to the formation of distinct vegetation communities (Moreno-Casasola, 1986; Oosting, 1954; Stallins & Parker, 2003; Young et al., 2011; Zinnert et al., 2017). Maximum exposure to abiotic stressors is experienced in the beach and foredune habitat, where vegetation is well adapted to the extreme conditions. More diverse grassland communities exist in the interdunal swales, protected by dunes, which often lead to succession of shrub thickets and/or maritime forest. Back-barrier marshes are often found on the bayside of islands. Beyond the chronic stressors, coastal storms cause abrupt change to the system through high winds, increased salt spray, and overwash events (i.e., when storm surge crests the foredune and floods interior habitats), which deliver pulses of saltwater and sand deposition into low-lying swale and upland communities (Leatherman, 1979; Matias et al., 2009). The frequency of overwash events is a product of elevation, tidal reach and storm frequency. Climate change is causing rising sea levels and is likely to bring an increase in severity and frequency of coastal storms to the North American Atlantic coast (Bender et al., 2010; Emanuel, 2005).

Overwash frequency is a major driver of vegetation zonation on barrier islands (Ehrenfeld, 1990; Fahrig et al., 1993; Miller et al., 2009). It can be difficult to tease apart the influence of salinity and deposition in nearshore and dune environments as both are constant sources of stress often co-occurring in marine coastal environments. There is disagreement regarding which factor is more important in determining vegetation zonation (Maun & Perumal, 1999; Wilson & Sykes, 1999), but there is no doubt that sediment deposition is a strong independent driver of vegetation zonation in marine coastal (Kent et al., 2001; Moreno-Casasola, 1986; Oosting, 1954) and inland systems (Brown, 1997; Cowles, 1899; Qu et al., 2017). Sand movement decreases with distance from the shoreline and declining elevation on barrier islands (Young et al., 2011). Generally, rates of sediment movement and frequency of overwash occurrence correlate well with species burial intolerance, thus burial tolerant species are often found closer to the shoreline (Ehrenfeld, 1990; Fahrig et al., 1993).

Most coastal burial research has focused on dune species (Brantley et al., 2014; Brown & Zinnert, 2018; Franks & Peterson, 2003; Gilbert et al., 2008; Harris et al., 2017; Stallins & Parker, 2003) and illustrates the strong role sediment deposition plays in shaping the dune vegetation community. Limited attention has been paid to burial impacts on the plant communities behind dunes, especially woody species, which will be impacted by overwash with increases in sea-level rise and storm frequency/intensity. In non-saline, sandy systems, burial is a major factor of woody plant zonation (Dech & Maun, 2005; Gilbert et al., 2008; Qu et al., 2017) and may be important in coastal woody vegetation zonation (Gilbert, 2007).

Sediment deposition is a source of stress to many coastal plants, apart from some dune-building grasses which have evolved to be burial dependent. Deposition stresses plants by altering the micro-environment through reductions in oxygen and temperature in the root zone as well as alterations in soil moisture and nutrient loads (Kurz, 1939; Maun, 1998). If deep enough, burial may significantly reduce photosynthetic area and be a physical barrier against growth. Surviving burial depends on the ability to reallocate resources to compensate for this stress, especially for lost photosynthetic tissues. Plants may do this by increasing vertical growth, increasing density (by sprouting new stems or branches), increasing photosynthetic rate of leaves, and/or developing adventitious roots in the burial space (Gilbert, 2007; Gilbert et al., 2008; Maun, 1998). Often, these strategies come at the cost of belowground biomass (D. Harris & Davy, 1988). The strongest adaptation to burial is the ability to develop adventitious roots in the burial space. Adventitious roots are new roots formed from non-root tissues. As a response to burial or flooding, these roots develop off the stems (Steffens & Rasmussen, 2016) and are an adaptation thought to improve stability, aeration, and nutrient absorption (Ayi et al., 2016; Steffens & Rasmussen, 2016). Maun (1998) identified the development of adventitious roots as the determinant factor in whether woody plants survive burial.

Certain patterns in sediment deposition, characterized in a variety of coastal species, include: i) an immediate decline if the species is not well adapted; ii) a delayed initial response followed by eventual decline after a certain depth or time threshold has been surpassed, or iii) a stimulated response that increases with burial for well adapted species (Dech & Maun, 2006; Gilbert & Ripley, 2010). Of course, all species have a maximum tolerance to burial beyond which death is unavoidable, even in species adapted to survive >100% burial. Life stage plays an important role in survival. Seedlings have smaller energy and resource reserves to support compensatory growth and younger plants typically fair worse under proportional burial (Harris & Davy, 1988; Li, Werger, et al., 2010; Yu et al., 2019). Few studies have examined the response of juvenile woody species, but if burial reduces seedling survival sufficiently, it can effectively hinder a species' continuance, regardless of the resilience of mature plants.

A major shift in the vegetation community has occurred on the mid-Atlantic and Gulf coast barrier islands. At the Virginia Coast Reserve, woody vegetation cover, composed primarily of *Morella cerifera* (previously *Myrica cerifera*), increased 40% from 1984-2011 predominantly through grassland encroachment (Huang et al., 2018; Zinnert et al., 2016) and continues to expand today. The primary driver of woody shrub encroachment into the interdunal swales is climate change, especially warmer wintertime temperatures, combined with engineering the microenvironment (D'Odorico et al., 2013;

Wood et al., 2020; Zinnert et al., 2011). Establishment is typically limited to stable areas of the barrier islands where chronic sediment movement and disturbance frequency is lowest (Miller et al., 2008).

Fahrig et al. (1993) documented that the presence of *M. cerifera* on Hog Island, VA strongly correlated with very low overwash probability. Characterizing *M. cerifera* thickets on Hog Island, VA the following year, Young et al. (1995) again correlated thicket establishment with accretion, showing that seedling recruitment occurred only after land stabilized. Brantley et al. (2014) showed that *M. cerifera* seedlings on Hog Island were found in recovering overwash zones, but not in areas that had experienced significant overwash disturbance in the last 1-2 years. It is unknown to what extent *M. cerifera* is truly intolerant of sediment burial, or if salinity is the primary limiter in overwash zones. *Morella cerifera* is moderately tolerant of soil chlorides and salt spray (Sande & Young, 1992) and to extended saltwater flooding (Naumann et al., 2008; Tolliver et al., 1997). Burial tolerance of *M. cerifera* has never been examined but is essential for modeling future responses of barrier islands to storms and sea-level rise scenarios.

