

Salt Marsh Plant Community Structure on Horse Island, South Carolina

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Sea level rise is causing an increase in salt water encroachment and flooding in many coastal habitats, and increasing salinity can have negative impacts on plant communities. The objective of our research was to determine the impact of salinity on salt marsh plant community structure on Horse Island, South Carolina. We investigated variation in plant cover and height with distance from a tidal creek and the effect of increasing salinity on seedling emergence from the seed bank. We established three transects in the salt marsh habitat and recorded plant species presence, percent cover of each species, and height of the tallest individual of each species in 11 plots along each transect. Total plant cover was consistent from 0 to 24 m and increased from 24 to 40 m from the tidal creek; several species only occurred 36-40 m from the tidal creek. Percent cover of *Spartina alterniflora*, the dominant species, increased from 24 to 36 m from the tidal creek. The height of *S. alterniflora* was negatively correlated with percent cover of *S. alterniflora* and distance from the tidal creek. To assess the seed bank, we established 12 plots in the salt marsh-maritime forest ecotone, and soils collected from plots were assigned to each of four salinity treatments (0, 6, 12, and 26 ppt). Across all treatments, only one seedling emerged from the soil. The cover, height, and distribution of salt marsh species on Horse Island are likely to change as sea level continues to rise, but the role of the seed bank in affecting plant community structure remains unclear.

Keywords: height, maritime forest, percent cover, salinity, seed bank, *Spartina alterniflora*

Introduction

Coastal ecosystems, which provide a multitude of ecosystem services including purification of water, prevention of erosion, and protection from waves (Barbier et al. 2011), are threatened by sea level rise. Melting of glaciers and thermal expansion of the ocean has contributed to an average rise in sea level of 19 cm over the past century, and sea level could rise 70 cm or more by 2100 (IPCC 2014). Environmental gradients of salinity and flooding influence the spatial distribution of plant communities in coastal ecosystems (Shao et al. 1996, Pennings et al. 2005) such that sea level rise has the potential to cause shifts in the distribution of species and loss of coastal plant communities (Michener et al. 1997, Williams et al. 1999, Feagin et al. 2010, Saha et al. 2011). The persistence of coastal plant species depends in part on their survival, growth, and recruitment with increasing salinity.

Coastal plant species have a variety of adaptations that allow them to persist in saline soils, such as excluding salt from uptake by roots (Munns et al. 1999, Volkov and Amtmann 2006), secreting salt (Munns et al. 1999, Yuan et al. 2016), sequestering sodium ions (Lv et al. 2012) or chloride ions (Jiménez-Becker et al. 2019), and seed dormancy induced by salt stress (Ungar et al. 1979). However, increasing salinity can have negative impacts on salt-tolerant species. For example, relative growth rate, biomass, and height of mangrove species decreased at high salt concentrations (Ball and Pidsley 1995, Suárez and Medina 2005). Among grass species, sublethal levels of salinity reduced biomass of *Panicum hemitomon* and *Spartina patens* (Hester et al. 2001), and biomass, number of shoots, and height of *Spartina alterniflora* decreased with increasing salinity (Vasquez et al. 2006). Furthermore, germination of the seagrass *Zostera japonica* (Yue et al. 2019) and the halophyte *Haloxylon recurvum* (Khan and Ungar 1996) and emergence of seedlings from soil seed banks (Baldwin et al. 1996) decreased with increasing salinity. At the current rate of sea level rise, coastal plant species may not be able to tolerate increasing submergence and salinity.

