

FACILITATION PLAYS A KEY ROLE IN MARSH-MANGROVE INTERACTIONS ALONG
A SALINITY GRADIENT IN SOUTH TEXAS

A Thesis

by

MIKAELA J ZIEGLER

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MIKAELA J ZIEGLER

This thesis meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

Ed Proffitt, PhD
Chair

Lee Smee, PhD
Committee Member

Donna Devlin, PhD
Committee Member

August 2018

ABSTRACT

Climate change is resulting in fewer and less intense freezes which allows tropical mangroves, *Avicennia germinans*, to expand into saltmarshes in the Gulf of Mexico, causing a regime shift from herbaceous to woody plant dominance in many areas. Species interactions may affect the extent and rate of this regime shift. The Stress Gradient Hypothesis (SGH) predicts that at low stress plant-plant interactions will be competitive and shift to facilitative at high stress. Climate models show rising temperatures and changing precipitation patterns may lead to prolonged hypersaline conditions in some areas. Hypersalinity stress converts salt marsh dominance from *S. alterniflora* to succulent forb species or unvegetated tidal flats. Understanding how interactions between marsh species along stress gradients affect different life stages of *A. germinans* can provide more insight into which salt marsh habitats are vulnerable to encroachment. We utilized a transplant experiment and two observational field studies within different habitats to investigate *A. germinans* seedling survival, growth, and reproductive output under moderate and hypersaline conditions.

Seedlings were observed at moderate and hypersaline sites in four habitats: *A. germinans* canopy cover, shoreline and inshore succulent marsh habitats, and tidal flats. Propagules were collected from moderate and hypersaline sites along the south Texas coast and transplanted within three habitats: *A. germinans* canopy cover, succulents, and tidal flats. Reproductive branches of mature trees were monitored for the development of propagules at moderate and hypersaline sites.

By the predictions of the SGH, *A. germinans* canopy was competitive with seedlings under moderate salinity as succulents had higher seedling densities and mean heights, but canopy became facilitative at hypersalinity due to high seedling recruitment and growth. Propagules in moderate salinity had slightly lower survival rates than those in hypersalinity; propagule survivability was similar in succulent forbs and *A. germinans* canopy. Survival rates based on natal sites were marginally different, suggesting there was no local adaptations to hypersalinity. No difference was found in the quantity or size of propagules between both sites, while survival and growth conformed to SGH predictions, reproduction did not. Estuaries of moderate salinity with succulents or hypersalinity with mangroves are most vulnerable to mangrove encroachment.

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CHAPTER I: INTRODUCTION

The Stress Gradient Hypothesis (SGH) predicts that plant interactions will change from competitive to facilitative as stress increases (Menge & Sutherland 1987, Bertness & Callaway 1994, Maestre et al. 2009). In low stress conditions, such as moderate salinities, rainfall, and soil moisture, species are theorized to be more competitive for resources and space. For example, species grown together may allocate more resources to above-ground growth to be taller than their neighbors and compete for light availability. In high stress conditions, such as hypersalinity, intense heat, or drought, species are predicted to be more facilitative; the canopy of one species may provide shade and change the microclimate or soil conditions thus facilitating the survival of another species (Devaney et al. 2017, Wright et al. 2017).

Climate change is altering seasonal temperatures and some tropical species are moving poleward, leading to unique transitional regions of different biological communities, or ecotones (Walther et al. 2002, Saintilan et al. 2014). In the northern Gulf of Mexico (Texas, Louisiana, and Florida panhandle), winter freezes have become less frequent and less severe, leading to mangrove stand expansion and marsh-mangrove ecotones (Osland et al. 2013, Cavanaugh et al. 2014). As the climate continues to warm, the plant species composition of salt marsh communities may shift from graminoid-dominance to forb-dominance (Gabler et al. 2017). Also, estuaries may experience hypersaline conditions more frequently and for longer durations (Dore 2005). Along a salinity stress gradient, marsh and mangrove species interactions may change from competitive to facilitative, which has potential to change the coastal landscape. Here, two observational studies and a transplant experiment on black mangroves, *Avicennia germinans*, were conducted to test the validity of the SGH in this marsh-mangrove ecotone, to further understand *A. germinans* seedling survival and growth under moderate salinity and hypersaline

conditions, and to assess how hypersalinity affects reproductive output, all of which contributes to mangrove colonization potential.

Mangroves are tropical to sub-tropical intertidal trees and have been observed to expand their latitudinal range on five continents with the genus *Avicennia spp.* having the widest ranging migration patterns (Saintilan et al. 2014). In the northern Gulf of Mexico, *A. germinans* is limited by winter freeze events, which can cause mass mortality or stunt their growth, depending on the severity and duration of each freeze. Black mangroves in this region have more branching and are shorter due to physiological changes for freeze tolerance, creating a more shrub-like appearance, compared to their counterparts in Florida and other tropical locations (Madrid et al. 2014). Since the 1970s, this region has experienced fewer freezing events. Mild winter temperatures at the geographic boundary of *A. germinans* lessens the severity of freeze damage and alleviates cold-temperature stress thus allowing *A. germinans* to expand its range and encroach into temperate salt marshes (Osland et al. 2013). Climate models created from winter temperature data of the northern Gulf of Mexico from 1970-2000 predicted that mangrove presence occurs when mean annual minimum temperatures are at or above -8.9 °C and mangroves are dominant when minimum temperatures are -7 °C. This means that even a 2-4 °C increase in mean annual minimum temperature would leave majority of the northern Gulf of Mexico coastal saltmarshes vulnerable to mangrove encroachment, with 100% of the Texas coastal marshes converted to mangroves by 2100 (Osland et al. 2013).

In addition to reduced freezing events, increasing temperatures and variable rainfall in this region may lead to higher salinities and seasonal hypersaline conditions for some coastal estuaries, which can affect plant species distributions and interactions (Dore 2005). Using regional and local climate data, Gabler et al. (2017) created models identifying thresholds for

mangrove, graminoid, and forb distribution and dominance in the northern Gulf of Mexico based on mean annual rainfall (MAP) and minimum temperature. At lower minimum temperatures, graminoids were dominant but sharply decline as minimum temperatures increased and shifted to mangrove dominance. At moderate to high MAP, graminoids and mangroves are co-dominant, but decline as MAP declines causing dominance to shift to forbs (Gabler et al. 2017). Even small changes in regional climate could translate to larger shifts in plant functional group dominance, which may change the coastal landscape and affect ecological function and community assembly.

Both marsh and mangroves are foundation species that facilitate the creation of ecological communities; however, a state-shift from grassy salt marshes to woody mangroves would greatly affect ecosystem functions and services (Dayton 1972, Ellison et al. 2005). Carbon sequestration rates and soil carbon content are higher in mangroves than marsh due to their woody structure and greater above-ground biomass (Doughty et al. 2016), particularly in regions of low rainfall and high salinities (Yando et al. 2016). Complex cable root systems can more efficiently trap sediment and strengthen soils compared to marsh root systems, making mangrove habitats more resistant to storm-induced wave action and sea-level rise (Comeaux et al. 2012). Wood and leaf litter compared to grassy litter can change soil chemistry and decomposition rates, which in turn can affect nutrient cycling and primary productivity (Bianchi et al. 2013). The differences in the physical structure of marsh and mangrove habitats can also have an impact on the fauna community composition; marsh habitats have higher abundance and biomass of invertebrate nekton and infauna while mangroves have been associated more with crabs and fish (Smee et al. 2017).

To understand the mechanisms for mangrove encroachment, many studies in the northern Gulf of Mexico have focused mainly on interactions between the smooth cord grass *Spartina alterniflora* and *A. germinans* under a gradient of environmental conditions, such as increased minimum temperatures, CO₂ levels, and different marsh elevations. The relationship between *A. germinans* and salt marsh vegetation can be highly variable depending on environmental conditions. Along a winter temperature gradient on the Texas coast, *S. alterniflora* outcompetes *A. germinans* seedlings and juvenile trees except near their northern boundary. There, it was found that *S. alterniflora* can have facilitative effects due to their roots trapping and shielding propagules from cold winter temperatures (Guo et al. 2013). Increased CO₂ and nitrogen availability caused greater biomass in *A. germinans* when grown alone, but when mixed with *S. alterniflora*, *A. germinans* growth was greatly suppressed, even with increased CO₂ and nitrogen (McKee & Rooth 2008). In Louisiana and Texas, *S. alterniflora*, is highly competitive with *A. germinans* at varying marsh elevations; *A. germinans* can grow at most marsh elevations but at low elevations, growth is suppressed due to *S. alterniflora* competition (Patterson et al. 1993, Guo et al. 2013). Marsh-mangrove interactions have been highly studied under gradients of temperature, CO₂, and nutrients; however, it is not known how marsh-mangrove interactions would change with increased frequencies of hypersaline conditions and changes to salt marsh species composition.

Texas has a unique coastline with temperature and rainfall gradients that are inversely related; the northern coast has low winter temperatures and high rainfall while the southern coast is typically has mild winters and little rainfall. In addition to a climate gradient, the Texas coast contains part of the Laguna Madre system (Laguna Madre of Texas and the Laguna Madre de Tamaulipas), the largest hypersaline system in the world, extending 445 km along the Gulf coast

from Corpus Christi, Texas to Rio Soto la Marina, Mexico. Laguna Madre of Texas (the US portion of the system, and further referred to as Laguna Madre) is the largest estuarine system on the Texas coast, extending 185 km from Corpus Christi, Texas to South Padre Island, Texas (Tunnell & Judd 2002).

Laguna Madre is shallow and narrow, averaging 7 km wide and 1 m deep, except for the 3.5 m deep channel dredged to create the Gulf Intracoastal Waterway for barges and ships. Rainfall is the primary source of freshwater as no major rivers flow into Laguna Madre. High evaporation rates and limited exchange with the ocean result in high salinities (Tunnell & Judd 2002). Typically, salinities are higher (40-55 PSU) further from inlets and declining to about sea water strength near the Gulf inlets, such as Packery Chanel, Port Mansfield, and Port Isabel (McMahan 1968, Tunnell & Judd 2002). The Laguna Madre has numerous spoil islands and Padre Island, the longest barrier island in the world, is lined with sand dunes and flats dominated by salt marsh forbs such as *Batis maritima*, *Salicornia spp.*, and *Sesuvium portulacastrum* (Judd et al. 1977, Diamond et al. 2017). *A. germinans* can be found in patchy clusters near Packery Channel and on spoil islands in upper Laguna Madre and forms dense canopies on South Padre Island in lower Laguna Madre. Small stands are spotted throughout the remaining areas of the lagoon (Tunnel & Judd 2002).

S. alterniflora grows ideally in brackish estuaries but can survive at seawater salinities. Lonard et al. (1978) notes occasional, dense stands of *S. alterniflora* on the lower portion of Padre Island and stands in the tidal flats near the Queen Isabel Causeway of Port Isabel, Texas. Other stands have been observed on tidal flats of adjacent islands near Laguna Atascosa National Wildlife Refuge in lower Laguna Madre (Lonard & Judd 1980).

S. alterniflora out competes *A. germinans* in brackish conditions at low marsh elevations, but interactions can change depending on environmental conditions (Patterson et al. 1993, McKee & Rooth 2008, Guo et al. 2013, Guo et al. 2017) . With increasing temperatures and variable rainfall leading to higher salinities in south Texas estuaries and more forb coverage in marshes, Laguna Madre is an ideal study site to assess how hypersaline conditions can alter marsh-mangrove interactions in the northern Gulf of Mexico. The composition and complexity of marsh vegetation has a strong influence on the entrapment and establishment of *A. germinans* propagules. Salt marsh habitats with a variety of marsh forb species can have a facilitative effect on propagules by entrapping them in a matrix of roots and stems (Peterson & Bell 2012). It is possible that *A. germinans* expansion may be facilitated by warming winter temperatures and increases in forb coverage, thus changing the coastal landscape

A. germinans is known to tolerate high salinities and drought conditions. Their root systems can exclude some salts from entering the tree-body, but the most common mechanism is by excreting salt through specialized glands on the backs of leaves (Sobrado 2001). *A. germinans* is crypto-viviparous, meaning that the embryo, or propagule, begins to germinate on the parent tree before dropping, thus reducing the time needed to establish. Propagules are buoyant and can withstand a wide salinity range, *Avicennia sp.* have been recorded in 0-90 PSU (Yan et al. 2007); cotyledons provide the enclosed embryo with maternal starches and reserves. Propagules can establish within 30 days; however, they may remain in the water column for months in stressful environments which allows for an extended dispersal period (Alleman & Hester 2011). Once established, cotyledons provide nutrients until roots can be established and can act as an ion sink and minimize the effects of salinity stress (Yan et al. 2007).

The ability of *A. germinans* to respond to changing conditions can be attributed to local adaptations, phenotypic plasticity, and maternal contribution. The relative importance and interactions of these factors can affect species interactions and population dynamics. As temperatures warm and hypersaline events become more frequent, *A. germinans* may develop local adaptations to survive through these conditions. Local adaptations can be determined by how well an individual and its offspring respond to changing environmental conditions revealing increased fitness over generations. However, some studies show plasticity is the determining factor in phenotypic response; in a marsh forb, seedlings responded similarly to salinity stress regardless of previous exposure (Richards et al. 2009). In mangroves, only a few studies have explored the effects of maternal contribution, the interaction between genotype and environmental factors. The red mangrove, *Rhizophora mangle*, was influenced by genetic and environmental factors when planted on various coastal islands in Florida. Among 86 half-siblings (propagules from the same maternal tree), survival and growth response varied between tidal elevation and genotype. Some differences could be attributed to variation between physical factors of the islands, such as island size and slope, but other differences were rooted in genotype and their ability to respond to environmental variations (Proffitt & Travis 2010). Another study found that half-siblings of *R. mangle* greatly varied in resistance and mortality to a burrowing beetle (Devlin 2004). With a unique life history of cryptovivipary, it is thought that *A. germinans* will exhibit significant maternal contribution. This may be noticeable in propagule size, indicating the amount of reserves available, or the quality of such reserves, all of which play a key role in survival and success.