To better understand the controls of *M. cerifera* range expansion, I tested burial response of *M. cerifera* shrubs at two life stages. I measured morphological growth response to multiple levels of burial to detect any threshold responses. I hypothesized that *M. cerifera* would be mildly tolerant of burial, and would exhibit a neutral, then negative response with increasing burial depth (Figure 1). Low levels (< ½ plant height) of burial would not induce a significant change in resource allocation or survival, but severe burial (> ½ pant height) would correspond with a decline in growth and

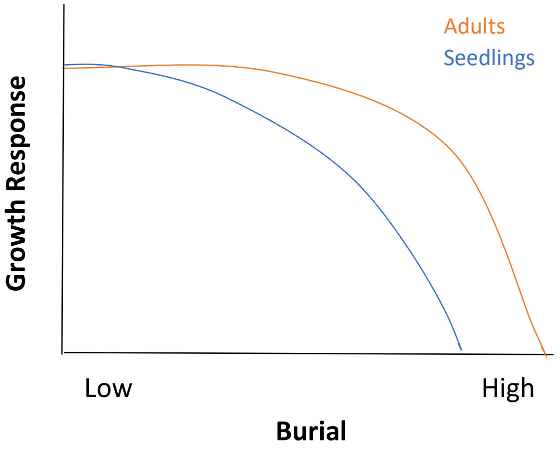

Figure 1 Hypothesized response curve of Morella cerifera to burial at two life stages.

survival. I also predicted that seedlings would be more susceptible to burial and would experience higher mortality from burial.

Methods

Burial simulation

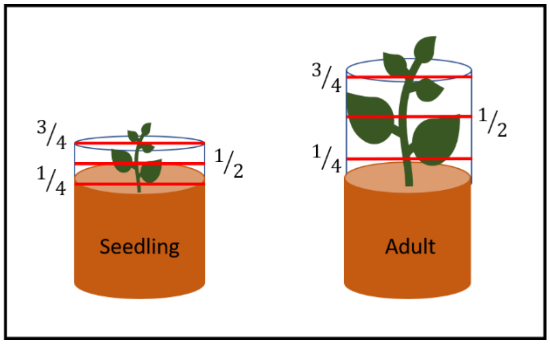

Figure 2 Schematic of proportional burial design for seedling and adult shrubs

To test *Morella cerifera* response at different life stages to sand burial, I applied four levels of sand burial, as a proportion of plant height. Using a random number generator, individual shrubs were distributed among four treatment groups: no burial, ¼ burial, ½ burial, or ¾ burial (n=36 adults, n=34 seedlings) (Figure 2). Adult plants (2 gal pot, ~61 cm tall) were purchased in March 2019 from Cross Creek Nursery in Richmond, VA. Plants remained in plastic pots for the duration of the experiment and were grown in a glasshouse at Virginia Commonwealth University for two months prior to the start of the experiment. Seeds were collected in fall 2018 from the Virginia Coast Reserve LTER and germinated in February 2019 in a CONVIRON growth chamber (25° - 30° C, 16hr day/8hr night cycle). As seedlings grew, they were re-potted into individual 2.5 L plastic pots until all reached at least 10 cm tall. I recorded initial height and diameter along two axes before trimming adult plants to 70 cm height and seedlings to 30 cm height. All plants sat in plastic pots for watering during the experiment.

To simulate burial, collars as tall as the sediment line (based on proportional burial treatments) were constructed around plants using vinyl, supported by bamboo dowels on adult shrubs and recycled plastic pots on seedlings. Where needed, shrubs were trimmed to fit within the diameter of the collar. Control plants did not receive treatment. Collars were filled with a 3:1 mix of play sand and sand collected from the beach of Hog Island, VA. All plants received water daily from the bottom. Hoagland nutrient solution (Hoagland & Arnon, 1950) was added to the water (20 ml for adults; 10 ml for seedlings) weekly in the first month of the experiment and pests were controlled with periodic spraying of Ortho Malathian 50 Plus. The adult shrub experiment ran from May to October 2019; the seedlings experiment from August to November 2019.

Figure 3 Examples of the burial set-up. The first two images are of adult shrubs buried at 50% (A) and 75% (B) of starting height. The third image is of technician Eddie Long tending to buried seedlings in a growth chamber (C).

Measurements

I tracked morphological response in three regions of the plant: 1) growth above the burial line; 2) adventitious root development in the buried portion; and 3) belowground root mass. For aboveground growth, I recorded aboveground height to the sand line, diameter along two perpendicular axes, and counted the number at stems at the sediment surface, as well as the number of branches on seedlings. These measurements were repeated at the conclusion of the experiment. After taking final measurements, I harvested all biomass above the sediment line into paper bags. Sand-buried biomass was recovered, the sediment removed, and adventitious roots separated from the plant. Aboveground and buried biomass was dried at 60° C for at least 24 hours and weighed. Due to extensive binding in belowground roots, root balls were broken up by hand and dried inside paper bags at 60° C for at least 96 hours. Roots were sifted from the soil through a 3.35mm sieve and weighed.

Statistics

All statistics were performed in R. Extreme outliers were identified and removed using the identify_outliers method of rstatix package. One-way Analysis of Variance was used to compare aboveground biomass, canopy volume, height, diameter, changes in stem count, branching (in seedlings only), adventitious root biomass, and belowground root biomass between burial treatments within each life stage. When appropriate, Tukey post-hoc tests were used to differentiate treatment level. Where ANOVA assumptions were violated, Kruskal-Wallis rank test with a Nemenyi post-hoc test was used. Regression analysis was also used to examine relationships between burial depth and adventitious root biomass and height. Correlations between burial proportion, biomass production in the three zones of the plant, and final height were examined using Pearson's correlation test

Results

All shrubs survived the experiment, regardless of burial severity. The ability of adult shrubs to regenerate aboveground biomass decreased at higher burial levels ($F=26.98$, $p<0.0001$; Figure 4a). Aboveground biomass in adult shrubs was affected only after ½ burial. Plants buried at ¼ height were able to completely recover with no statistical differences from controls, producing only an average of 9% less biomass than the controls by the end of the experiment. Adult shrubs at ½ and ¾ burial were significantly different from controls with 45% and 63% less aboveground biomass, respectively. Conversely, seedlings were able to overcome aboveground biomass deficits due to burial at all levels ($F=3.08$, $p=0.584$; Figure 4b).