Salt marsh plant communities have pronounced zonation due to spatial variation in salinity and flooding and variation in the competitive ability of plant species (Bertness and Ellison 1987, Odum 1988, Bertness 1991, Rand 2000, Pennings et al. 2005). In the southeastern United States, *Juncus roemerianus*, which has lower salt tolerance and higher competitive ability, dominates the upper marsh, while *Spartina alterniflora* dominates the lower marsh due to higher salt tolerance and lower competitive ability (Pennings et al. 2005). In addition, *S. alterniflora* can tolerate low oxygen soils by oxygenating the rhizosphere and its roots (Teal and Kanwisher 1966). Biomass of *J. roemerianus* did not increase after removal of *S. alterniflora* at the border between species; in contrast, *S. alterniflora* biomass increased after removal of *J.*

roemerianus (Pennings et al. 2005). This suggests that the lower range limit of *J. roemerianus* is determined by its tolerance to flooding and salinity, while the upper range limit of *S. alterniflora* is determined by competitive exclusion (Pennings et al. 2005). Thus, an increase in sea level has the potential to cause a shift in the distribution of salt marsh species.

The goal of our research was to gain a better understanding of the potential effects of sea level rise, particularly increasing salinity, on salt marsh plant communities in South Carolina. We assessed percent cover and height of salt marsh species in relation to distance from a tidal creek. We predicted that percent cover and height of salt marsh species would increase with distance from the tidal creek due to lower salinity. We also investigated the effect of salinity on seed germination from the seed bank collected from the ecotone between salt marsh and maritime forest communities. Seed banks can have a large impact on population growth rates (Adams et al. 2005); thus, knowledge of the presence of seeds and effect of salinity on germination of seeds in the ecotone seed bank could provide insight into the future composition of the salt marsh community (Kottler and Gedan 2020). We predicted that emergence of seedlings would decrease with increasing salinity.

Methods

Study Site

We conducted this study on Horse Island (32° 35' 10" N, 80° 11' 55" W), which is located in Charleston County, South Carolina. Horse Island is partly developed on the northwest tip of the island, so our field sampling occurred on the southeastern, uninhabited end of the island. Our study focused on the salt marsh habitat along a tidal creek and the ecotone between the salt marsh and maritime forest plant communities. The salt marsh is located on the outer part of the island in the intertidal zone; water submergence occurs during high tides. The maritime forest is in the interior of the island, behind and at a higher elevation than the salt marsh. Maritime forests are dominated by salt tolerant trees and shrubs (Shao et al. 1996, Connor et al. 2005), and cabbage palm (*Sabal palmetto*) and southern red cedar (*Juniperus virginiana* var. *silicicola*) are the most salt tolerant species (Williams et al. 1999).

Plant Cover and Height

During August 2020, we randomly selected points along the edge of the tidal creek and established three transects in the salt marsh habitat. Transects started at the edge of the tidal creek and extended 40 m, to the edge of the salt marsh habitat. The transects extended from north to south and were parallel to each other. We established 11 1 x 1 m plots along each transect; the first plot was at the edge of the tidal creek (0 m),

and plots were spaced 4 m apart. Overall, a total of 33 plots were established. We recorded the species present in each plot and estimated the percent cover of each species to the nearest 5%, except for when cover of a species was very low and recorded as 1% cover. We also measured the height of the tallest individual of each species found in each plot.

Soil Seed Bank

On June 4, 2021, we randomly established twelve plots in the ecotone between the salt marsh and maritime forest habitats. Each plot was 30 x 30 cm and was divided into four equal-sized quadrats, and plots were spaced 5 to 20 m apart. Two soil samples (5 cm depth, 2.5 cm diameter) were taken from each quadrat and combined to have one sample per quadrat (49 cm³ soil total) and four samples per plot (N = 48). We recorded the species present in each plot and occurring within 1 m of each plot. Soil samples were returned to Winthrop University and stored in the refrigerator until September 2021.

We investigated the effect of salinity on seed germination by assigning one soil sample per plot to each of the following treatments: control (deionized water), 6 ppt salinity, 12 ppt salinity, or 26 ppt salinity (n = 12 per treatment). Our highest salinity concentration corresponds to the intermediate to high range of groundwater salinity in a South Carolina salt marsh (Thibodeau et al. 1998). We made solutions with different salinity by dissolving Instant Ocean Sea Salt (Spectrum Brands, Inc.) in deionized water (Baldwin et al. 1996).