Cold tolerance is a large factor in determining survival of mangroves in the northern Gulf of Mexico; winter freezes restrict xylem tissues which interrupt the flow of water and minerals

from roots to shoots, reduce stomatal activity, and cause leaf loss, all of which result in stunted growth or death (Kao et al. 2004, Stuart et al. 2007). In a comparison study of cold stress response, *A. germinans* was shown to be the most cold-tolerant genus with populations from Louisiana and Texas having the least injury (McMillan 1975a, Markley et al. 1982). Cold tolerance is linked to narrow vessel structures, which reduce the risk of embolisms from freeze events; it was also found that narrow vessels is more strongly linked with higher soil salinities since *A. germinans* from Veracruz, Mexico had similar vessel structures to populations in Texas, yet Veracruz rarely, if ever, has freeze events (Madrid et al. 2014). Leaf chemistry analysis showed differences in fatty acid composition which affect membrane fluidity. Seedlings also showed similar tolerance and leaf chemistry, suggesting that tolerance is based on inheritance and maternal contribution (Markley et al. 1982). If *A. germinans* stands in this region can develop local adaptations for cold-stress, it is possible that local adaptations for hypersalinity can also develop as climates continue to warm.

The primary objectives of this research project were to test the validity of the SGH for marsh and mangrove interactions along a salinity stress gradient and to better understand which habitats may be more vulnerable to mangrove encroachment. Three separate studies were done; a transplant experiment of establishing propagules, an observational study of older established seedlings, and an observational study of the reproductive output of mature *A. germinans*. Competitive interactions are expected to be more common at moderate salinities while facilitative interactions may be more common in hypersalinity.

Propagules are dispersed in the water column and then stranded ashore by tidal activity. Establishment success and survival can be dependent upon the interactions with surrounding vegetation as well as other environmental factors. Marsh forbs and adult mangrove canopies may

be facilitative by trapping propagules and lowering heat stress; or, forbs and mangroves may shade out propagules and have a competitive effect on this early life stage. It is hypothesized for the transplant experiment that propagules will be facilitated by marsh and mangrove vegetation under salinity stress but will be in competition with vegetation under lower salinity stress. A secondary hypothesis is that propagules from a hypersaline environment would have local adaptations to hypersaline conditions and therefore have better survival rates in hypersalinity than their counterparts from areas with moderate salinities.

For the observational study on naturally occurring seedlings, it is hypothesized that salt marsh forbs will have the highest seedling recruitment, density and growth rates due to facilitative interactions such as trapping and partial shading, compared to full shading from the mangrove canopy. Hypersalinity requires additional energy for salt regulation; therefore, it is hypothesized for the observational study on reproduction that sexually mature trees in hypersalinity will have reduced quantity of propagules or smaller propagule size.

About midway through data collections for the two observational studies, Hurricane Harvey made landfall in Port Aransas, TX on August 25, 2017 as a Category 4 storm and caused both field sites to be flooded for a 5-week period. For the observational seedling study, inundation stress altered trends in survival and growth. For the observational reproductive study, some broken pedicles were noted and its likely some flowers and fruits were knocked off by winds. The transplant experiment was not affected. Further details are given in the later section.

CHAPTER II: METHODS

Three studies were conducted to assess survival, growth and reproduction of *Avicennia germinans* under moderate salinity (Oso Bay) and hypersaline conditions (Laguna Madre), a transplant experiment and two observational field studies. A field experiment involving *A. germinans* propagules from Oso Bay and lower Laguna Madre transplanted within three habitat types at both moderate and hypersaline field sites was done to evaluate the potential for local adaptations in propagules to hypersaline conditions. An observational study assessed *A. germinans* seedling growth in three different marsh habitats (*A. germinans* canopy, salt marsh forbs, and tidal flats) at both sites; the other observational study assessed *A. germinans* reproduction at both sites by tracking the quantity and timing of buds, flowering, fruiting, and propagules.

All studies had response variables measured over time so multivariate statistical analysis accounting for the temporal nature of the data were used to address trends over time and the covariance structure inherent in many time-series datasets; SAS 9.4 was used to analyze each study.

Study Sites

Oso Bay

Oso Bay is a small bay within the Corpus Christi Bay system in Corpus Christi, Texas (Figure 1). The bay receives freshwater inflow from Oso Creek and saline water from Corpus Christi Bay (Nicolau 2001). Salinity measurements are typically 3-28 PSU depending on seasonal variation and on rare occasions of drought, can reach 45 PSU (Nicolau 2001). During the period of this study, open water salinities ranged from 19-35 PSU, with highest salinities occurring in July and August (M Ziegler, unpublished data). On the northern shores, *S.*

alterniflora stretches 1-2m from the shoreline, followed by a stretch of *A. germinans* before shifting to tidal flats (Figure 2a). In this study, *A. germinans* height ranged from 40-180 cm depending on age and were found in non-continuous stands (M. Ziegler unpublished data). Salt marsh forbs like *Batis maritima*, *Salicornia bigelovii*, and *Sesuvium portulacastrum* are found in the canopy gaps and between stands of *A. germinans* (Figure 2b).

Laguna Madre

Laguna Madre can be further divided into upper and lower sections due to a 20-km stretch of salt flats called the Saltillo Flats. In the 1940's during the creation of the Gulf Intracoastal Waterway, a channel, called the Land Cut, was created to permanently connect the upper and lower Laguna Madre (Figure 3) (Tunnel & Judd 2002). The upper Laguna Madre receives Gulf waters through Packery Channel and some exchange through Port Mansfield; the Lower Laguna Madre receives tidal exchange through Port Mansfield and Brazos Santiago Pass near Port Isabel.

The Laguna Madre is lined with sand dunes and flats and has numerous spoil islands dominated by salt marsh forbs such as *B. maritima*, *S. bigelovii* and *Salicornia depressa*, *S. portulacastrum*, *Lycium carolinianum*, *Borrchia frutescens*, *Monanthocloe littoralis*, and occasionally cactus like *Opuntia engelmannii* (Lonard et al. 1978, Lonard et al. 1999). *A. germinans* can be found in clusters near Packery Channel in upper Laguna Madre and in dense canopies in South Padre Island in lower Laguna Madre near Brownsville but stands are not as large or dense throughout the remaining areas of the lagoon (Tunnel & Judd 2002). However, field observations indicate that they have become more abundant in the Laguna Madre system in

the last decade, as they have also throughout much of coastal Texas (Osland et al. 2013, Armitage et al. 2015, Gabler et al. 2017).

Upper Laguna Madre

In the upper Laguna Madre, spoil islands, created during construction and maintenance dredging for the Gulf Intracoastal Waterway, extend roughly 40 km from the John F. Kennedy Causeway in Corpus Christi, Texas to the mouth of Baffin Bay (Figure 4). *A. germinans* can be found in clusters on spoil islands and on the lagoon-side of Padre Island but become less frequent continuing south. Texas A&M University-Corpus Christi has a field station on a spoil island that is about 10 km south of the John F Kennedy Causeway (Figure 5). A variety of forbs, including *B. maritima*, *S. bigelovii*, and *S. portulacastrum*, are found in discontinuous patches along the island's shoreline (Figure 6). Tidal flats with annual *S. bigelovii* are between the patches of salt marsh forbs and can reach further landward. The center of the island is dominated by high marsh species such as the grass *Monanthochloe littoralis* (Lehman 2013). There are three sexually mature *A. germinans* shrubs on the island, two on the east shoreline and the third (and smallest) on the northwest side of the island at the mid-marsh elevation.

Lower Laguna Madre

The lower Laguna Madre extends from the Land Cut to Brazo's Pass (Figure 7). *A. germinans* can be found in dense coverage in South Padre Island near the Queen Isabella Causeway and in the adjacent connected water bodies such as South Bay (Figure 8). *B. maritima* is the most common forb found in *A. germinans* canopy gaps as well as on the edge of stands (Figure 9).

Study 1: Reciprocal transplant experiment

In this study, propagules were collected from a moderate salinity site (Oso Bay) and hypersalinity site (South Padre Island in lower Laguna Madre) then planted reciprocally within the three habitat types at the hypersaline upper Laguna Madre and the moderate salinity Oso Bay sites. It was hypothesized that propagules from a hypersaline area would better survive hypersaline conditions than their counter-parts due to their parents' exposure to high salinities resulting in local adaptations.

Propagule collection and tethering

A. germinans propagules were collected in February-March 2017 from Oso Bay and lower Laguna Madre at South Padre Island (Figures 1 and 8). Propagules with minimal initial root development were preferred so that growth can be attributed to the experimental treatments. Propagules were rinsed with deionized water to remove all sediment and kept in filtered tanks with water collected from their natal collection locations until planting on March 24, 2017. Salinity was checked every other day and deionized water added to maintain the following ranges; Oso Bay, 16-20 PSU and lower Laguna Madre (South Padre Island) 32-36 PSU. Propagules showing signs of fungal infection or rot were removed from tanks.

For tethering, propagules were removed from tanks and placed on clean, damp paper towels with a moist paper towel on top of propagules. Propagules remained on moist towels overnight to remove majority water weight. Then, propagules were left to dry for 15-20 minutes on fresh paper towels before being weighed on a digital scale (0.01g accuracy). Length and width of the propagule and root length were measured with a caliper and recorded. Propagule

quality was graded on a scale of 1-3 with 1 indicating a majority green root with healthy white root tips, 2 indicating a yellowing root, and 3 indicating a browned root.

Propagules were strung on an elastic line by piercing the center of the entire propagule with a needle and then the line threaded through the cotyledons (Figure 10). Each elastic line had six propagules, three from Oso Bay and three from Lower Laguna Madre. The arrangement of propagules on the line was randomly assigned so neighboring effects are minimized. Each line has a compression tag labeled for habitat type and plot number, each propagule had a small compression tag indicating its natal site. Each habitat type has 10 plots for a total of 30 plots per planting site.

Planting

Propagules were planted at Oso Bay (at Ward Island) and upper Laguna Madre (at the Laguna Madre Field Station). At each site, propagules were planted in three habitat types—*A. germinans* canopy cover, a mixture of succulent forb vegetation, and tidal flats with 10 replicate plots per habitat per site. Plots were 1.5 m away from another plot. Plots were placed an equivalent distance from shoreline and similar tidal elevation. Each propagule was planted with root tips facing down into the sediment. Plots were secured in the sediment by placing unfolded paperclips through each tag, then pushed into the sediment. Neon ribbon was tied to vegetation next to each plot to assist in visual recognition (Figure 11).

Field data collection

Sites were checked weekly to ensure plots have not been altered by factors not relating to the experiment (human activity, storms etc). Each seedling was individually assessed for root establishment, cotyledon and root color (viability), total height, development of leaves, and

mortality; all seedlings were monitored until mortality (March-November 2017) which was determined when a seedling had brown cotyledons or root for two consecutive weeks (Figure 12). Roots were assessed by gently moving the sediment near the base of the seedling; if a root could be seen, it was assessed as 1, 2, or 3 using the same index in pre-planting root assessment. If a root could not be seen without breaking tissues or uprooting the seedling, then no assessment was made.

For every field site assessment, pore salinity and soil salinity of each habitat type was recorded. For pore salinity, a hole was dug until water was reached. Sediment was left to settle before taking a water sample to read on a refractometer. The depth to water was recorded. Top soil samples were collected, and salinity measured in the lab following Pennings & Richards (2006) protocol.

Study 2: Observational study of naturally occurring seedlings

In this observational field study, naturally recruited *A. germinans* seedlings were tagged and monitored at both moderate salinity (Oso Bay) and hypersalinity (upper Laguna Madre) to determine if species interactions followed predictions from the SGH and the effects of salinity and type of surrounding habitat on survival and growth. It was hypothesized that hypersaline conditions would limit the growth of seedlings and survival would be low compared to seedlings in moderate salinity, but that seedlings recruited into areas of salt marsh forbs would have better survival and growth as marsh vegetation facilitates seedlings by providing a degree of shade which reduces desiccation and soil salinities. However, *A. germinans* shrubs provides more shade which tends to reduce biomass and occurrence of marsh plants, and it was hypothesized that at the hypersaline site, *A. germinans* canopy would be facilitative for its seedlings, but at the

moderate salinity site, would be competitive. As seedlings grow taller than surrounding vegetation, there will be less competition for light, unlike in *A. germinans* canopies.

Study-design

In this observational field study, naturally recruited seedlings were tagged and monitored at both moderate salinity (Oso Bay) and hypersalinity (upper Laguna Madre) from May-December 2017. At both field sites, four habitats were identified: *A. germinans* canopy cover, inshore salt marsh forbs (mixture of *Batis sp.*, *Salicornia sp.*, and *Sesuvium sp.* two or more meters from the waterline), shoreline salt marsh forbs (mixture of *Batis sp.*, *Salicornia sp.*, and *Sesuvium sp.* at the waterline), and tidal flats (Figure 13).

Once habitats were identified, plots 2 x 1 m were randomly located 1-4 m apart with the long axis parallel with the shoreline. Bamboo stakes marked the corners of each plot with labeled flagging tape for identification. Within each plot, all seedlings were individually tagged and identified with flagging tape (Figure 14). For plots with over 20 seedlings, a small quadrat of 15 cm x 30 cm was haphazardly tossed into the plot four times; seedlings captured within the quadrat were tagged.

Field data collection

Every two to three weeks, seedlings were measured for survival, total height (tallest point to the nearest 0.5 cm), apical stem height (root to apical tip to the nearest 0.5 cm), leaf count, and signs of herbivory (present or not present). Hurricane Harvey made landfall on August 25, 2017 producing a 5-week long period of flooding at both field sites from mid-September to end of October 2017. Water depth at both sites ranged from 10-20 cm (Figure 15). Seedlings were not

measured during this time as water depth made it difficult for accurate measurements to be taken and for seedlings to be correctly identified. Once waters receded, seedlings were re-assessed.

During each assessment, open water salinity, pore water salinity, and soil salinity were recorded in each habitat type. For open water salinity, a water sample at least 2 m from the shoreline was measured using a refractometer; for pore salinity, a hole was dug until water was reached (typically about 25-45 cm deep). The sediment was left to settle before taking a water sample to read on a refractometer and the depth to water was recorded. Soil samples 5-10 cm deep were collected and salinity measured in the lab following Pennings & Richards (2006) protocol. Briefly, 50 ml of soil are weighed and placed in a dry oven for 2-3 days to remove water weight, then 50 ml of freshwater was added and mixed with the soils and allowed to sit overnight; soils were stirred again then sat for 2 hours before the supernatant was measured for salinity. The true soil salinity was calculated by multiplying the supernatant salinity by the volume of freshwater added, then divided by the volume of water lost during drying.

Study 3: Observational study of reproductive output

In this study, reproducing stems of *A. germinans* were tagged and monitored to quantify the reproductive output at moderate and hypersaline sites to assess differences in quantity and size of propagules. It was hypothesized that hypersalinity will limit propagule production and size due to the parent tree allocating additional energy to salt regulation.