Despite these differences in aboveground biomass in adult plants, there was no difference in canopy volume (i.e., vertical and horizontal growth) between treatment groups at the end of the experiment (F=0.81, p=0.50, Figure 5a). Shrubs buried at ½ or ¾ height were slightly smaller on average than control or ¼ buried shrubs, but the difference were not significant. Amongst the seedlings, the average final volumes of each treatment group were all within 18% of each other, which was not statistically significant (F=0.32, p=0.81, Figure 5b). Disentangling vertical and horizontal growth revealed that burial stimulated height growth in both life stages. In adults, the relationship between height and burial was moderate (r^2=0.23, F=3.09, p=0.04; Figure 6a). Shrubs in the ¾ burial group were 23% taller than controls at the end of the experiment. Horizontal expansion was similar among all adult groups (F=0.77, p=0.51). In seedlings, the relationship between height and burial was stronger than seen in adults (r^2=0.37, F=5.69, p=0.003; Figure 6b). Seedlings in the ¾ burial group were 40% taller than control plants after the three-month experiment and were significantly different from the controls and the ¼ burial group. There were no significant differences in horizontal expansion with burial (F=1.47, p=0.24).

The number of live stems at the sediment surface decreased due to death at every burial level in adults, with the ½ burial group losing the most. The difference was significant when compared to both the controls and the ¾ burial group (F=4.26, p=0.13, Table 1). There were no differences in stem count in seedlings (F=0.58, p=0.64, Table 1), nor any evidence that burial affected branching in seedlings (X^2=2.90, p=0.41, Table 2).

Morella cerifera shrubs developed adventitious roots at all burial levels and life stages and increased adventitious root production with burial severity. In adult plants, there was a moderate, positive relationship between burial depth and adventitious root production (r^2=0.23, F=3.16 , p=0.04) and a stronger relationship in seedlings (r^2 = 0.48, F =8.78, $p < 0.001$) (Figure 7). Of all buried adult shrubs, 93% produced adventitious roots. At low or moderate burial levels, average root production was low (0.32 ±0.14 g and 0.58 ±0.17 g, at ¼ and ½ burial respectively), but this was not statistically different from the highest (¾) burial level, which produced an average root biomass of 1.18 ±0.51 g. Of the buried seedlings, 88% produced adventitious roots; the three that produced none were all in the ¼ burial treatment group. Like the adults, there were no statistical differences among ¼, ½, or ¾ burial levels in seedlings.

The impact of burial on belowground root biomass differed between the two life stages. Adult shrubs in the ¾ burial group developed 31% less belowground root biomass than controls, which was statistically different from both the control and the ¼ burial groups (F=4.62, p=0.01, Figure 8a). Reduction in belowground root biomass under high burial correlated with increased adventitious root development (r= -0.45, p=0.007, Table 3), but no such correlation was present in seedlings (Table 4). Although buried seedlings also trended towards lower root biomass than unburied seedlings, the effect was not significant (F=1.58, p=0.22, Figure 8b).

Discussion

Climate change has precipitated major changes in coastal areas, especially along the Virginia barrier islands which represent a biogeographical boundary in northern and southern species distributions. Sea level rise, increased coastal storm severity, and the proliferation of woody vegetation alter island ecology and have consequences for long-term island survival. My goal was to ascertain how the dominant, expanding shrub of the Virginia barrier islands, *Morella cerifera,* responds to sand burial. This knowledge is an important part of understanding the species' resilience to overwash disturbance. *Morella cerifera* was assumed to be intolerant of overwash, based on observations that it was uncommon in areas of semi-frequent disturbance (Brantley, 2009; Fahrig et al., 1993). Moderate tolerance to salinity and flooding have previously been established (Naumann et al., 2008; Sande & Young, 1992; Tolliver et al., 1997). This is the first study to examine the response of *M. cerifera* to burial, despite evidence that burial can be a primary determinant of woody species zonation in other environments (Dech & Maun, 2005; Gilbert et al., 2008; Qu et al., 2017).

My hypotheses of *M. cerifera* burial tolerance at two life stages were partially supported. Low-level burial (< ½ plant height) did not have any significant impact on plants, at either life stage, as hypothesized. However, rather than the expected negative growth response and increased mortality at higher burial levels (> ½ plant height), shrub growth response was stimulated and there was no mortality, but adult growth was impacted more than seedlings. At low burial, neither life stages were significantly impacted in any of the metrics I tracked. Burial at ½ plant height appears to be an important threshold for *M. cerifera's* response to sand burial in adult shrubs. At this point, adults were no longer able to recover aboveground biomass but produced significant adventitious roots. At ¾ burial, belowground root biomass in adult shrubs was reduced, likely to support this response. Seedlings recovered aboveground biomass production at all burial levels and increased vertical height adventitious root production at ½ and ¾ burial, but this stimulated growth response did not come at the expense of belowground roots at any point.

Aboveground Biomass

At low burial, adult shrubs were sufficiently able to increase biomass production to overcome the buried leaves. After ½ burial, this stimulated response was absent, and shrubs were unable to recover buried biomass. Though growth continued and no mortality occurred in adults, shrubs buried at ½ and ¾ height had significantly less biomass. Seedlings recovered biomass completely at all burial levels - evidence of a stimulated response and greater resilience to proportional burial than adults. Despite biomass differences, the canopy of all adult shrubs was approximately the same size by the end of the experiment. This means burial elicited an increasingly strong growth response, even if the canopy was less dense at the higher burial levels. Horizontal growth was similar regardless of burial depth, but burial prompted plants to grow taller relative to unburied. This was true for seedlings, as well; plants grew taller, but not wider with burial. Additionally, I found a burial effect on the number of stems in the ½ burial group in adults. However, this difference was fueled by several plants in the ½ burial group that lost a large number of stems. It may be a reflection of the fact that the middle of the shrub body has the most stems and therefore plants buried at that level experienced greater stem death than the ¼ burial or even the ¾ burial, which left very few stems above the sand line. Whereas stem count decreased across all treatment groups in the adults, seedlings grew new stems in all groups, with no difference between treatments.

Harris and Davy (1988) showed that burial can alter the nutrient allocation to plant organs, so it is possible, and perhaps worthy of further inquiry, that new tissue is constructed differently than pre-existing tissue and that new tissue construction may differ in adults versus seedlings. Stem elongation is a critical adaptation to burial survival, but this stimulated response due to loss of photosynthetic tissue is very costly. Observing a tradeoff between elongation and tissue density, Gilbert et al. (2008) suggested that to reduce the cost of elongating stems to overcome burial, new tissue density is sacrificed.

Adventitious Roots

The lag in biomass production observed in adults, despite stimulated vertical growth, is likely a consequence of resources diverted to adventitious root production. Burial caused plants to produce adventious roots at every burial level in adults, but significant production mirrored the reduction in aboveground biomass above ¼ burial. The relationship between coastal burial and adventitious root development in woody species is not always positive or linear (Dech and Maun 2006). Even among tolerant species, production may increase with burial to a point but decline beyond a certain threshold or decrease linearly as burial becomes more severe. Mature *M. cerifera* produced adventitious roots in a strong, positive, linear relationship to burial, indicating a high tolerance up to at least ¾ burial. Seedlings also produced adventitious roots at all burial levels, with significant production at and above the ½ burial threshold. They did not appear to make the tradeoff observed in adults (i.e., loss in aboveground biomass), but were able to increase aboveground biomass production with burial severity so that all plants had roughly the same amount of aboveground biomass at the end of the experiment, regardless of adventitious root production.