We homogenized soil samples and spread them in a thin layer across the top of 8.2 x 8.2 cm pots filled to a depth of approximately 6.3 cm with a 3:7 mixture of Miracle-Gro® moisture control potting soil mix and sand. We included four pots with only the mixture to serve as laboratory controls. We placed pots on trays on a shelf next to a window to provide ambient light availability and rotated trays weekly to control for variation in light. Treatment application began on September 30 and lasted for about two months. Approximately every other day during this period, we watered the pots with the appropriate solution. We added 80 mL of solution the first day, then we added 40 mL of solution to each pot for the first week, and we added 20 mL of solution to each pot for the next eight weeks; these volumes of solution were used to ensure that soil remained wet but not saturated. In December, we moved pots into a greenhouse where they were watered daily from an automated watering system. We monitored pots for germination through February 2022, and seedlings that emerged were grown in the greenhouse through June 2022 to facilitate identification.

Statistical Analyses

We calculated the total plant percent cover in each plot (sum of all species) and analyzed differences in total percent cover of salt marsh species among distances from the tidal creek using a Kruskal-Wallis test. We analyzed differences in percent cover of *Spartina alterniflora*, the most dominant species, among distances from the tidal creek using a Kruskal-Wallis test. *Spartina alterniflora* was the only species abundant enough to analyze variation in height. We analyzed the correlation between distance from the tidal creek and height of the tallest *S. alterniflora* and the correlation between percent cover and height of *S. alterniflora* using Kendall's tau. Seedling emergence was too low to analyze the effect of salinity on germination of seeds in the soil seed bank.

Results

Plant Cover and Height

We documented five plant species in the salt marsh plots. *Spartina alterniflora*, the most common species, was found in 31 of the 33 plots. *Salicornia virginica*, *Juncus roemarianus*, and *Borrhichia frutescens* were found only in plots 36-40 m from the tidal creek.

There was a significant effect of distance from the tidal creek on the total percent cover of salt marsh species ($\chi^2 = 26.00$, $df = 10$, $P = 0.004$). Total percent cover of salt marsh species stayed relatively stable from 0 m (Mdn = 20, range = 10) to 24 m (Mdn = 20, range = 5) from the tidal creek and increased from 24 to 40 m (Mdn = 56, range = 21; Figure 1a).