Branch selection and tagging

A. germinans within 2 x 1 m plots designated for the observational seedling study were sampled and tagged for this reproductive output assessment. Reproducing stems located higher

in the canopy were selected to minimize the effects of shading on the development and maturation of buds to propagules; stems with only primary pedicles were preferred (Figure 16). Thirty-three sexually mature trees were tagged in Oso Bay and two sexually mature trees were tagged in Laguna Madre. Each reproducing tree had five stems tagged and were spread across the surface of the upper canopy; some sexually mature trees were younger and did not have five reproducing stems, so only one to four branches could be tagged (Oso Bay, n=122 branches; Laguna Madre, n=10 branches). Once a branch was selected, flagging tape with a written number was secured at the base of the stem.

Measurements

Every two weeks, stem and pedicle lengths were measured to the nearest millimeter, and number of nodes and leaves were recorded. On each pedicle, the number of buds, flowers, fruits and propagules were recorded from June-December 2017. In the November and December 2017, a caliper was used to measure the length and wide of the largest propagule on each pedicle (Figure 17).

Statistical analyses

For the transplant experiment, a survival analyses using PROC PHREG in SAS 9.4 was done to test for differences in individual seedling survival rates based on natal site, field planting site, habitat type, and presence of crab burrows.

For the observational seedling study, separate mixed models using SAS 9.4 PROC MIXED were computed to test for differences in rooted seedling density (indicative of initial

survival to rooting), height, leaf count and stem count over time between field sites and habitat type. Following the procedures of Goldstein (2016), the data were plotted for normality and distribution patterns. Then, the mean for each variable was calculated per plot, which was nested in habitat and field. The random effect in this study was time; five random models (Slope, Intercept, Slope and intercept, repeated measures with compound symmetry, and repeated measures with auto-correlation, as described by Goldstein (2016)) were then tested. The fixed effects in this study were Field and Habitat; five fixed models (Simple linear regression, Linear regression with factor effects, Linear regression with factor effects and interaction, Linear regression with factor effects and interaction and time, and Quadratic effects, as described by Goldstein (2016)) were then tested. The best fit model was selected by AICc values; if two or more models were within two AICc points, they were considered comparable and the most biologically sound model was selected.

For the reproductive output study, separate MANOVAs were performed using the time points as response variables to test for difference in number of buds, flowers, fruits, and propagules per branch between the two field sites. The time series in which no buds, no flowers etc were present were excluded from analysis. A separate MANOVA was performed to test for differences in average propagule size (length in cm x width in cm) between both sites.

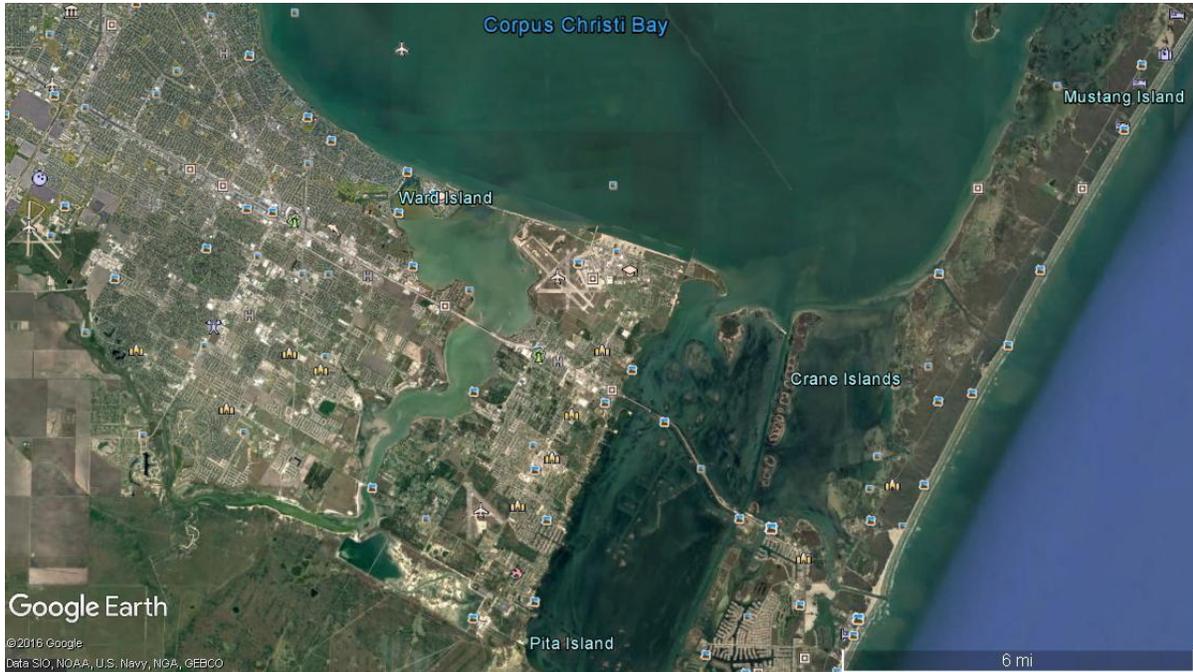


Figure 1: Oso Bay is connected to Oso Creek and Corpus Christi Bay within the Corpus Christi Bay system.



Figure 2: *S. alterniflora* dominates along the shoreline of Oso Bay with *A. germinans* landward of it (left). Succulent marsh forbes such as *Batis maritima* and *Salicornia bigelovii* most commonly occur between stands of *A. germinans* and can extend into the tidal flats (right).

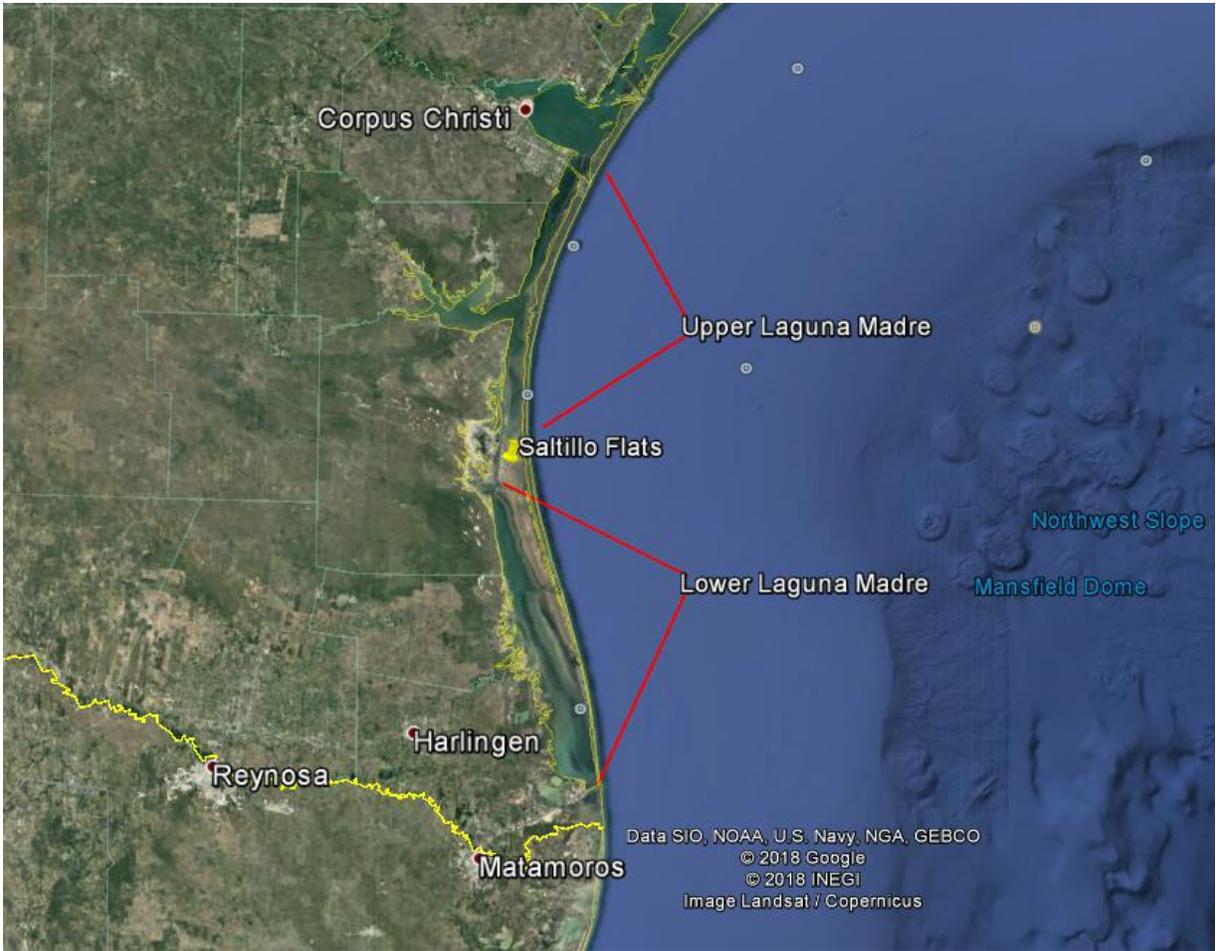


Figure 3: The upper and lower portions of Laguna Madre in Texas separated by the Saltillo Flats.

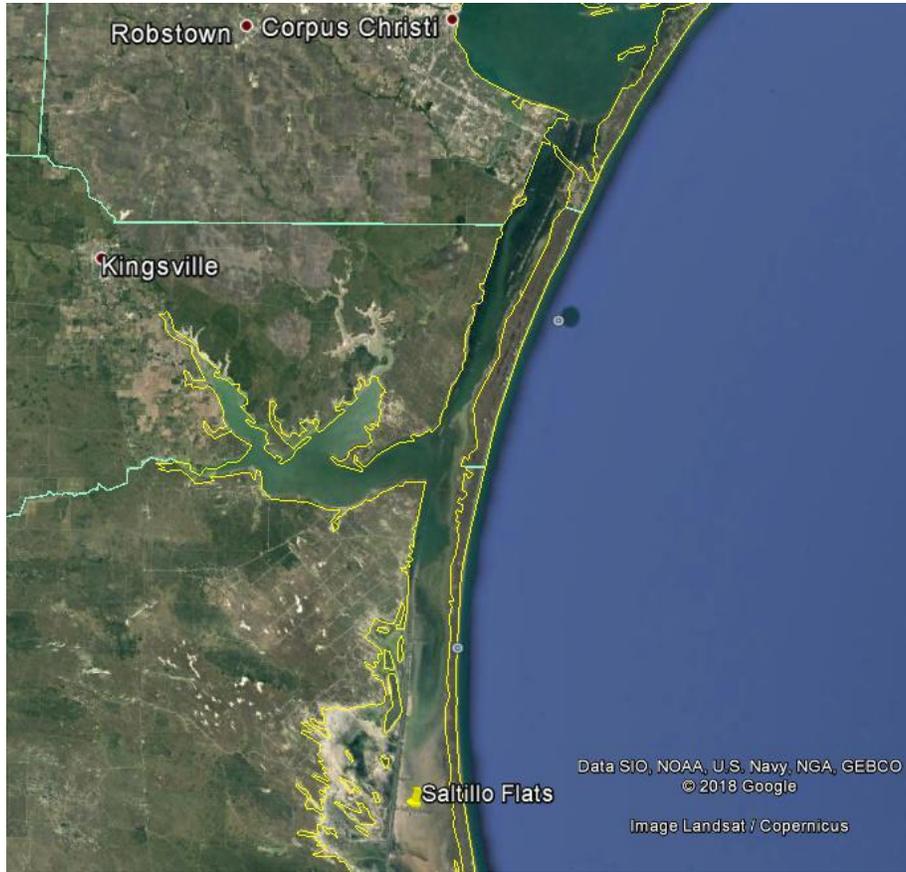


Figure 4: Upper Laguna Madre extends from Corpus Christi Bay to the Saltillo Flats near Port Mansfield.



Figure 5: The Laguna Madre Field Station is built on a spoil island in the upper Laguna Madre.



Figure 6: *B. maritima*, *S. depressa*, and *S. portulacastrum* grow along the spoil island's shoreline with tidal flats further inland.

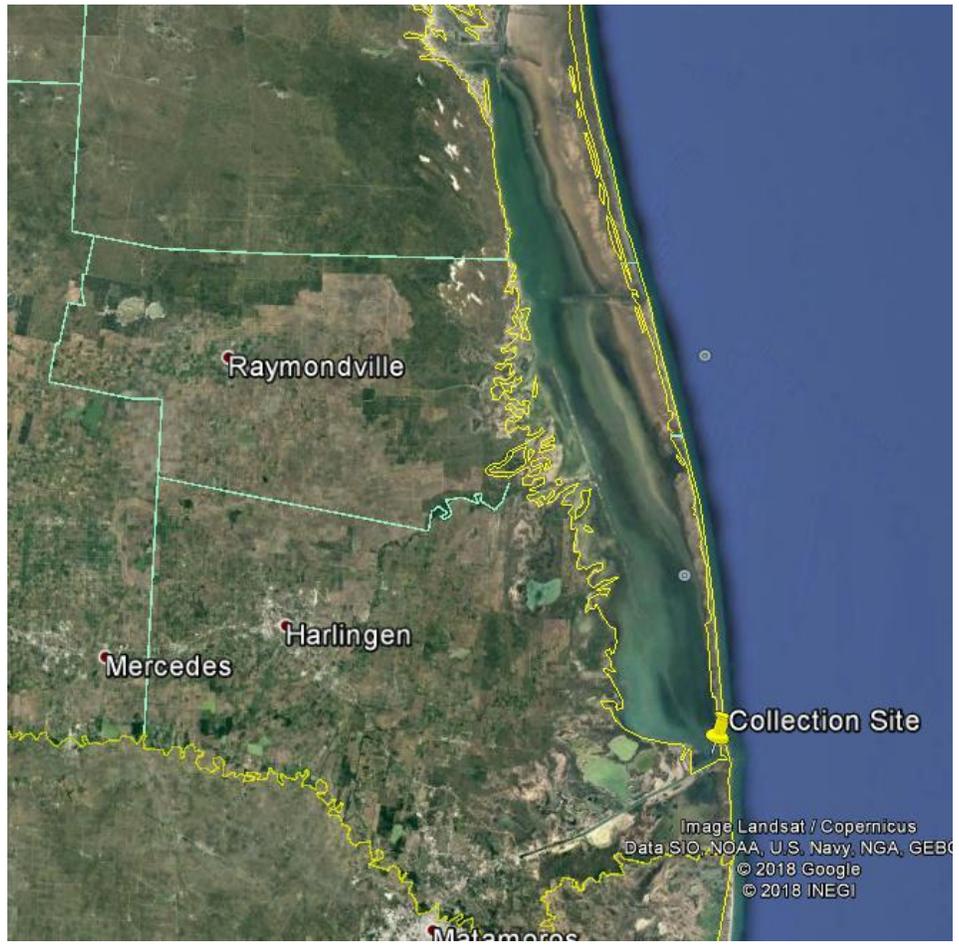


Figure 7: The lower Laguna Madre extends from the Saltillo Flats to Port Isabel.