Belowground Biomass

Belowground biomass was significantly reduced in adults at only the highest (¾ height) burial. This sacrifice of belowground production with increasing burial correlates with the production of adventitious roots (Table 3). Resources are likely diverted in adults to these high priority responses when burial is severe. In seedlings, there was no difference in belowground root biomass at any level, regardless of significant adventitious root production and stimulated aboveground biomass and vertical growth. This suggests that young plants can ramp up photosynthesis enough to support stimulated growth responses, without needing to divert resources from other parts of the plant.

Though I did not measure photosynthesis in this experiment, similar studies show a variety of photosynthetic responses to burial, but overall increased activity is typically minor and decreases over time (Gilbert & Ripley, 2010). It is possible that some of the energy and resources from the buried portion of the plant are recycled to support increased growth in either aboveground biomass and/or adventitious roots (Gilbert et al., 2008). This experiment shows that, at least at ¾ burial, belowground biomass is reallocated in adult *M. cerifera* shrubs, which is in agreement with documented studies in other species (Gilbert & Ripley, 2010).

My hypotheses of i) a neutral, then negative response to burial in *M. cerifera* shrubs and ii) higher mortality in seedlings were partially supported. My results indicate that *M. cerifera* is tolerant of sand burial at both adult and seedling life stage, with seedlings exhibiting greater tolerance at all burial levels. Contrary to my hypothesis and work on other species (Harris & Davy, 1988; Li, Zuidema, et al., 2010; Liu et al., 2008; Yu et al., 2019), *M. cerifera* seedlings seemed more resilient to proportional burial than adults. Seedlings had a stronger stimulated growth response in height and adventitious root development than adults, and recovered their aboveground biomass deficit completely at all burial levels. New growth seemed to come at a lower cost than in adult plants since there was no parallel sacrifice to aboveground or belowground tissue mass. The stronger response burial observed in seedlings may be partially explained by the differences in tissue structure between young and mature plants. Mature shrubs have undergone secondary growth, which requires production of a lot of carbohydrates. Juveniles are not burdened by these complex, secondary organs, which are expensive to produce and maintain, which may mean they can dedicate more resources to new primary production than adult shrubs (Kozlowski & Pallardy, 1997).

Although plant life history is a significant factor in recovery from overwash in many coastal species (Cheplick 2017), my results show that *M. cerifera* is resilient in both juvenile and mature forms. I did not assess complete burial of seedlings, but short of that, these results suggest burial will not reduce *M. cerifera's* competitive advantages in the barrier island landscape. Instead, this experiment provides evidence of a neutral, then positive response to burial in *M. cerifera* shrubs. Maun (1998) proposed a "multifactor hypothesis" which attributes increased plant 'vigor' after burial to a combination of 4 factors: i) increased soil volume, ii) increased mycorrhizal activity, iii) increased soil resources, and iv) reactive plant response. The experiment provides evidence that *M. cerifera* is capable of capitalizing on the new soil volume by producing adventitious roots and is adapted to allocate energy and resources to fuel a reactive growth response.

This study suggests that burial is not a strong factor influencing the zonation of *M. cerifera* in coastal systems. Although burial tolerance and exposure are often expected to co-occur, it is not always the case. Sykes and Wilson (1990) found that the strength of that relationship varied on a species by species basis and Gilbert (2007) also found that species in stable dune systems where burial rate was low had a greater growth response than species in mobile dunes. Gilbert (2007) also observed contrasting interactions between stimulated growth response to burial and nutrient availability among some coastal shrub species. As a nitrogen-fixing shrub, stimulated growth in *M. cerifera* is likely uninhibited by nutrient availability. Salinity, access to freshwater, and exposure to extreme wintertime temperatures are likely the primarily influence on *M. cerifera* zonation (Naumann et al., 2008; Sinclair et al., 2020; Wood et al., 2020; Woods et al., 2019).

Woody encroachment into grassland, especially of a species like *M. cerifera* that tends to form monotypic thickets, is a major cause for concern regarding plant diversity and sediment transport (Field et al., 2012; Zhang & Dong, 2014). Burial filters intolerant species from the landscape, resetting the conditions of competition and influences community composition on a multi-year scale (Cheplick, 2017). The strong, positive response of seedlings to burial may be evidence of an adaptation for colonization in frequent burial, in which case *M. cerifera* may have an advantage in the interdunal swales. *Morella* cerifera is a fast-growing evergreen species, not only capable of surviving burial up to at least ¾ of its height but stimulated by it, especially at the younger life stage. Burial disturbance may hasten shrub encroachment, especially given that most overwash events occur during winter months when most other island species are dormant. The persistence of *M. cerifera* seedlings after overwash may redirect the recovery trajectory of the grassland habitat towards a new steady state that is less diverse. There is also reason to believe that shrub thickets may inhibit island rollover (Zinnert et al., 2019). Sediment transport is reduced by woody vegetation (Breshears et al., 2009; Field et al., 2012). The results of this experiment suggest a possible positive feedback loop between burial and shrub growth, which had been previously obscured by the limitation of *M. cerifera* stands by cold temperatures. Further study must evaluate how community recovery in the interdunal swales is impacted by winter-time burial with encroaching shrub species. The burial tolerance of *M. cerifera* recorded here can also be incorporated into predictive models for barrier island response to disturbance.