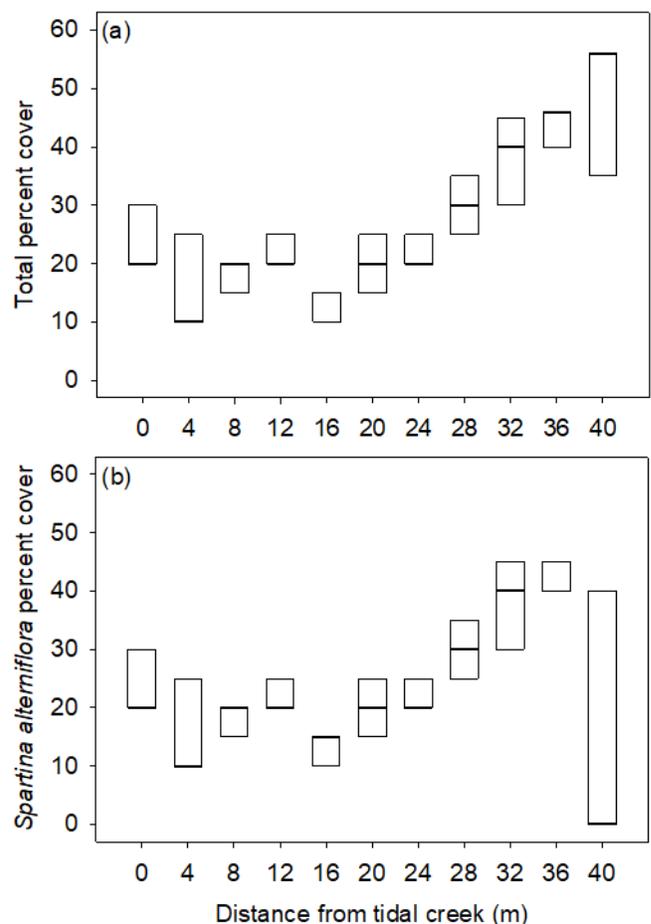


Figure 1. Boxplots of total percent cover of plants (a) and percent cover of *Spartina alterniflora* (b) in the salt marsh at each distance from the tidal creek. The thicker black horizontal line shows the median, and boxes show the interquartile range.

Spartina alterniflora accounted for all the percent cover in nine of the plots (0-32 m) in each transect. *Salicornia virginica*, *Juncus roemarianus*, and *Borrhichia frutescens* accounted for high percent cover in the 40 m plots.

There was also a significant effect of distance from the tidal creek on the percent cover of *S. alterniflora* ($\chi^2 = 20.78$, $df = 10$, $P = 0.023$). Percent cover of *S. alterniflora* was relatively consistent until 24 m (Mdn = 20, range = 5) from the tidal creek after which percent cover increased to 36 m (Mdn = 45, range = 5) and then dropped off in the 40 m plots (Mdn = 0, range = 40; Figure 1b). *Spartina alterniflora* was present in only one of the three 40 m plots.

Height of the tallest *S. alterniflora* individual in each plot ranged from 64 to 178 cm. The height of the tallest *Spartina alterniflora* individual was negatively correlated with distance from the tidal creek ($\tau = -0.67$, $P < 0.001$; Figure 2a) and with percent cover of *S. alterniflora* ($\tau = -0.41$, $P = 0.002$, Figure 2b).

Soil Seed Bank

Borrhichia frutescens occurred in all 12 plots. *Juncus roemarianus*, *Baccharis halimifolia*, and several grass species occurred in five or fewer plots. *Quercus virginiana*, *Ilex vomitoria*, and *Juniperus virginiana* occurred near the plots.

No seeds germinated during the two-month period when salinity treatments were applied. One seedling confirmed to be a salt marsh or maritime forest species emerged when the pots were in the greenhouse. A *Sabatia stellaris* seedling emerged from soil in the 26 ppt salinity treatment. No seedlings emerged from soils in the deionized water