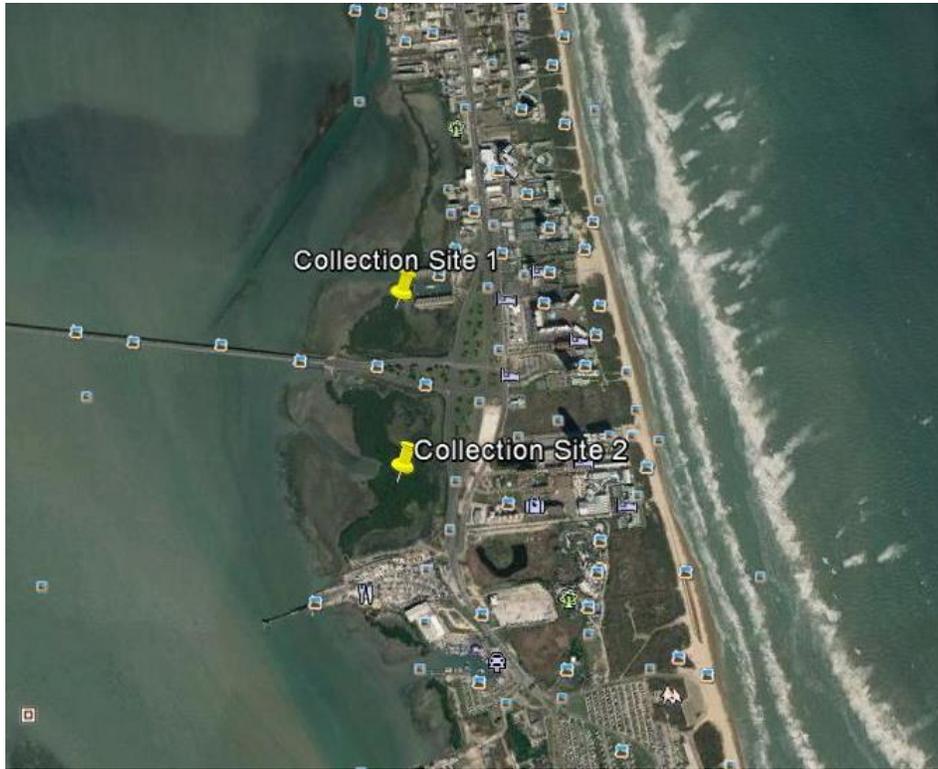


Figure 8: *A. germinans* grow in dense stands on either side of the Queen Isabel Causeway in lower Laguna Madre.



Figure 9: *B. maritima* grows along the edge of *A. germinans* stands in lower Laguna Madre near the Queen Isabel Causeway.



Figure 10: A propagule collected from South Padre Island in lower Laguna Madre and strung on elastic lining in preparation for planting.



Figure 11: A plot of tethered propagules planted under *A. germinans* canopy cover at Oso Bay



Figure 12: A healthy seedling with a green leaf bud (left) and an unhealthy yellow/brown seedling (right).



Figure 13: The four habitat types: *A. germinans* canopy cover (top left), tidal flats (top right), shoreline forbs (bottom left) and inshore forbs (bottom right).



Figure 14: A tagged *A. germinans* seedling in the inshore succulent habitat.



Figure 15: A tagged seedling in the inshore saltmarsh forb habitat during a flooding event after Hurricane Harvey.



Figure 16: A reproductive stem of *A. germinans* with three primary pedicels producing buds and flowers



Figure 17: *A. germinans* pedicles with mature, oval-shaped propagules.

CHAPTER III: RESULTS

Study 1: Reciprocal transplant experiment

Overall, there was a significant difference in seedling survival based on planting field site, habitat type, natal site, and burrows (Table 1). Seedling survival was lower in moderate salinity than in hypersalinity. At Oso Bay, seedling survival rates were better in marsh forbs and under mangrove canopy in comparison to the tidal flats, indicating vegetation had a facilitative effect on seedlings. At Laguna Madre, seedlings in tidal flats initially had better survival rates, but over time, vegetated habitats had higher seedling survival rates, indicating facilitation. Significant differences in survival based on natal site revealed that seedlings from moderate salinity (Oso Bay) had better survival rates at both planting sites, suggesting no evidence of local adaptations in seedlings from hypersaline environments. Overall survival was very low, only 1 of 356 seedlings (<1%) survived past 60 days; however, differences in survival rates based on natal site, field planting site, and habitat were apparent.

Source	DF	F-value	p-value
Field	1	12.00	0.0005
Habitat	2	10.80	0.0045
Natal site	1	11.58	0.0007
Crab burrows	1	27.96	<.0001

Table 1: Type III results from the survival analysis of transplanted seedlings from Oso Bay and lower Laguna Madre.

By field planting site

There was a significant difference in seedling survival rates between the field sites seedlings were transplanted into; burrows also had a significant effect on survival (Table 1). Seedlings at the hypersaline site had higher survival rates than their counterparts planted in moderate salinity, regardless of seedling natal site (Figure 18). Field observations note that crab burrowing activity appeared higher at the moderate salinity site and some seedlings were buried in pseudofeces from crabs or tethering lines were cut, which may explain the higher survival rate at the hypersalinity site where crabs were less abundant, and no burial was observed.

There were 176 seedlings transplanted to the moderate salinity site and 180 transplanted to the hypersaline site. Two weeks after transplanting, 63.1% and 73.9% of seedlings survived, respectfully. About one month after transplanting, 8.5% and 11.1% of seedlings survived, respectfully. At 47 days since planting, only one seedling was alive at the moderate salinity site and 6 alive at the hypersaline site. Only one seedling of all 356 transplanted survived past this point, it survived until November 2017.

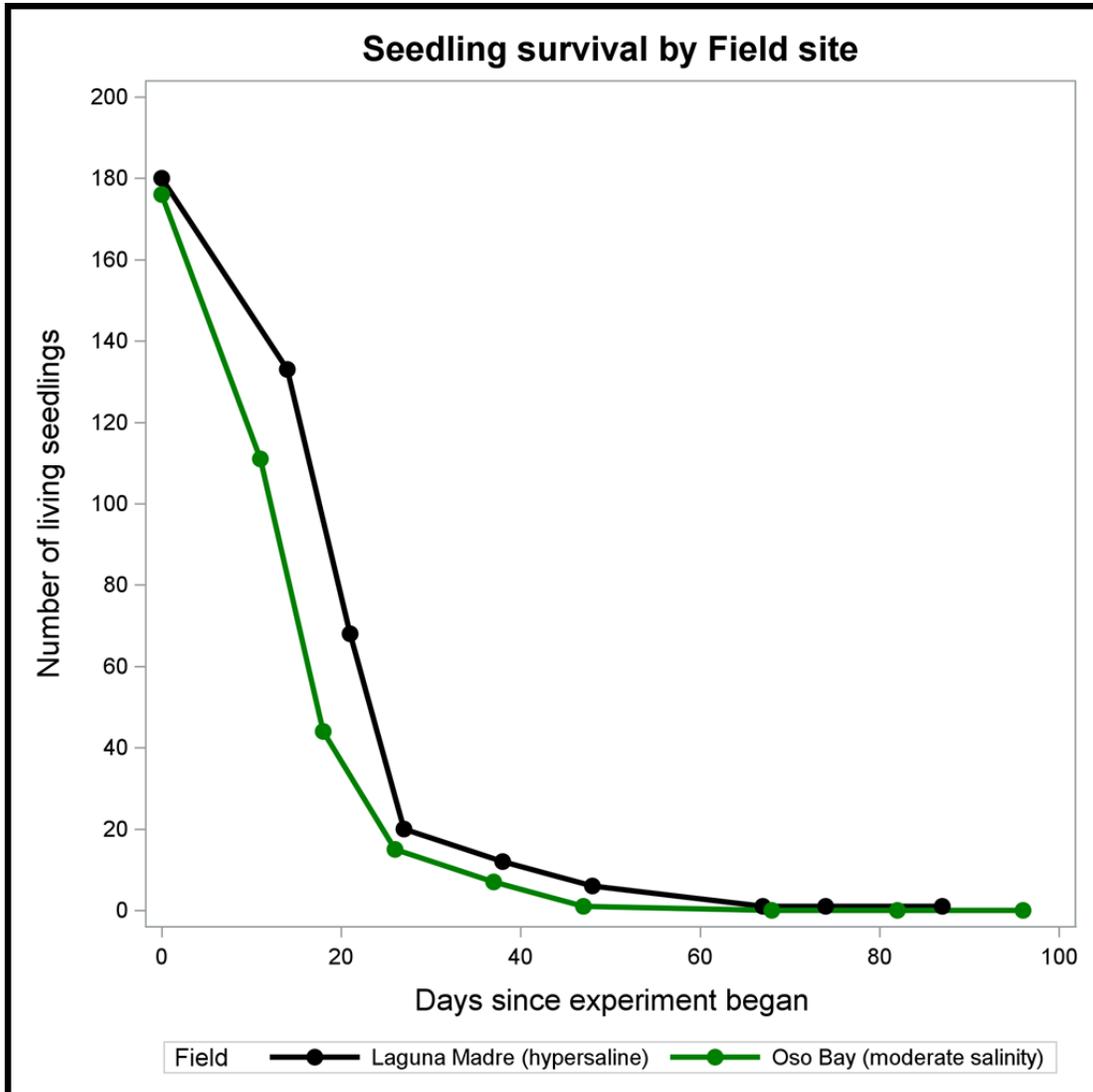


Figure 18: The total number of living seedlings over time at each field site, Oso Bay (moderate salinity) and Laguna Madre (hypersalinity).

By habitat type

There was a significant difference in seedling survival rates based on the habitat in which *A. germinans* seedlings were planted (Table 1). At Oso Bay, seedlings had higher survival rates in the marsh forbs and mangrove canopy cover compared to the tidal flats, suggesting vegetation was facilitative to seedling survival (Figure 19). At Laguna Madre, seedlings initially had lower survival rates in vegetation compared to the tidal flats during the first 10 days of the study, suggesting potential for competition. Through the remainder of the study however, survival rates

in succulent marsh forbs and under canopy cover remain higher than tidal flats, suggesting facilitative interactions (Figure 20).

At Oso Bay, there were 176 total seedlings planted: 60 under *A. germinans* canopy, 58 in succulent marsh forbs and 58 in tidal flats. In 11 days, 60%, 63.8% and 65.5% of seedlings survived, respectfully. After a month, survival was 11.7% under *A. germinans* canopy cover, 13.8% in succulent marsh forbs and no survival in tidal flats. In 47 days since planting, all seedlings under canopy cover died and one seedling remained in the succulent marsh forbs but died shortly after. At nearly one month, survival was 11.1% under canopy cover and 5.8% in succulent marsh forbs. Based on the natal site of seedlings, total mortality was reached in 68 days for seedlings from Oso Bay and 47 days for seedlings from South Padre Island.

At Laguna Madre, there were 180 total seedlings planted: 60 seedlings within each of the three habitat types. Within two weeks, 71.6% survived under *A. germinans* canopy, 58.3% within marsh forbs and 91.7% in tidal flats. At one month, survival was 21.7%, 8.3% and 3.3% respectfully. One seedling under *A. germinans* canopy survived until November 2017. Total mortality for seedlings in succulents was in 67 days, tidal flats in 48 days.

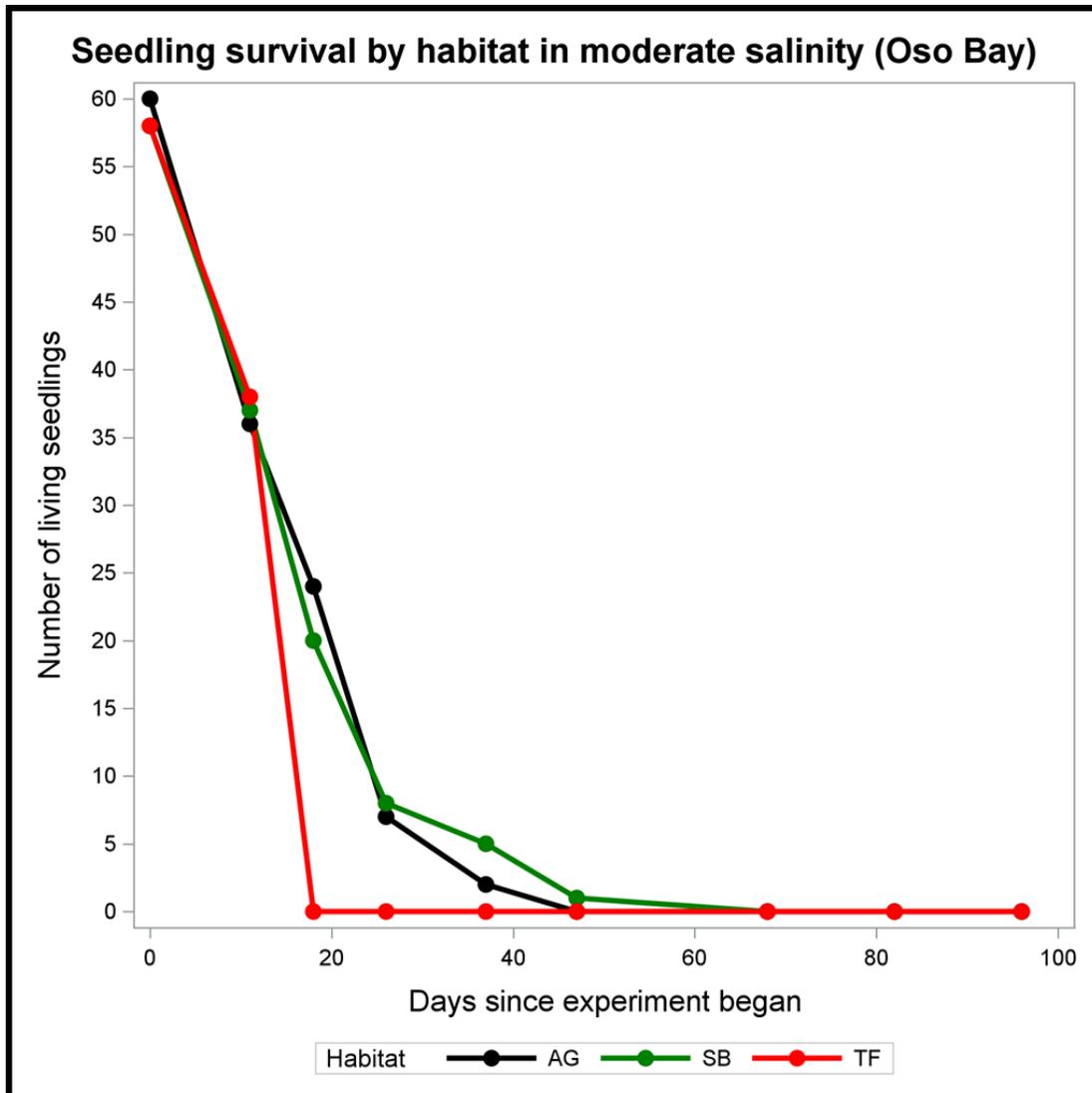


Figure 19: The number of living seedlings per habitat over time at Oso Bay (moderate salinity). AG= under *A. germinans* canopy; SB= mixture of succulent marsh forbs; TF= tidal flats.