Figures

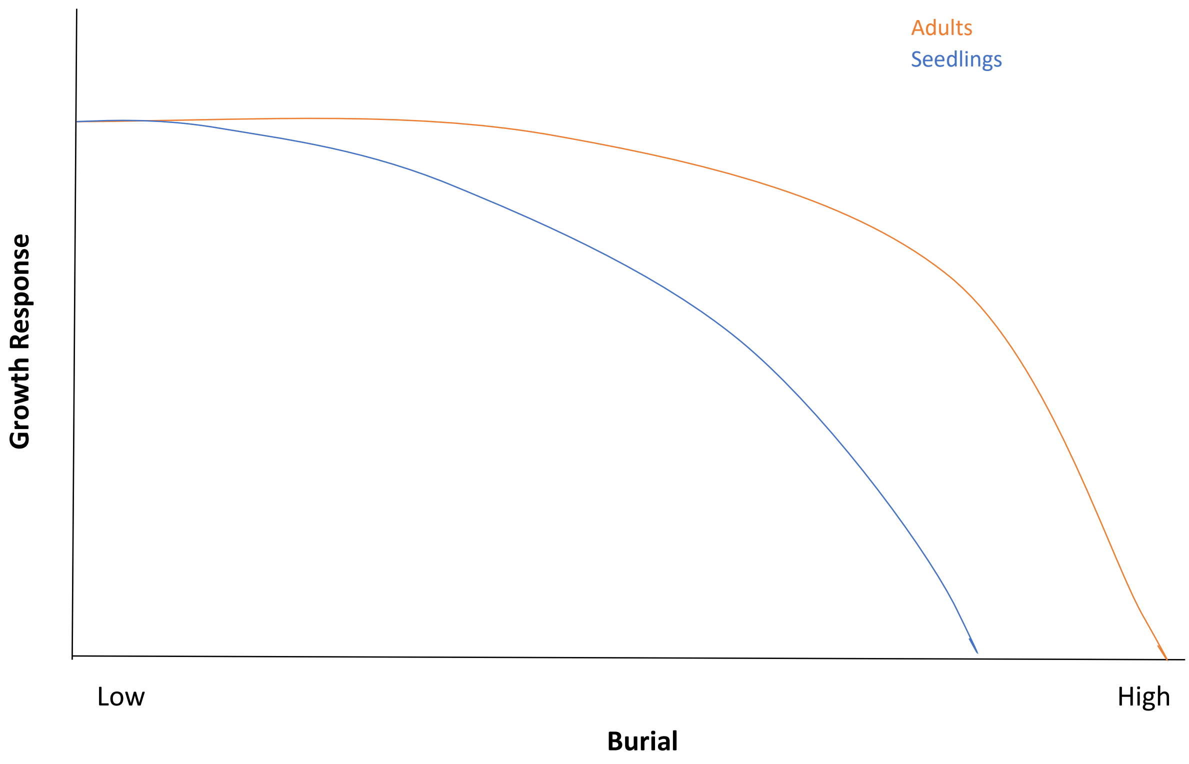

Figure 1 Hypothesized response curve of Morella cerifera to burial at two life stages.

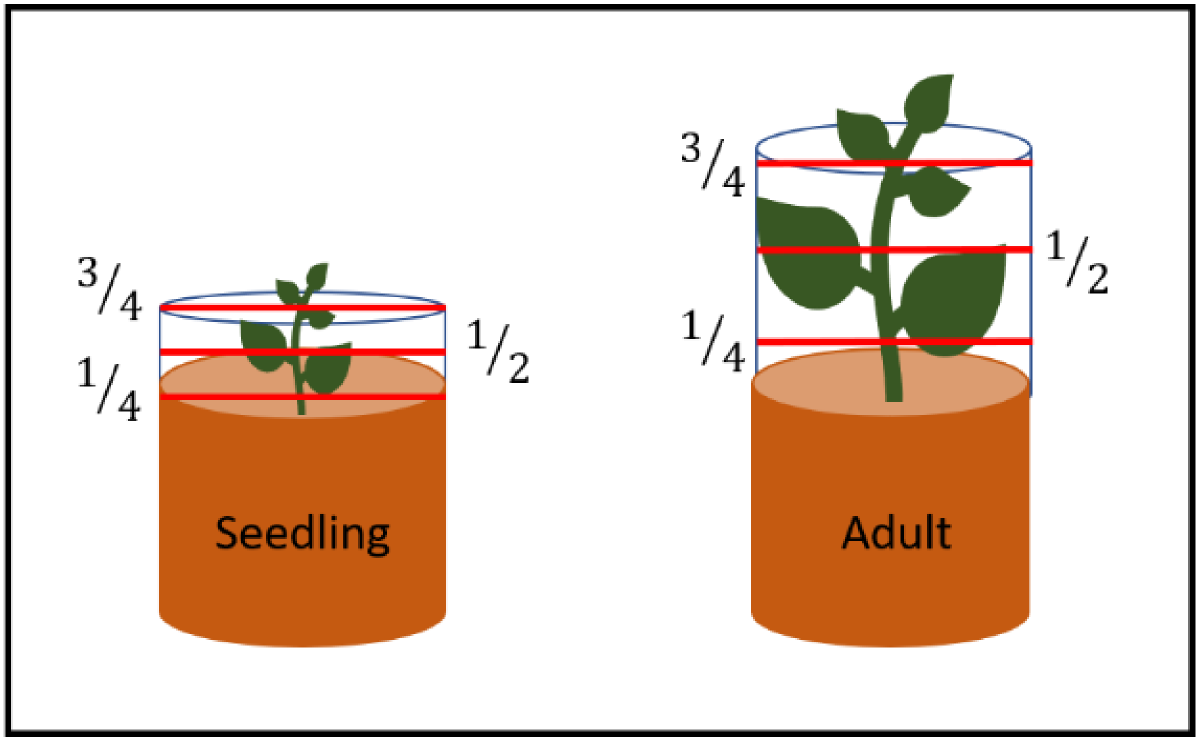

Figure 2 Schematic of proportional burial design for seedling and adult shrubs

Figure 4 Examples of the burial set-up. The first two images are of adult shrubs buried at 50% (A) and 75% (B) of starting height. The third image is of technician Eddie Long tending to buried seedlings in a growth chamber (C).