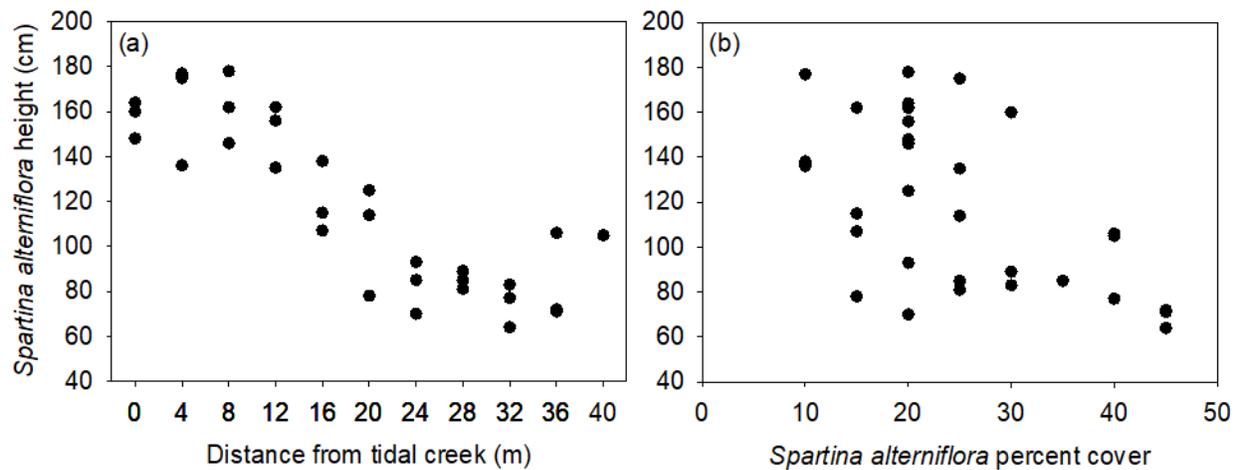


Figure 2. Correlation between distance from the tidal creek and the height of the tallest *Spartina alterniflora* individual in each plot (a) and between *Spartina alterniflora* percent cover and the height of the tallest *S. alterniflora* individual in each plot (b).

control group. We found a *Sabal palmetto* seed in one soil sample while spreading samples in pots, but the seed did not germinate during our study period.

Discussion

We found that cover of salt marsh species did not change close to the tidal creek but increased across distances further from the tidal creek. Height of *Spartina alterniflora* decreased with distance from the tidal creek as cover of *S. alterniflora* decreased. Only one seedling, of a salt marsh species, emerged from the salt marsh-maritime forest ecotone soil.

Our prediction that percent cover of salt marsh species would increase as distance from the tidal creek increased was partially correct. Percent cover of *Spartina alterniflora*, which was the only species present 0 to 32 m from the tidal creek, did not change from 0 to 24 m from the tidal creek. Percent cover of salt marsh species increased from 24 to 40 m from the tidal creek due to the increase in cover of *S. alterniflora* from 24 to 36 m and the occurrence and relatively high cover of *Juncus roemerianus*, *Salicornia virginica*, and *Borrchia frutescens* in plots 40 m from the tidal creek. Growth (Ball and Pidsley 1995, Suárez and Medina 2005) and stem density (Holm and Sasser 2001) of coastal plant species and number of shoots of *S. alterniflora* (Vasquez et al. 2006) decrease under high salinity. Lower cover of *S. alterniflora* closer to the tidal creek is likely due to lower growth and shoot production caused by high salinity.

The zonation of plant species we observed in the salt marsh on Horse Island aligns with other studies (Bertness and Ellison 1987, Bertness 1991) and can be explained by differences in stress tolerance and competitive ability among species. *Spartina alterniflora*, which can tolerate high salinity (Pennings et al. 2005) and low oxygen (Teal and Kanwisher 1966), occurred in the areas of the marsh that have higher salinity and are flooded more frequently. Plants further from the tidal creek are not submerged as long as plants closer to the tidal creek and thus are not exposed to high salinity to the same degree. *Salicornia* and *Juncus* species have lower salt tolerance than *Spartina alterniflora* (Bertness and Ellison 1987, Pennings et al. 2005), which likely limits their occurrence closer to the tidal creek. *Juncus roemerianus* is able to outcompete *S. alterniflora* where salinity is lower (Pennings et al. 2005), which likely limits the cover of *S. alterniflora* further from the tidal creek. As sea level continues to rise and salinity increases further from the tidal creek, *S. alterniflora* may increase in cover further from the tidal creek (Michener et al. 1997, Feagin et al. 2010). Species with lower salt tolerance (*J. roemerianus*, *S. virginica*, *Borrchia frutescens*), which already have a narrow distribution on Horse Island, may encroach into the maritime forest, if they are able to tolerate lower light availability, or

be lost from the salt marsh community.