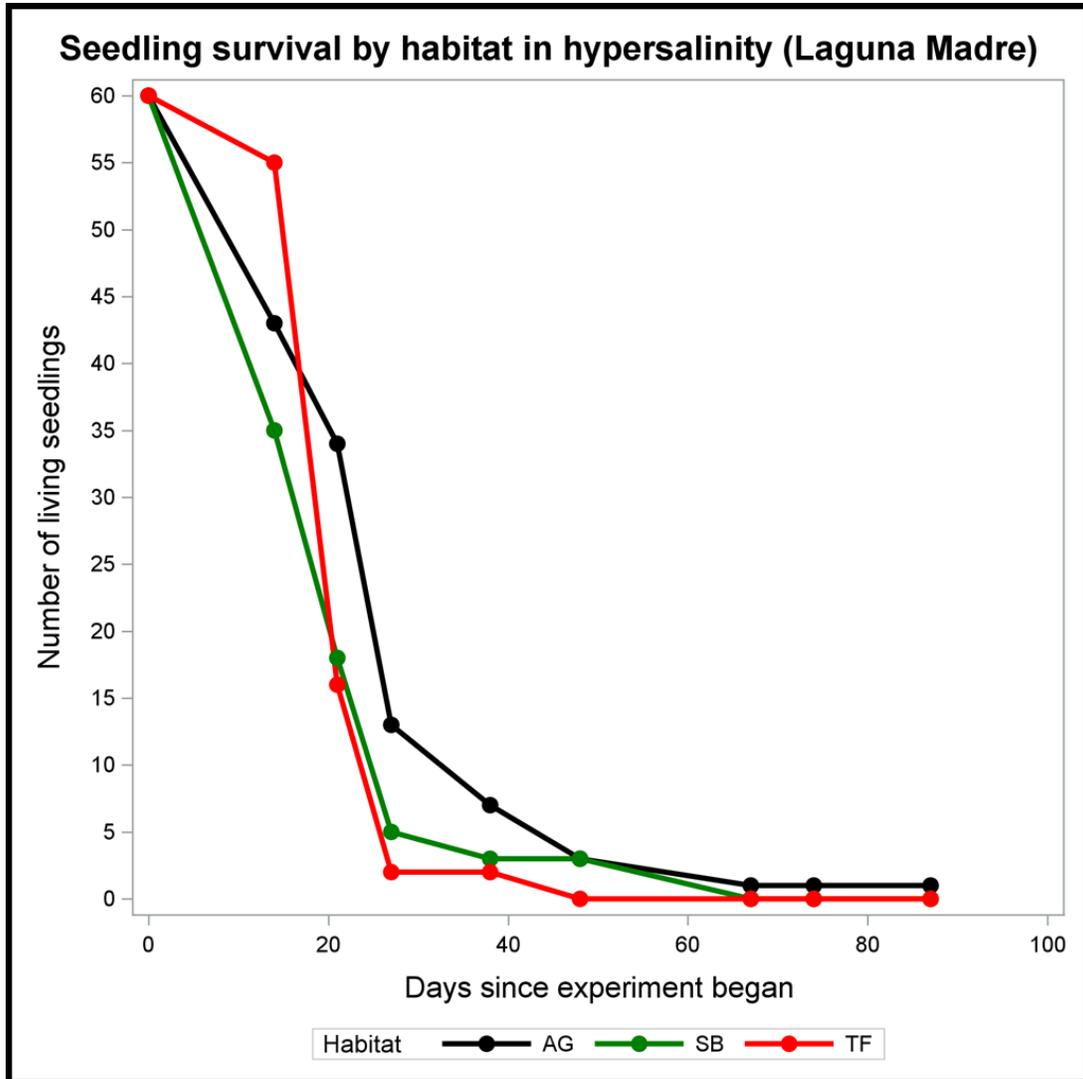


Figure 20: The number of living seedlings per habitat over time at Laguna Madre (hypersaline site). AG= under *A. germinans* canopy; SB= mixture of succulent marsh forbs; TF= tidal flats.

By Natal site

There was a significant difference in survival based on the natal site of seedlings (Table 1). Seedlings from South Padre Island (SPI) had lower survival rates at both Oso Bay (Figure 21) and Laguna Madre (Figure 22), suggesting that seedlings derived from a hypersaline environment are not better adapted for hypersalinity.

At the moderate salinity site, there were 90 seedlings from Oso Bay and 86 from SPI. Within 11 days, 70% of Oso Bay seedlings and 55.8% of SPI seedlings survived. At one month, survival was 11.1% and 5.8% respectively. Total mortality was reached in 68 days for Oso Bay seedlings and 47 days for SPI seedlings.

At the hypersaline site, there were 90 seedlings each from Oso Bay and SPI. Within 14 days, 78.8% of Oso Bay seedlings and 68.8% of SPI seedlings survived. At one month, survival was 17.7% and 4.4% respectively. Total mortality for seedlings from Oso Bay was in 67 days; at that time, one seedling from SPI was still alive and remained so until November 2017, after Hurricane Harvey. This seedling grew 12.2 cm tall and had nine leaves.

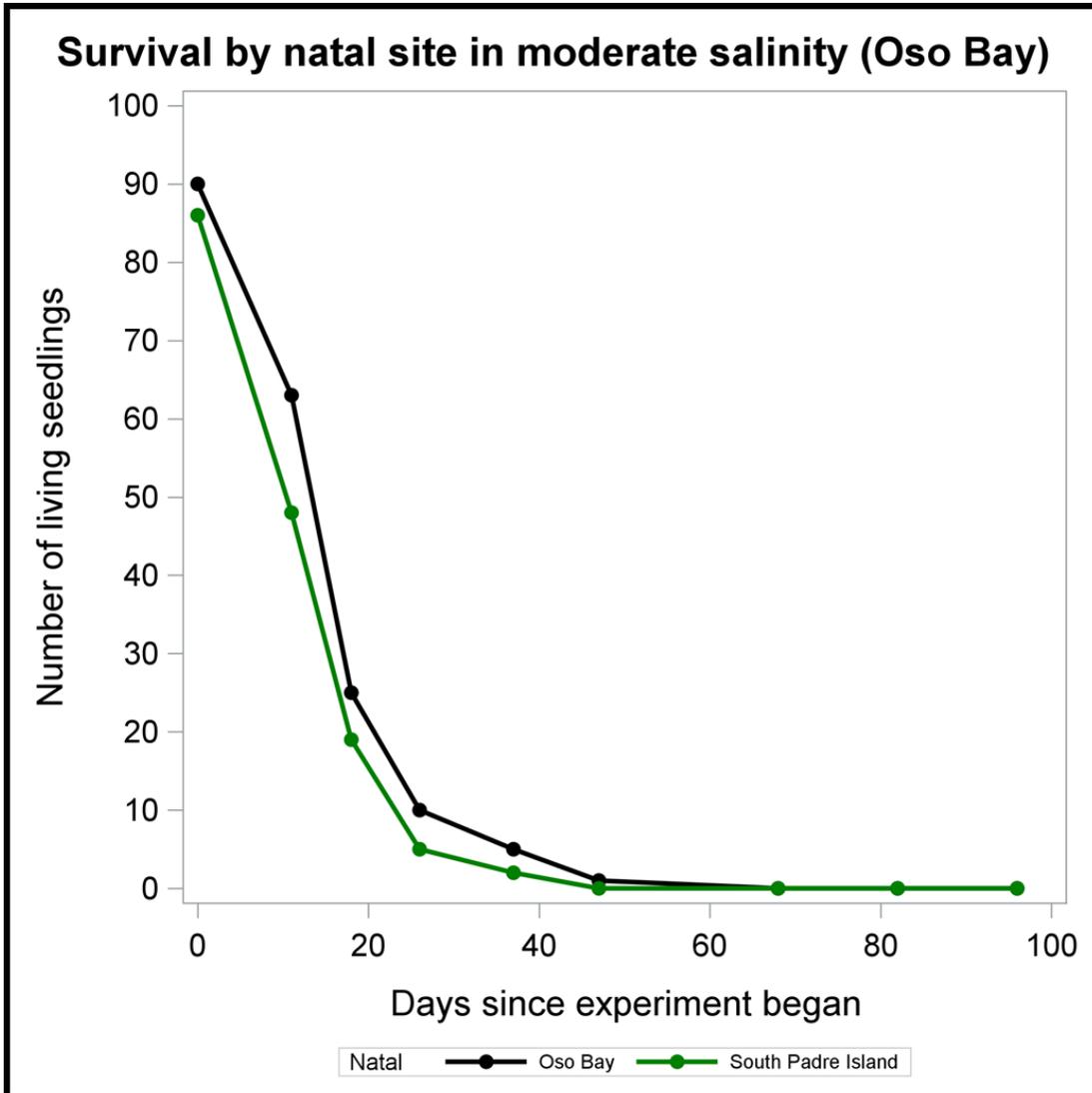


Figure 21: The number of surviving seedlings over time at the moderate salinity site (Oso Bay) based on seedling natal site: Oso Bay (black) or South Padre Island (green).

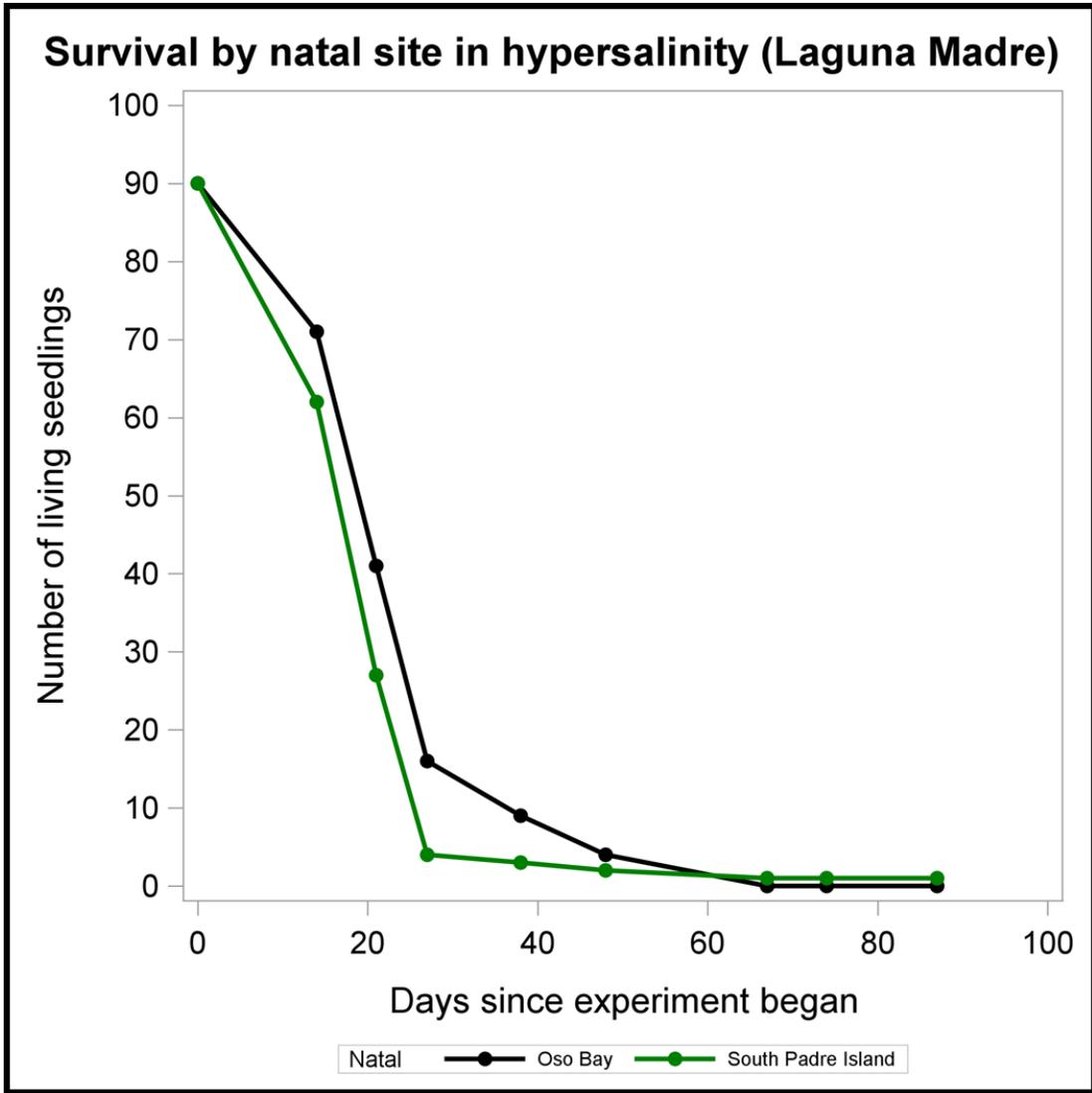


Figure 22: The number of surviving seedlings over time at the hypersaline site (upper Laguna Madre) based on seedling natal site, Oso Bay or South Padre Island.

Study 2: Observational study of naturally occurring seedlings

Model selection for random effects and fixed effects was based on AICc values and followed the procedure outlined in Goldstein (2016). For random effects (time; the number of days since the study began), an auto-regressive model was the best fit for seedling density, leaf count and stem count, while random slope model was the best fit for seedling height. For fixed effects (field site and habitat type), the quadratic model was the best fit for all variables. An auto-regressive model for random effects demonstrates serial correlation, or timepoints closest to one another are most correlated compared to more distant timepoints; the random slope model demonstrates that time has a different effect on each group (eight field x habitat combinations) resulting in different slopes. The quadratic effect shows that response variables change over time in a non-linear fashion.