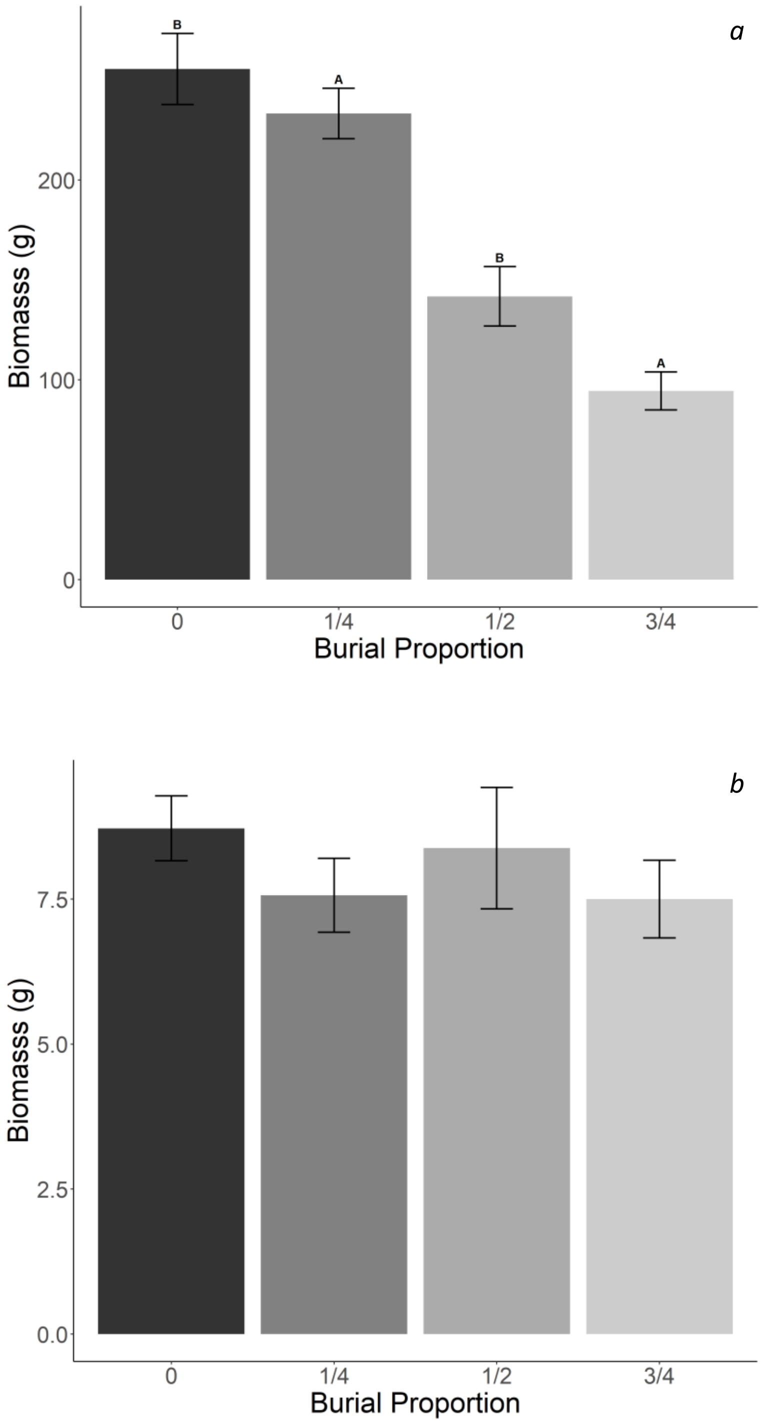

Figure 5 Effect of burial proportion on (a) adult and (b) seedling aboveground biomass above the sediment line. Bars represent mean ±SE and letter codes denote statistical significance ($p<0.05$) among treatments.

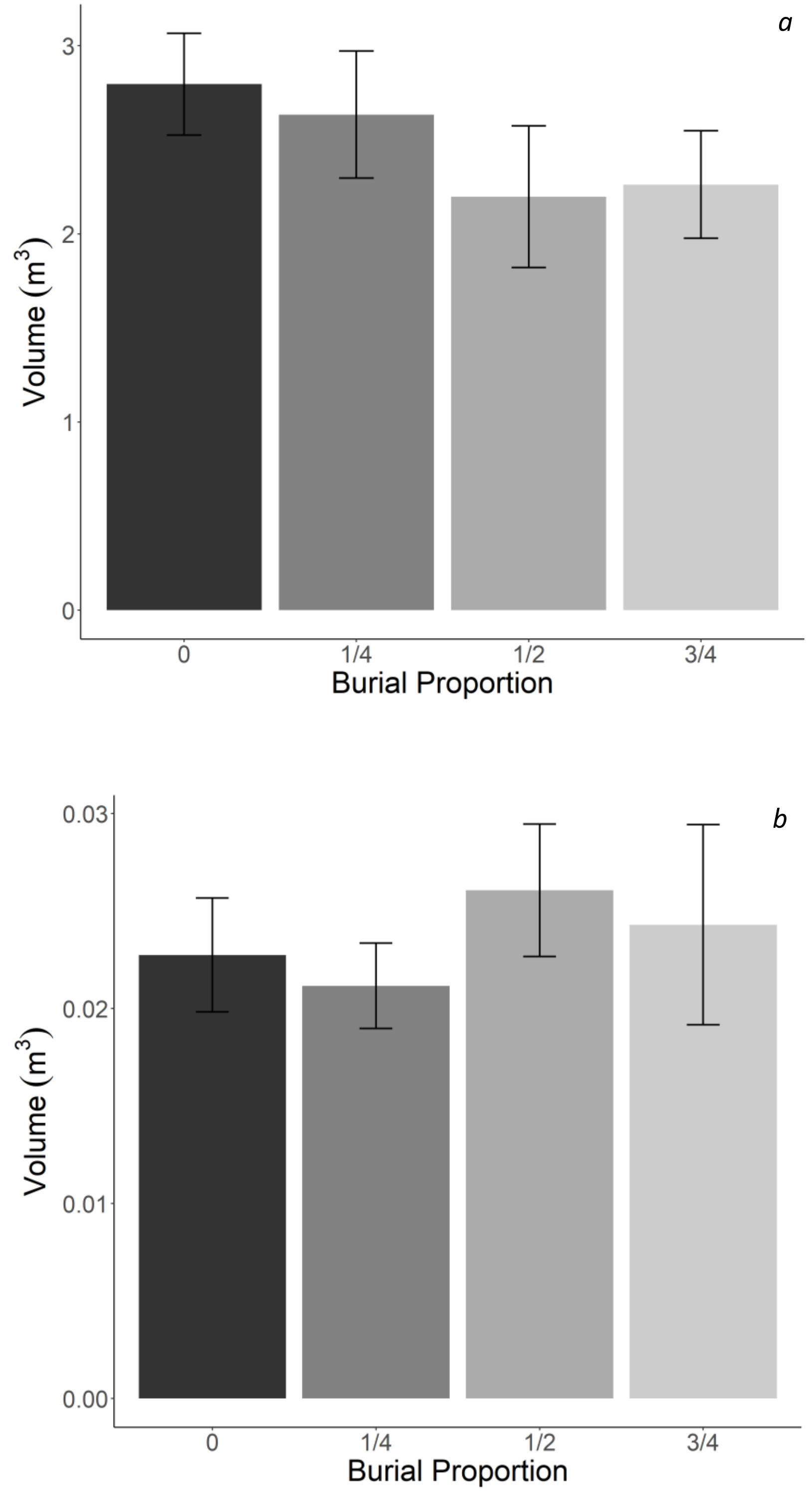

Figure 6 Effect of burial proportion on (a) adult and (b) seedling canopy volume. Bars represent ±SE.