In contrast to our prediction that plant height would increase with distance from the tidal creek, we found that height of *S. alterniflora* decreased as distance from the tidal creek increased. Vasquez et al. (2006) found that height of *S. alterniflora* decreased with increasing salinity; our results suggest that salinity is not the driving factor affecting *S. alterniflora* height in our study site. There are several potential mechanisms that could contribute to the decrease in *S. alterniflora* height with distance from the tidal creek. Height of *S. alterniflora* decreased as percent cover increased; allocation of resources may have shifted from vertical growth to horizontal spread. *Spartina alterniflora* may grow taller closer to the tidal creek due to increased submergence. Greater height contributes to higher survival in flooded habitats (Garssen et al. 2015), and plants closer to the tidal creek experience a longer duration of flooding; by growing taller, part of *S. alterniflora* individuals are able to stay above the water during flooding. *Spartina alterniflora* may have been taller closer to the tidal creek due to higher nutrient availability; *S. alterniflora* allocates a lower proportion of biomass belowground as nutrient availability increases (Darby and Turner 2008), and lower allocation of resources to belowground biomass could allow for greater allocation to aboveground growth. Finally, the decrease in height of *S. alterniflora* with distance from the tidal creek may be due to a shift from the tall form to short form of *S. alterniflora* (Mendelsohn 1979).

Increasing salinity can have a negative effect on the number (Baldwin et al. 1996, Rand 2000) and diversity (Kottler and Gedan 2020) of seedlings that emerge from the soil seed bank; however, we were not able to assess the effect of salinity in our study due to overall low seedling emergence. No seedlings emerged from the salt marsh-maritime forest ecotone soils during the treatment application phase of our seed bank study, and only one seedling confirmed to be a salt marsh species emerged during the period when soils were automatically watered in the greenhouse. Baldwin et al. (1996) found that the majority of seedlings emerged from coastal marsh soils within a month, so our study period should have been long enough for seeds present in the soil to germinate. There are several factors that could have contributed to the low seedling emergence during our study. First, there could be a relatively low abundance of seeds in the salt marsh-maritime forest ecotone soil seed bank on Horse Island. Second, some viable seeds in the soil could have germinated before we collected soil samples; in other salt marsh seed bank studies, soil samples were collected in March (Kottler and Gedan 2020) or May (Rand 2000). Third, our soil samples may not have been large enough to include many seeds, especially if there is high spatial variability in seed density in the soil; higher seedling emergence from salt marsh and ecotone soils has been documented in studies that sampled a larger volume of soil (Baldwin et al. 1996, Kottler and Gedan 2020). Methodological factors could have also affected our

seed bank study results. Storing soils in the refrigerator could have affected germination; however, Baldwin et al. (1996) found that storing soils at 4°C did not affect seedling emergence. Seed germination only occurred when samples were in the greenhouse, which suggests that there might not have been enough water to facilitate germination while salinity treatments were applied. In addition, when our samples were in the greenhouse, seeds of surrounding plants (forbs and ferns) recruited into the pots. Seedlings of salt marsh species could have died before we were able to distinguish them from seedlings of greenhouse species. The lack of seedling emergence from the control (deionized water) samples suggests that salinity did not contribute to low seedling emergence in our study.

Our results suggest that salinity and submergence impact the cover and distribution of plant species in the salt marsh community on Horse Island, SC. We found little overlap between the lower and upper salt marsh communities. *Spartina alterniflora* dominated the community 0 to 36 m from the tidal creek, where conditions are stressful due to submergence and high salinity, while *J. roemarianus* and *B. frutescens* only occurred 40 m from the tidal creek, where conditions are less stressful. The role of the soil seed bank in affecting salt marsh plant community structure requires further investigation. As sea level continues to rise, salt water encroachment will occur in areas where less salt-tolerant species occur, which could allow *S. alterniflora* to expand its range into the upper marsh. Where human development limits the upward movement of coastal ecosystems, less salt-tolerant species may be lost from the community. Changes in the structure of coastal ecosystems due to sea level rise will likely diminish the ecosystem services they provide (Barbier et al. 2011).

Acknowledgements

We thank David Maybank III for allowing us to conduct research on his island. We thank Peter Jenkins for his help with field work and aid in transportation and Roberta Jenkins for the use of her boat, gas, and dock. This research was funded by a Winthrop University Research Council Grant.

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