Overall, it was found that hypersaline conditions reduced seedling survival and growth, and seedling success varied by habitat type. The moderate salinity site had higher seedling recruitment and survival rates, faster growth rates leading to taller seedlings, but less leaf and stem growth. The hypersaline site had low seedling recruitment and survival, slower growth rates and shorter seedlings, but more leaf and stem growth

Density

Field, habitat, and the field x habitat interaction were significant while time was not significant (Table 2). Seedling densities were relatively consistent over time, except during the flooding period. Time may not be significant in the model because density only changed for one of the 10 time-points and changes were only seen in five of the eight possible field x habitat combinations. Total recruitment was higher in Oso Bay with 285 total seedlings tagged than in

hypersaline Laguna Madre with 38 total seedlings tagged at the beginning of the study. At Oso Bay, the 'Inshore Succulent' habitat had the highest recruitment with a mean of 12 seedlings per 2x1 m plot (total 118 seedlings) while the 'Tidal Flats' had the lowest recruitment with a mean of 2 seedlings per plot (total 21 seedlings) (Figure 23). At Laguna Madre, the highest recruitment was under *A. germinans* canopy with a mean of 7.5 seedlings per plot (total 15 seedlings) while the lowest recruitment was in tidal flats and 'Inshore Succulents' with a mean of 0.5 seedlings per plot (Figure 24). At both field sites, vegetated habitats had higher seedling densities compared to tidal flats, indicating vegetation has facilitative effects on seedling recruitment.

Seedling densities were relatively consistent for the first three months of the study (June-August 2017), until the 5-week flooding period caused by Hurricane Harvey greatly decreased seedling density at Oso Bay in all habitats (Figure 23). Of the 275 living seedlings before the flooding event, only 137 survived (49.8%) at Oso Bay immediately after the flooding (141 days into the study); under *A. germinans* canopy cover was the lowest survival rate (19.1%) with a decrease in density from a mean of 9.5 to 2 seedling per plot. The Laguna Madre site saw a small decrease in seedling density (Figure 24). Of the 26 living seedlings before the flooding event, 24 survived (92.3%); under *A. germinans* canopy cover was the only habitat with significant changes in seedling density, but there was a lag in mortality compared to Oso Bay (Figure 23). Seedlings in this habitat at Laguna Madre died a few weeks after floods receded as compared to during the flooding event, like seedlings at Oso Bay. Seedling density decreased from a mean of 6 to 2 seedlings per plot, a 36% survival rate a few weeks after the flooding event.

Seedling densities remained consistent across all habitats at both field sites after the flooding period. Overall, 48.8% of seedlings at Oso Bay survived the flooding event while 92.3% of seedlings at Laguna Madre survived.

Source	DF	F-value	P-value
Day	631	0.38	0.5355
Field	64	47.05	<.0001
Habitat	64	18.84	<.0001
Field x Habitat	64	12.97	<.0001

Table 2: The Type III Tests of random and fixed effects for mean seedling density.

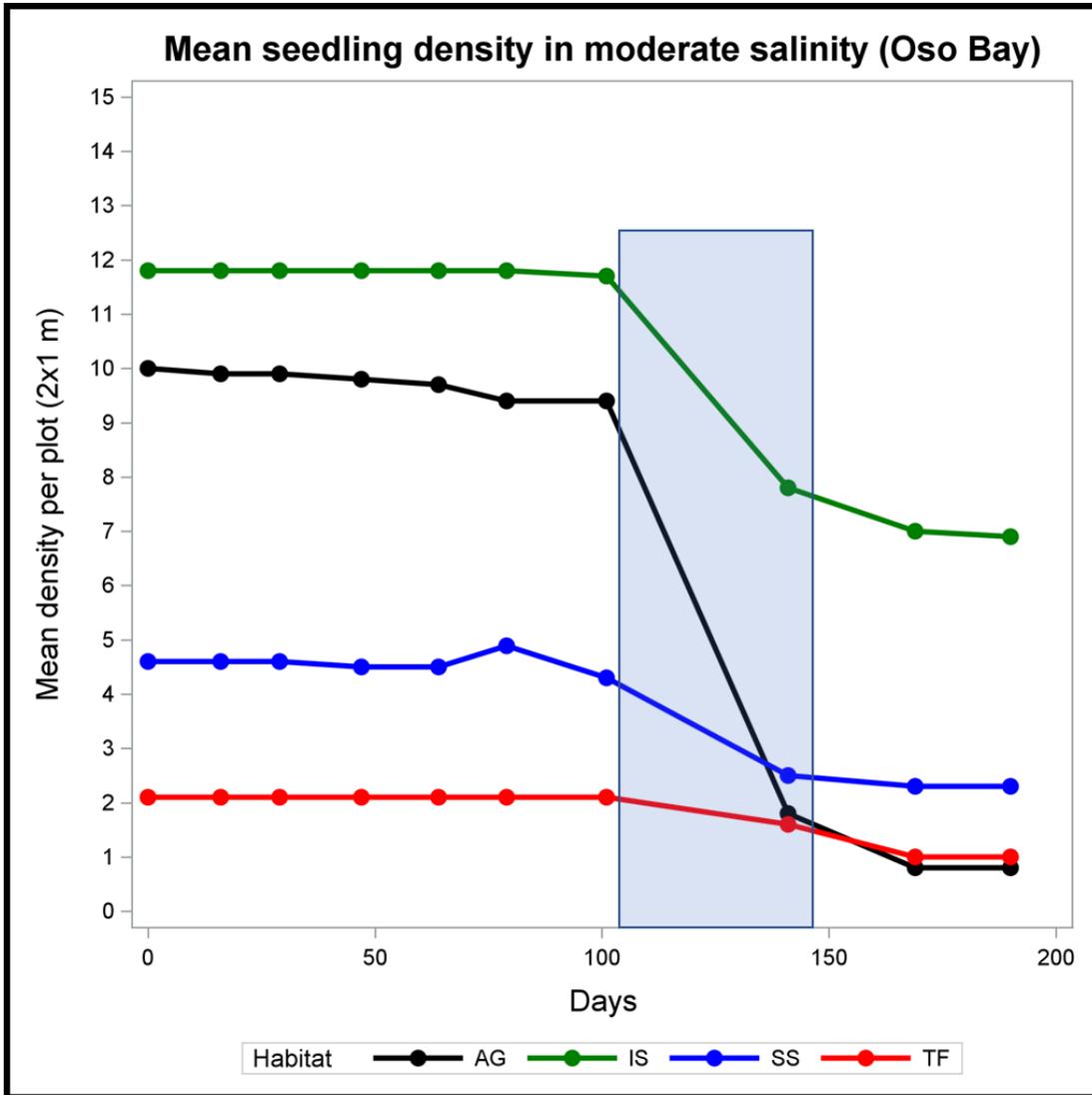


Figure 23: Mean seedling density for habitats in moderate salinity (Oso Bay). The blue box indicates the 5-week flooding period. (AG-*A. germinans* canopy cover, IS-inshore succulents, SS-shoreline succulents, TF-tidal flats).

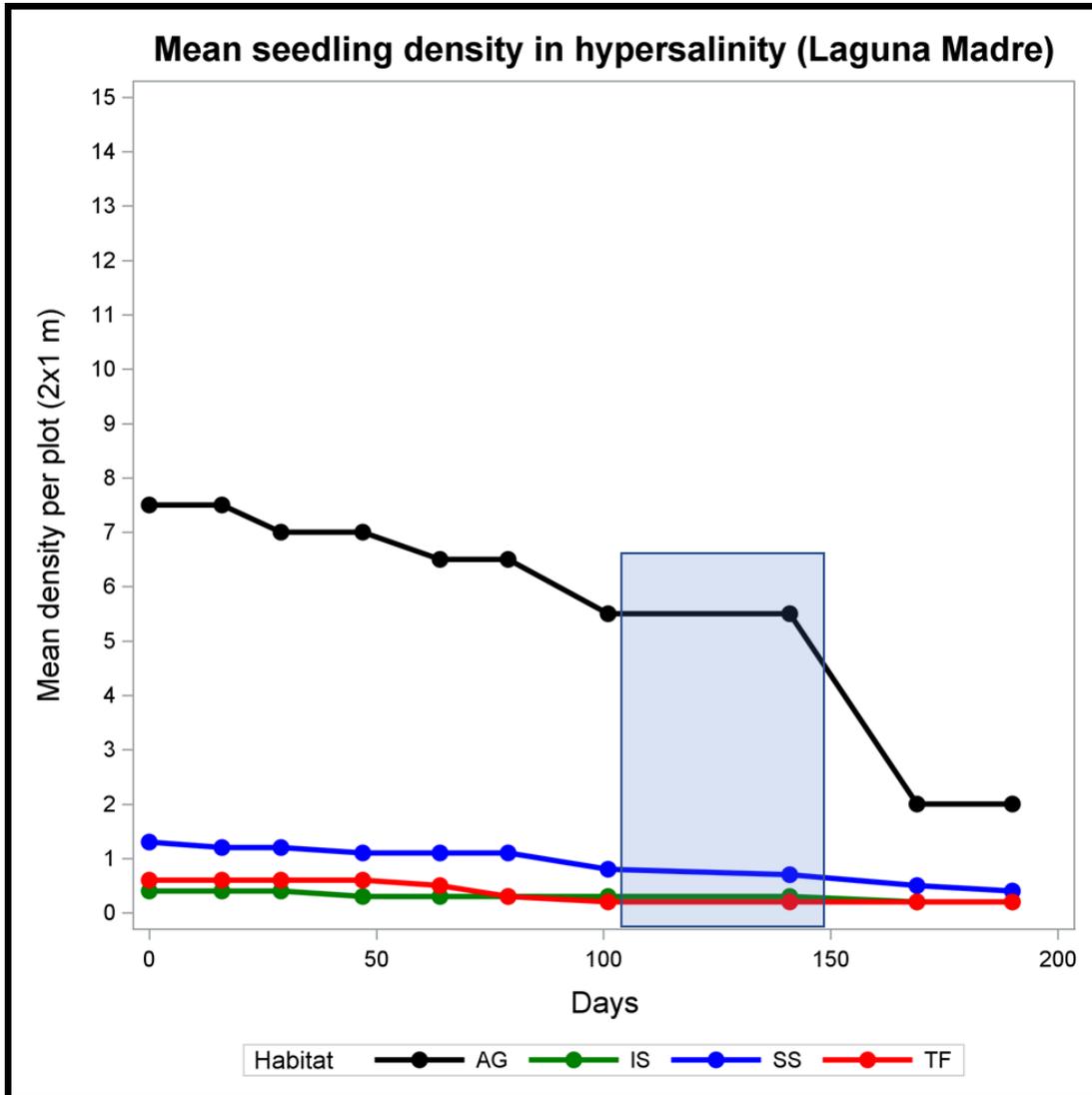


Figure 24: Mean seedling density for habitats in hypersalinity (Laguna Madre). The blue box indicates the 5-week flooding period. (AG-*A. germinans* canopy cover, IS-inshore succulents, SS-shoreline succulents, TF-tidal flats).

Height

Mean seedling height was the only variable where random slope was the best model for random effects instead of auto-regression. The random slope model shows that time has different effects on seedling heights, resulting in varying slopes. For the fixed effects, three models (Linear regression with factors and interaction; Linear regression with factors, interaction and

interactions with time; or Quadratic effects) were within two AICc points and considered comparable; the quadratic model was selected because graphing residuals showed a curve in slopes over time.

Field, habitat type, their interaction term, and time were all significant for mean seedling height (Table 3). At Oso Bay, seedlings in all habitats had a positive growth rate over time, with seedlings in the ‘Shoreline Succulent’ habitat attaining the greatest height during the 200 days of the study (Figure 25). Initial mean heights ranged from 14.6-19.9 cm. Seedlings at hypersaline Laguna Madre had variable growth across habitats, the ‘Shoreline Succulent’ habitat was the only habitat to have an overall positive growth rate (Figure 26). Initial mean heights were 10.2-18.5 cm, with seedlings in the ‘Inshore Succulent’ habitat being the tallest.

During the 5-week flooding period, many shorter seedlings died from inundation while taller seedlings survived. At Oso Bay, seedlings were on average tallest in the ‘Shoreline Succulent’ habitat and remained so through the flooding event, averaging 27 cm tall immediately after the flooding (Figure 25). Seedlings under *A. germinans* canopy had the greatest shift in mean height from 18.2 cm immediately after flooding, to 32 cm a few weeks later, and were on average equally as tall as seedlings in the ‘Shoreline succulent’ habitat. At Laguna Madre, the ‘Inshore Succulent’ habitat was tallest with an average height of 19.3 cm just before the flooding event (Figure 26). After floods receded, the ‘Shoreline succulent’ habitat had the greatest shift in height, from 17.5 cm to 23.6 cm and surpassed the mean height of seedlings in the ‘Inshore succulent’ habitat.

Statistical analysis was not done for maximum seedling height (the most successful individuals) but trends show evidence of competition and facilitation. At Oso Bay, the tallest seedlings were under *A. germinans* canopy cover, followed by both succulent marsh forb

habitats, and then tidal flats having the shortest seedlings (Figure 27). Through the flooding event, all maximum seedling heights increased except for those under *A. germinans* canopy cover, which remained relatively unchanged. The tallest seedlings in both succulent marsh forb habitats exceeded the height of seedlings under *A. germinans* canopy cover. After the flooding event, all maximum seedling heights increased and height in the tidal flats was similar to height under *A. germinans* canopy cover (Figure 27). This shows that adult *A. germinans* had competitive effects on seedlings as shading limited growth. and succulent marsh forbs had facilitative effects on seedlings since they had higher growth rates. Mean heights under *A. germinans* canopy cover dropped during the flooding period, then had a drastic increase afterward. Since the tallest seedlings in this habitat had very little growth during the flooding, this would confirm that the shift in mean height was due to shorter seedlings dying and not overall growth for most seedlings.

At Laguna Madre, the tallest seedlings were in the ‘Shoreline succulent’ habitat, followed by ‘Inshore succulent’, then under *A. germinans* canopy cover, and then tidal flats having the shortest seedlings (Figure 28). During the flood, all habitats had little to no change in maximum height, except for a small increase in the ‘Shoreline succulent’ habitat. After the flooding event, seedlings in the ‘Shoreline Succulent’ habitat continued to grow at a greater rate than seedlings in other habitats. Here, seedlings were facilitated by all vegetation, but more so in the shoreline marsh forbs. Seedling mortality from the flooding event was low and trends in maximum height are similar to mean height.