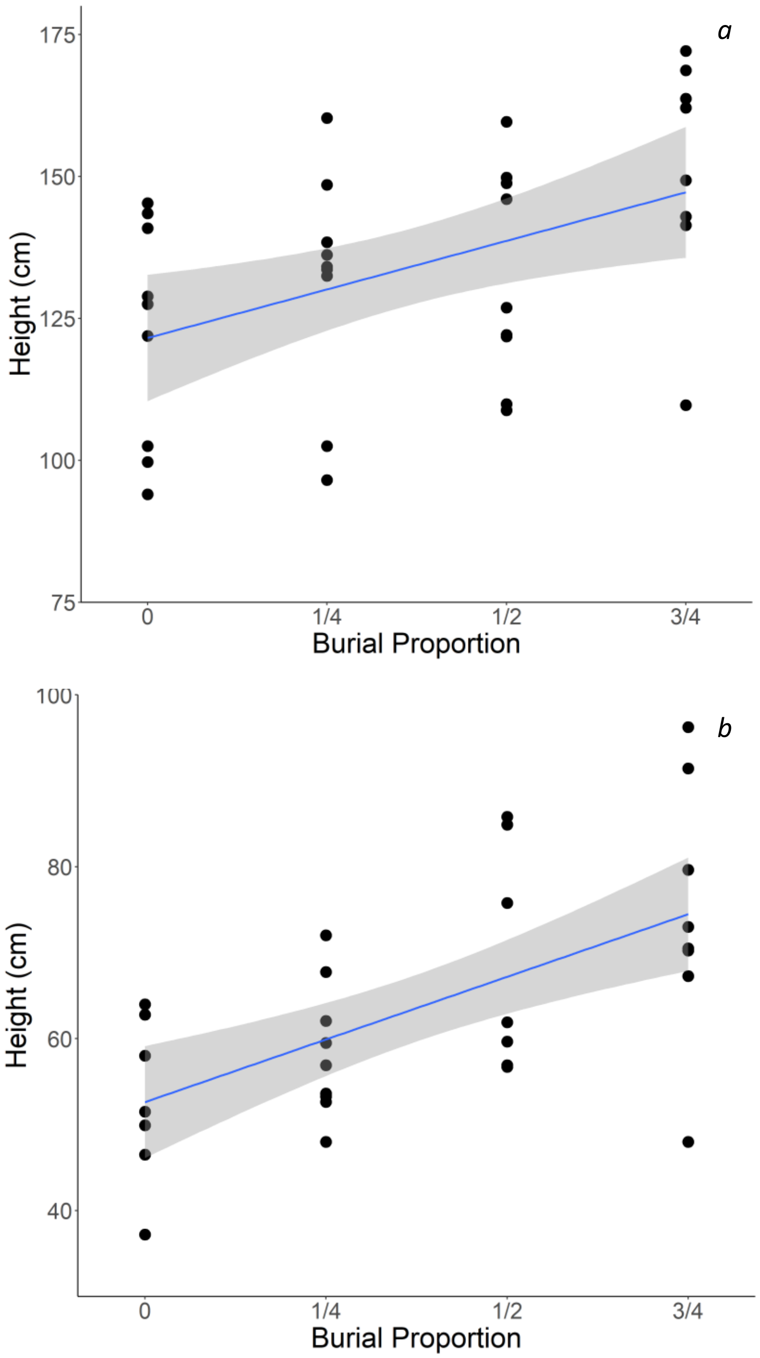

Figure 7 Relationship between burial proportion and plant height in (a) adults and (b) seedlings. Shading around the regression line represents standard error.

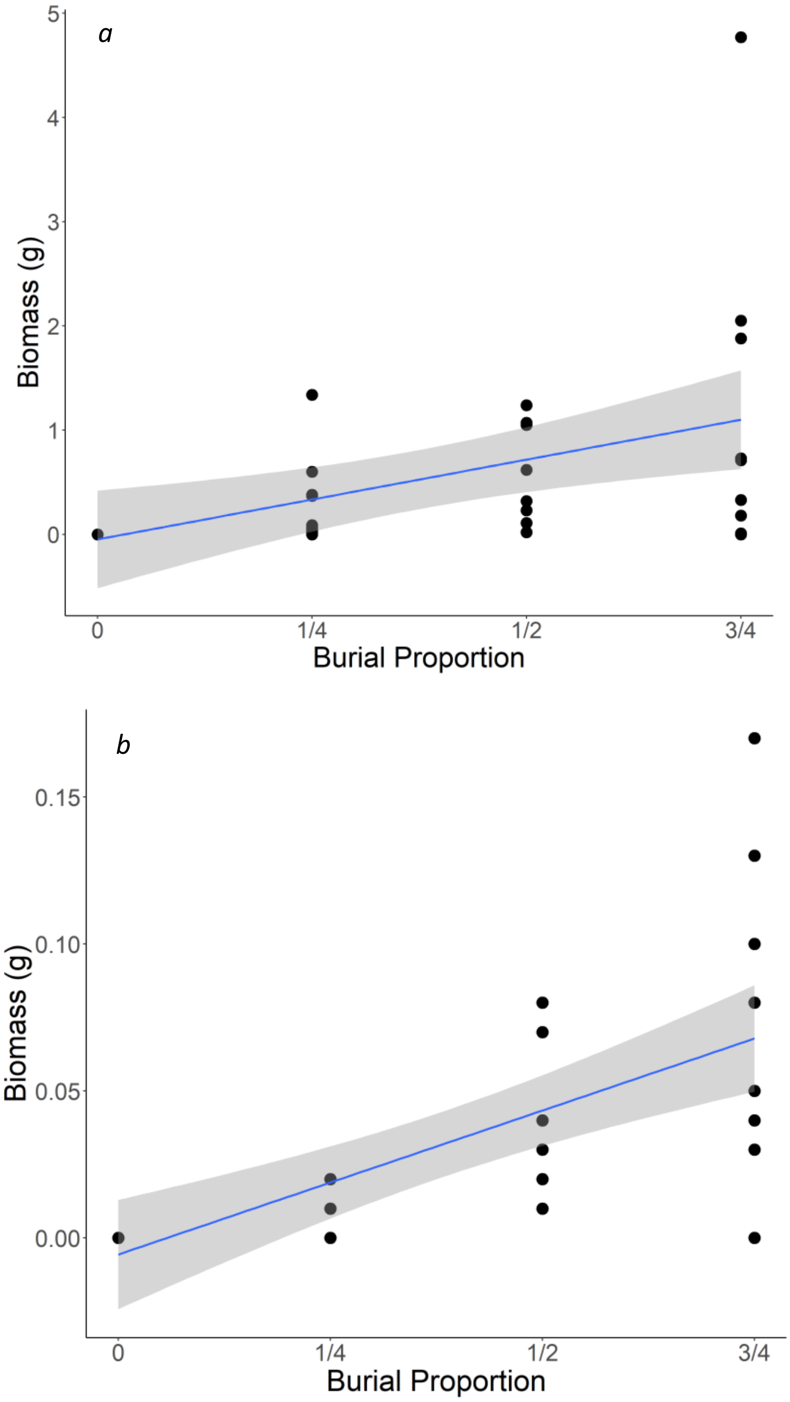

Figure 8 Relationship between burial proportion and adventitious root biomass in (a) adults and (b) seedlings. Shading around the regression line represents standard error.