Source	DF	F-value	P-value
Day	45	18.94	<.0001
Field	45	16.68	0.0002
Habitat	45	8.05	0.0002
Field x Habitat	45	4.81	0.0055

Table 3: The Type III Tests of random and fixed effects for mean seedling height.

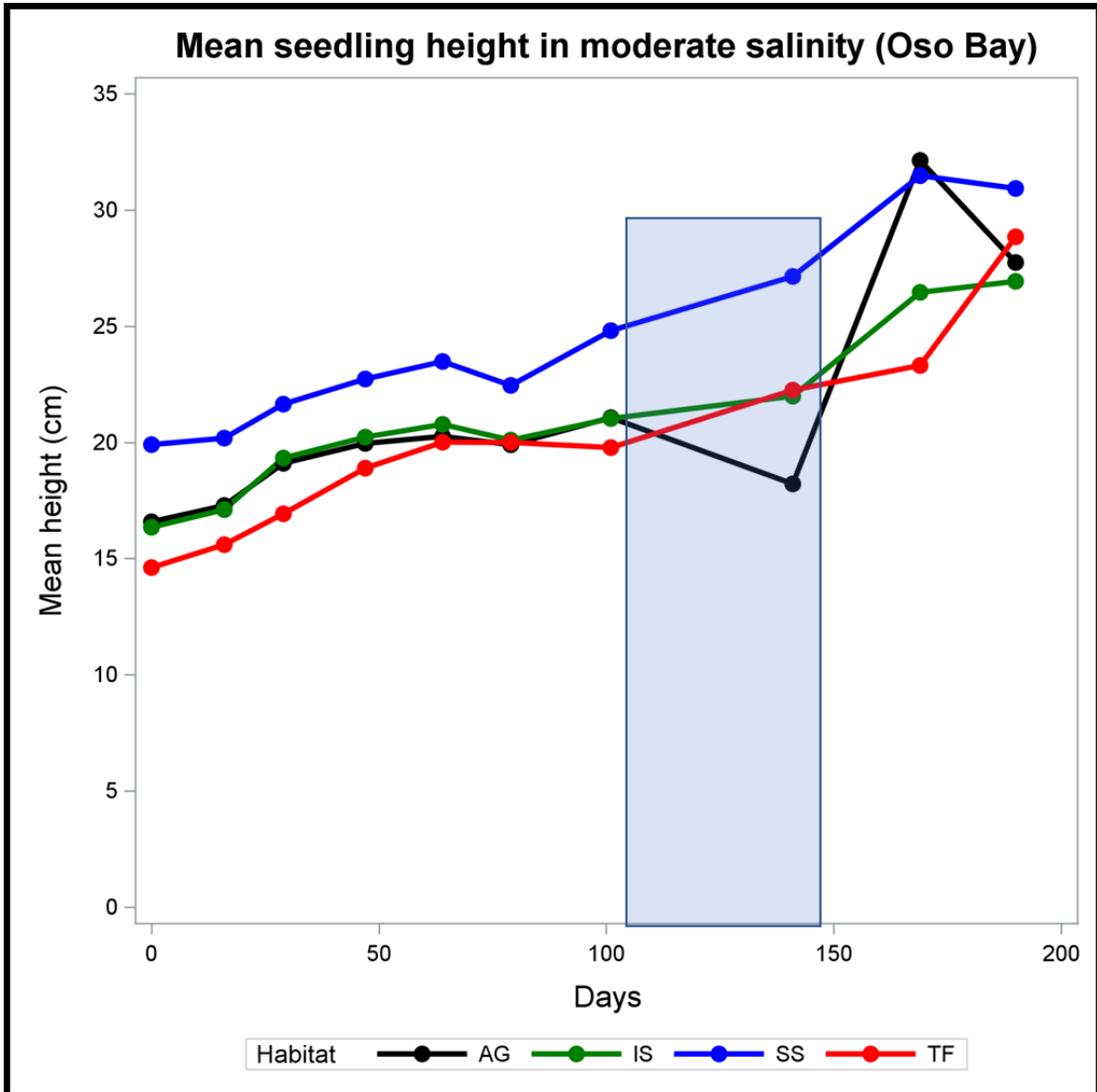


Figure 25: Mean seedling height for habitats in moderate salinity (Oso Bay). The blue box indicates the 5-week flooding period. (AG-*A. germinans* canopy cover, IS-inshore succulents, SS-shoreline succulents, TF-tidal flats).

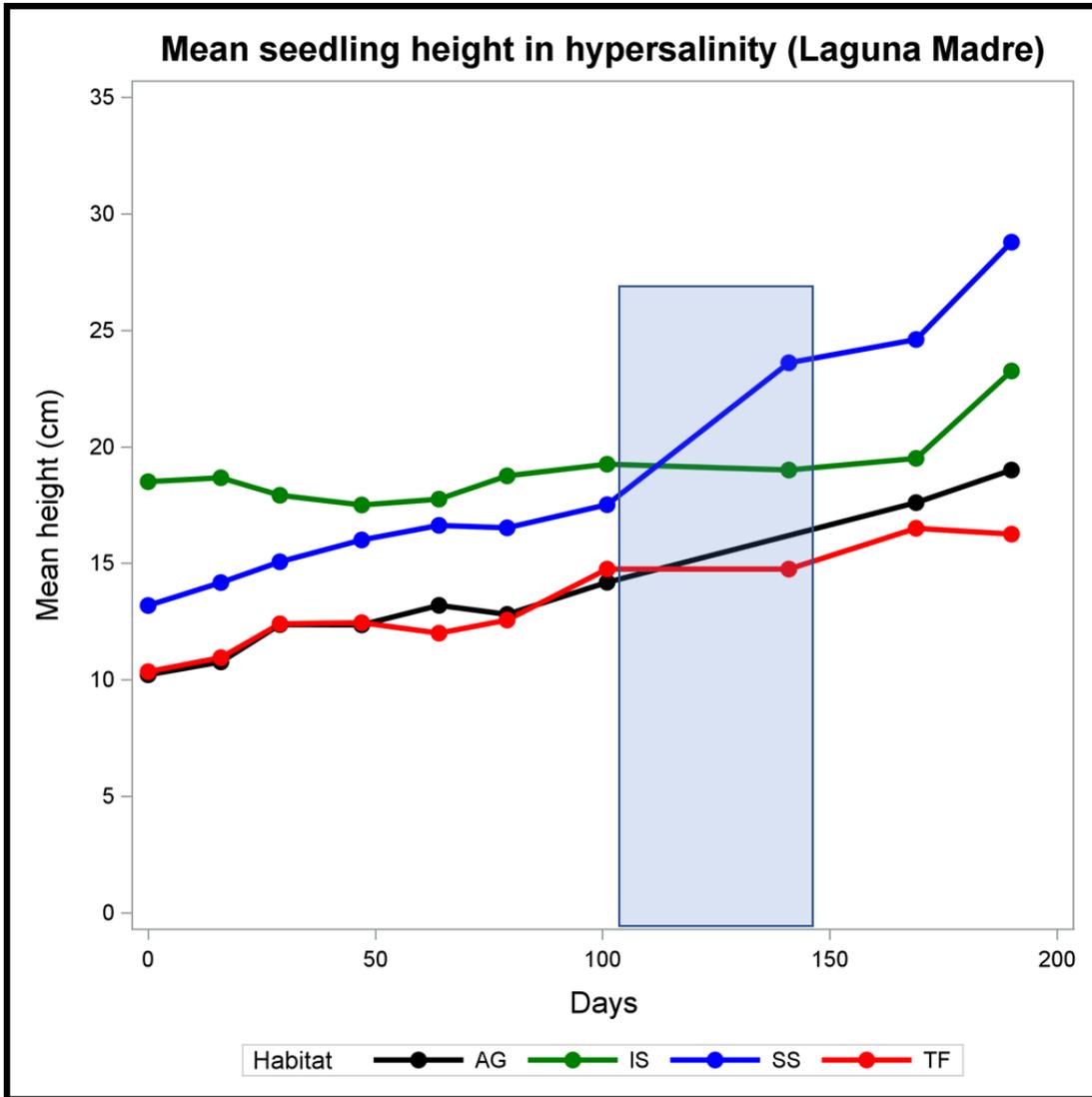


Figure 26: Mean seedling height for habitats in hypersalinity (Laguna Madre). The blue box indicates the 5-week flooding period. (AG-*A. germinans* canopy cover, IS-inshore succulents, SS-shoreline succulents, TF-tidal flats).

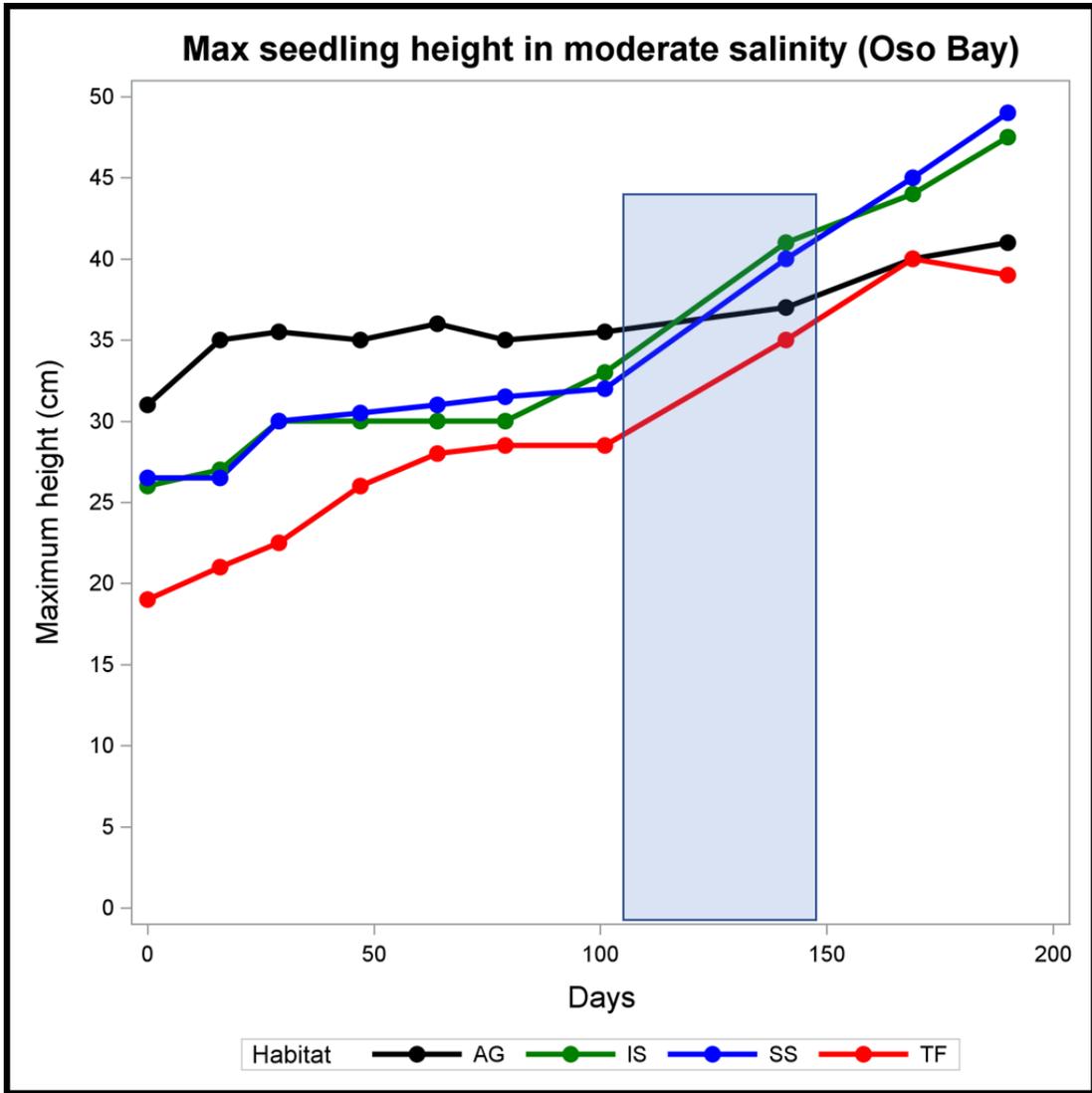


Figure 27: Maximum seedling height for habitats in moderate salinity (Oso Bay). The blue box indicates the 5-week flooding period. (AG-*A. germinans* canopy cover, IS-inshore succulents, SS-shoreline succulents, TF-tidal flats).