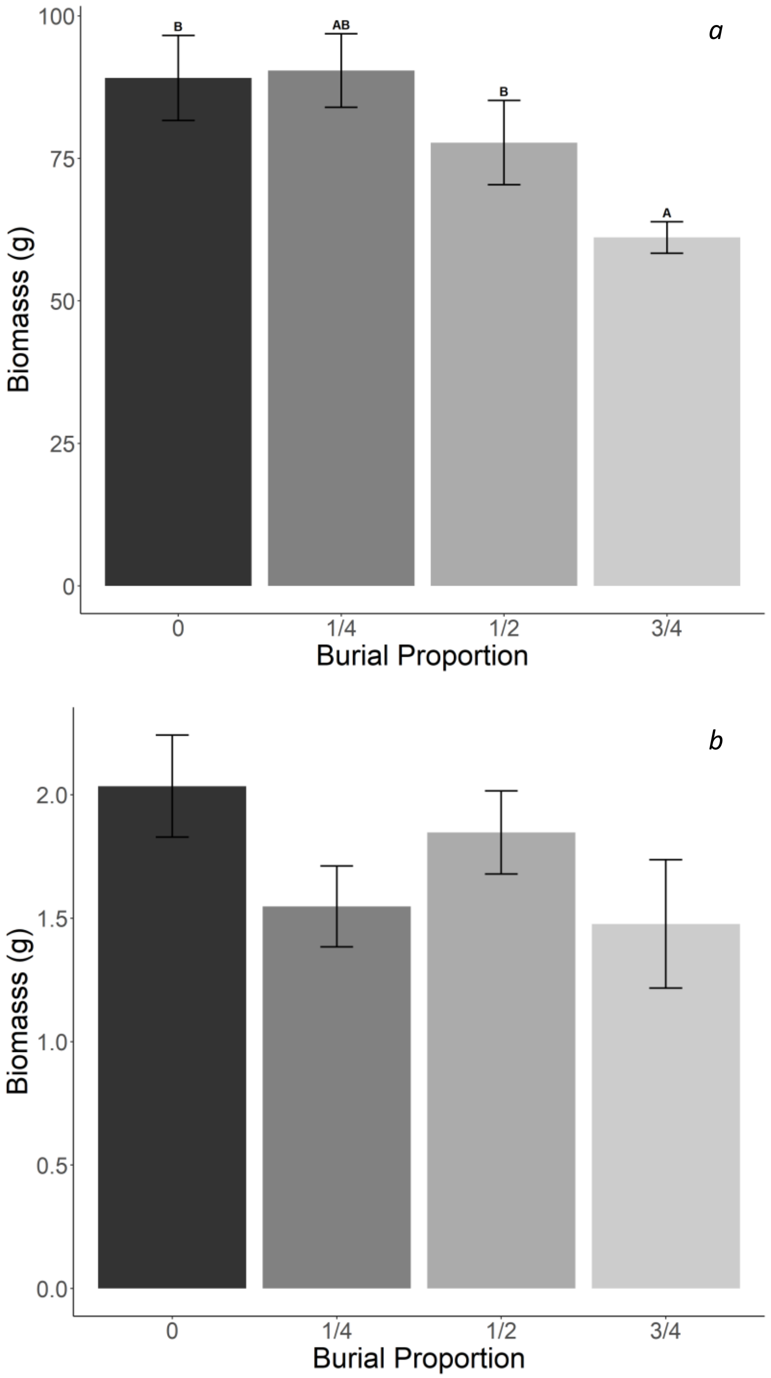

Figure 9 Effect of burial proportion on (a) adult and (b) seedling belowground biomass. Bars represent ±SE and letter code denote statistical significance (p<0.5) among treatments.

Tables

Table 1 Mean stem change and final stem count for adults and seedlings

	Burial Proportion	**Mean Change**	**SE**	**Mean Total Stems**	**SE**
Adults	0	-2.78	0.78	3.89	2.03
	1/4	-4.48	0.68	8.89	4.59
	1/2	-8.44	2.01	9.78	4.63
	3/4	-3.12	1.08	6.38	3.34
Seedlings	0	-0.25	0.16	1	0
	1/4	0	0	1	0
	1/2	0	0	1	0
	3/4	0	0	1	0

Table 2 Mean branches on seedlings

Burial Proportion	Mean Branches	SE
0	3.75	1.26
1/4	3.88	1.63
1/2	2.56	0.78
3/4	1.33	0.69

Table 3 Pearson 's correlation coefficient matrix for burial proportion, biomass production in three plant zones, and height in adult plants. Asterisks indicate significance levels.

		Correlation Coefficient	P
Burial Proportion	Aboveground Biomass	-0.84	<0.001 ***
Burial Proportion	Adventious Roots	+0.48	0.004 **
Burial Proportion	Belowground Biomass	-0.51	0.002 **
Burial Proportion	Height	+0.32	0.054
Aboveground Biomass	Adventious Roots	-0.32	0.07
Aboveground Biomass	Height	-0.09	0.63
Aboveground Biomass	Belowground Biomass	+0.48	0.004 **
Adventitious Roots	Belowground Biomass	-0.45	0.007 **
Adventitious Roots	Height	+0.36	0.032 *
Belowground Biomass	Height	-0.28	0.096

Significance Codes: 0.05 ‘*’ 0.01 ‘**’ 0.001 ‘***’

Table 4 Pearson 's correlation coefficient matrix for burial proportion, biomass production in three plant zones, and height in seedling plants. Asterisks indicate significance levels.

		Correlation Coefficient	P
Burial Proportion	Aboveground Biomass	-0.15	0.40
Burial Proportion	Adventious Roots	+0.68	<0.001 ***
Burial Proportion	Belowground Biomass	-0.27	0.12
Burial Proportion	Height	+0.60	<0.001 ***
Aboveground Biomass	Adventious Roots	+0.17	0.35
Aboveground Biomass	Belowground Biomass	+0.56	<0.001 ***
Aboveground Biomass	Height	+0.27	0.13
Adventitious Roots	Belowground Biomass	+0.07	0.68
Adventitious Roots	Height	+0.53	0.002 **
Belowground Biomass	Height	+0.14	0.43

Significance Codes: 0.05 ‘*’ 0.01 ‘**’ 0.001 ‘***’

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