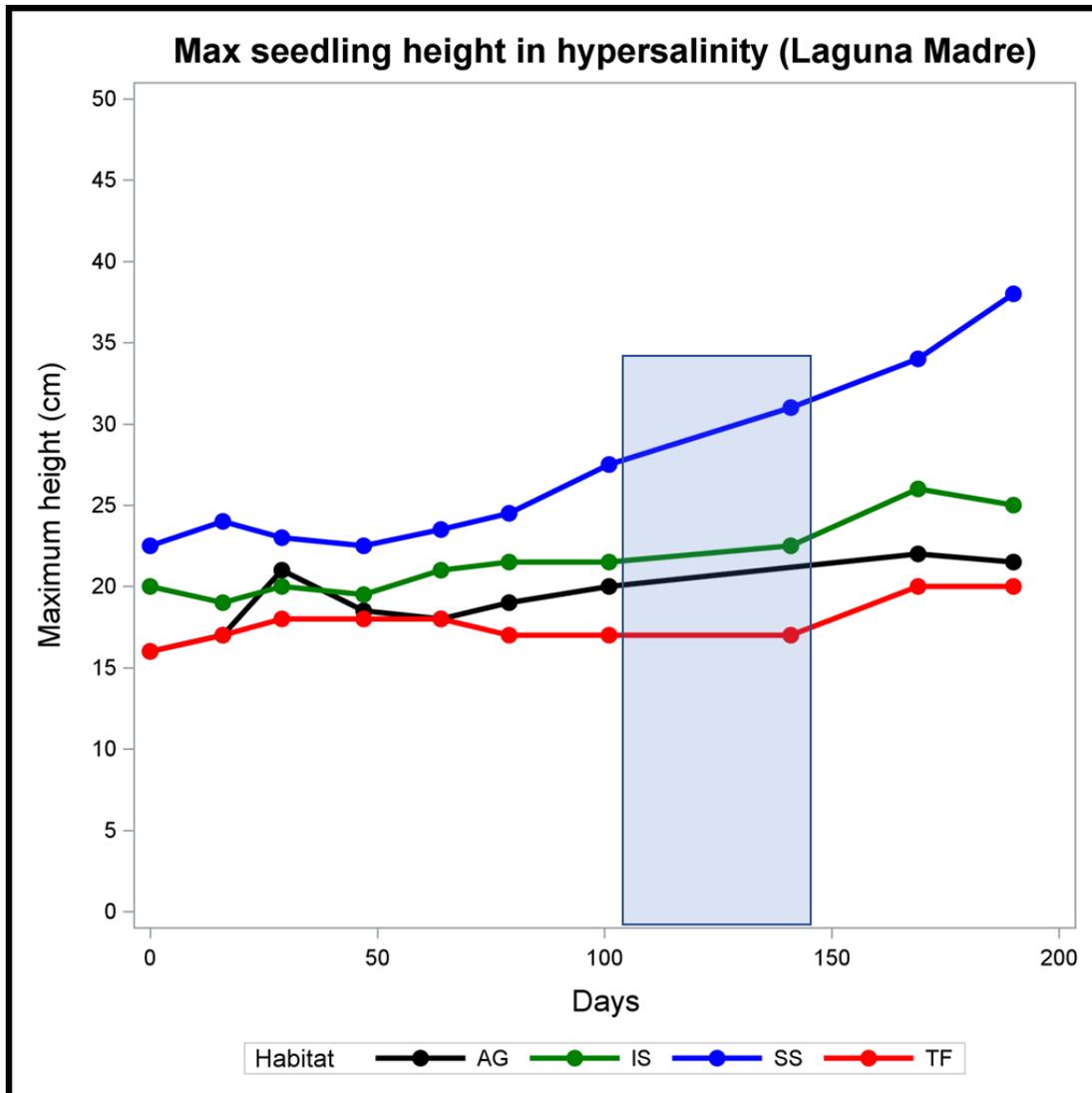


Figure 28: Maximum seedling height for habitats in hypersalinity (Laguna Madre). The blue box indicates the 5-week flooding period. (AG-*A. germinans* canopy cover, IS-inshore succulents, SS-shoreline succulents, TF-tidal flats).

Mean leaf count

Habitat and the field x habitat interaction had significant effects on the number of leaves, while field and time did not (Table 4). At Oso Bay, seedlings in all habitats except tidal flats had relatively consistent counts of 4.8-5.8 mean leaves until the flooding period. Seedlings in the tidal flats had a mean of 9.7 leaves initially and leaf count doubled to 20.8 leaves in the first three months of the study (June-August 2017) (Figure 29). At Laguna Madre, leaf count was

variable across habitats (Figure 30). Only seedlings in the 'Shoreline Succulent' habitat had linear leaf growth over time. Initial counts were between 3.3-15.5 mean leaves with the 'Inshore Succulent' habitat having the highest mean leaf count while seedlings under *A. germinans* canopy had the lowest mean leaf count. Generally, mean leaf counts are somewhat higher at the hypersaline Laguna Madre, but are not statistically different.

During the flooding period, many seedlings were defoliated at Oso Bay and leaf counts dropped for all habitats except the 'Inshore Succulents' (Figure 29). About four weeks after floods receded, leaf count began to increase as seedlings produced new leaf pair to continue photosynthesizing. Seedlings under *A. germinans* canopy cover had the greatest rate of leaf growth, increasing from a mean of 0.9 to 7.8 leaves. At Laguna Madre, flooding had variable effects on leaf count (Figure 30). Seedlings in both succulent habitat types had an increase in leaf count during the flooding, seedlings in '*A. germinans* canopy cover' had little to no change, and seedlings in the tidal flats saw a decrease in leaf count. Through the flooding event, seedlings in the 'Inshore Succulents' had a large increase in the mean leaf count from 13.5 to 22 leaves, then to 43 leaves in the following six weeks. Seedlings in the 'Shoreline succulent' habitat had a similar increase during the flooding event, from 13.3 to 23.4 leaves, but declined in the time after the flooding event before recovering. Seedlings in the tidal flats also had an increase in mean leaf count directly after the flooding, from 6 to 14.5 leaves in several weeks.

Source	DF	F-value	P-value
Day	405	1.93	0.1650
Field	45	2.37	0.1309
Habitat	45	5.73	0.0021
Field x Habitat	45	7.46	0.0004

Table 4: The Type III Tests of random and fixed effects for mean seedling leaf count.

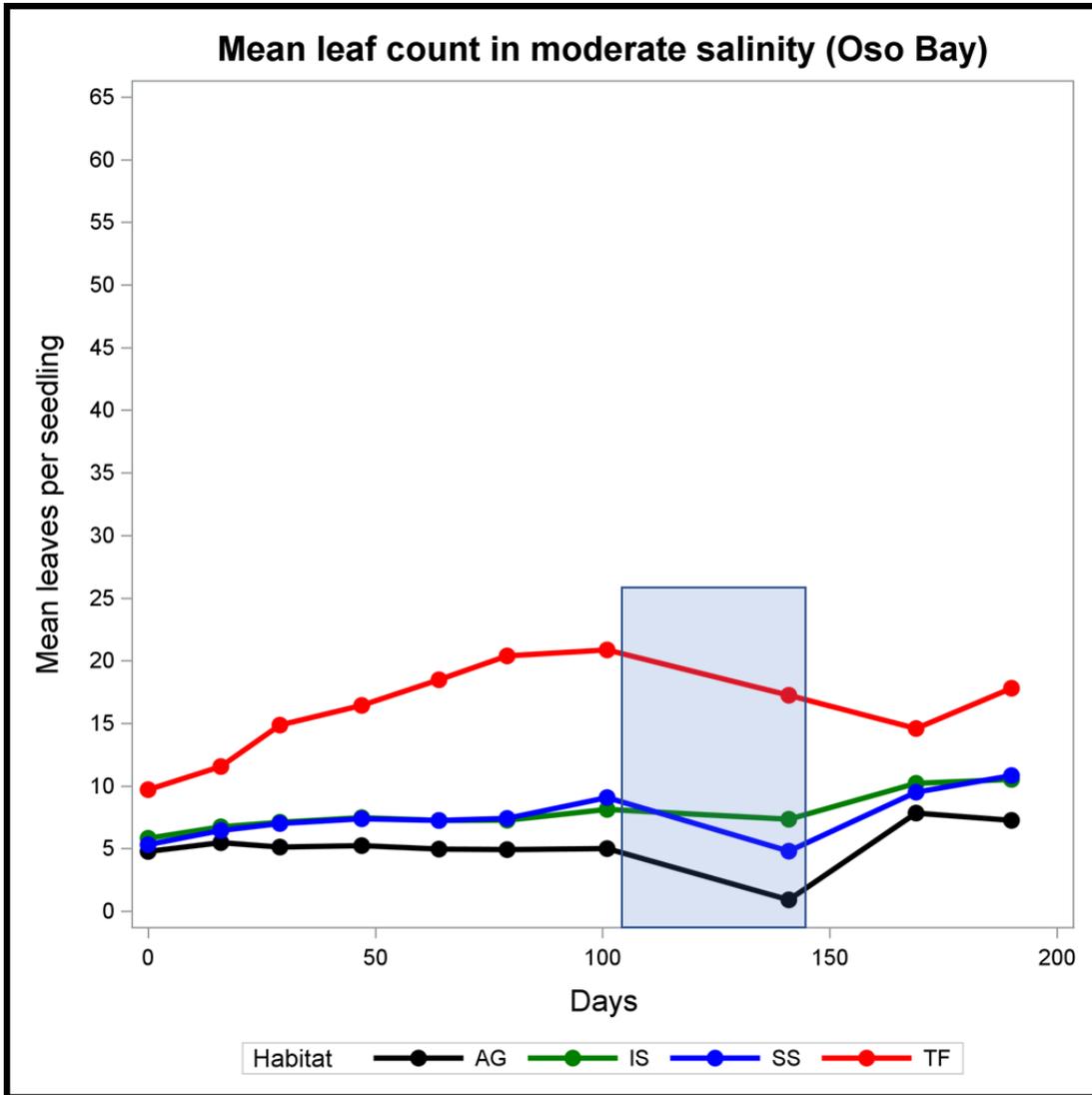


Figure 29: Mean seedling leaf count for habitats in moderate salinity (Oso Bay). The blue box indicates the 5-week flooding period. (AG-*A. germinans* canopy cover, IS-inshore succulents, SS-shoreline succulents, TF-tidal flats).

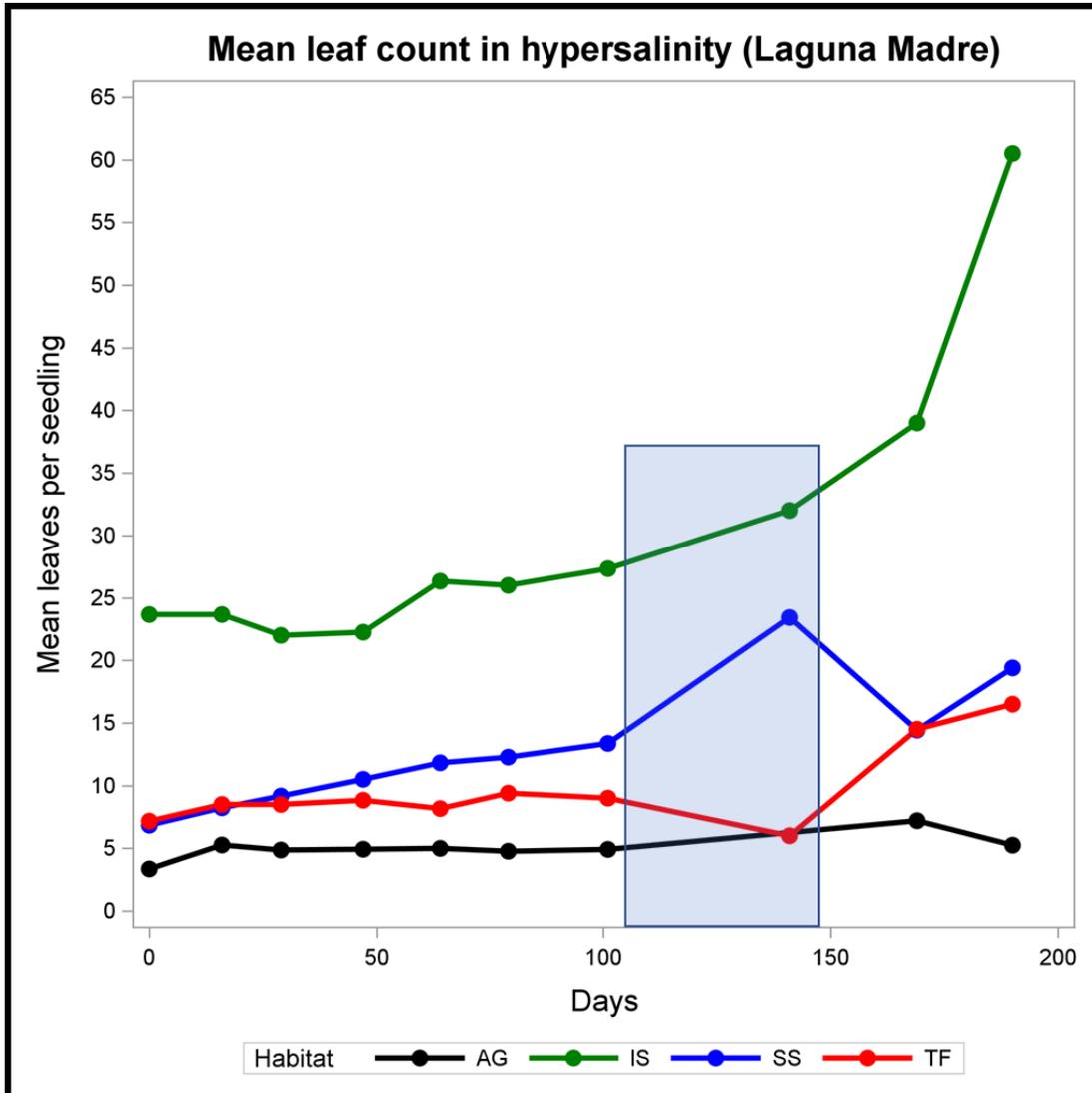


Figure 30: Mean seedling leaf count for habitats in hypersalinity (upper Laguna Madre). The blue box indicates the 5-week flooding period. (AG-*A. germinans* canopy cover, IS-inshore succulents, SS-shoreline succulents, TF-tidal flats).

Stem count

Habitat and the field x habitat interaction were significant while field and time were not significant (Table 5). At Oso Bay, seedling in all habitats except tidal flats consistently had 1 stem, until after the flooding period (Figure 31). Seedling in the tidal flats had an initial mean of 1.4 stems, which doubled to three stems in the first three months of the study (June-August 2017)

(Figure 31), a similar trend was seen in mean leaf count. At Laguna Madre, stem count was variable across habitats (Figure 32). Only seedlings in the 'Shoreline Succulent' habitat had generally a linear growth of stems over time. Initial mean stem counts were between 1.1-4.7 stems with the 'Inshore Succulent' habitat having the highest mean stem count and seedlings in the '*Avicennia* canopy cover' habitat had the lowest mean stem count.

During the flooding period, there was no change in stem count at Oso Bay (Figure 31). After floods receded, all habitats saw an increase in means stem count in the following weeks with seedlings under *A. germinans* canopy cover having the greatest change, from 1-2.8 stems. Seedlings in the tidal flats had little change in mean stem count immediately after the flooding, but later increased from 3.1-4.6 stems. At the hypersaline Laguna Madre, flooding had variable effects on mean stem count; seedlings in 'Inshore succulent' and tidal flat habitats declined, seedlings under *A. germinans* canopy cover had little change, and seedlings in 'Shoreline Succulents' had a slight increase (Figure 32). After the flooding, seedlings in all habitats, except under *A. germinans* canopy cover, saw an increase in mean stem count, a similar trend was seen for mean leaf count. Seedlings in the 'Inshore succulent' and tidal flat habitats had the greatest rate of change immediately after flooding, then 'Tidal flats' slightly declined from three stems to 2.5 stem. Seedlings in the 'Inshore succulent' habitat continued to drastically increase stem count after the flooding and had a mean of eight stems at the end of the study.

Source	DF	F-value	P-value
Day	402	1.99	0.1593
Field	46	3.30	0.0758
Habitat	46	2.97	0.0413
Field x Habitat	46	3.25	0.0301

Table 5: The Type III Tests of random and fixed effects for mean seedling stem count.

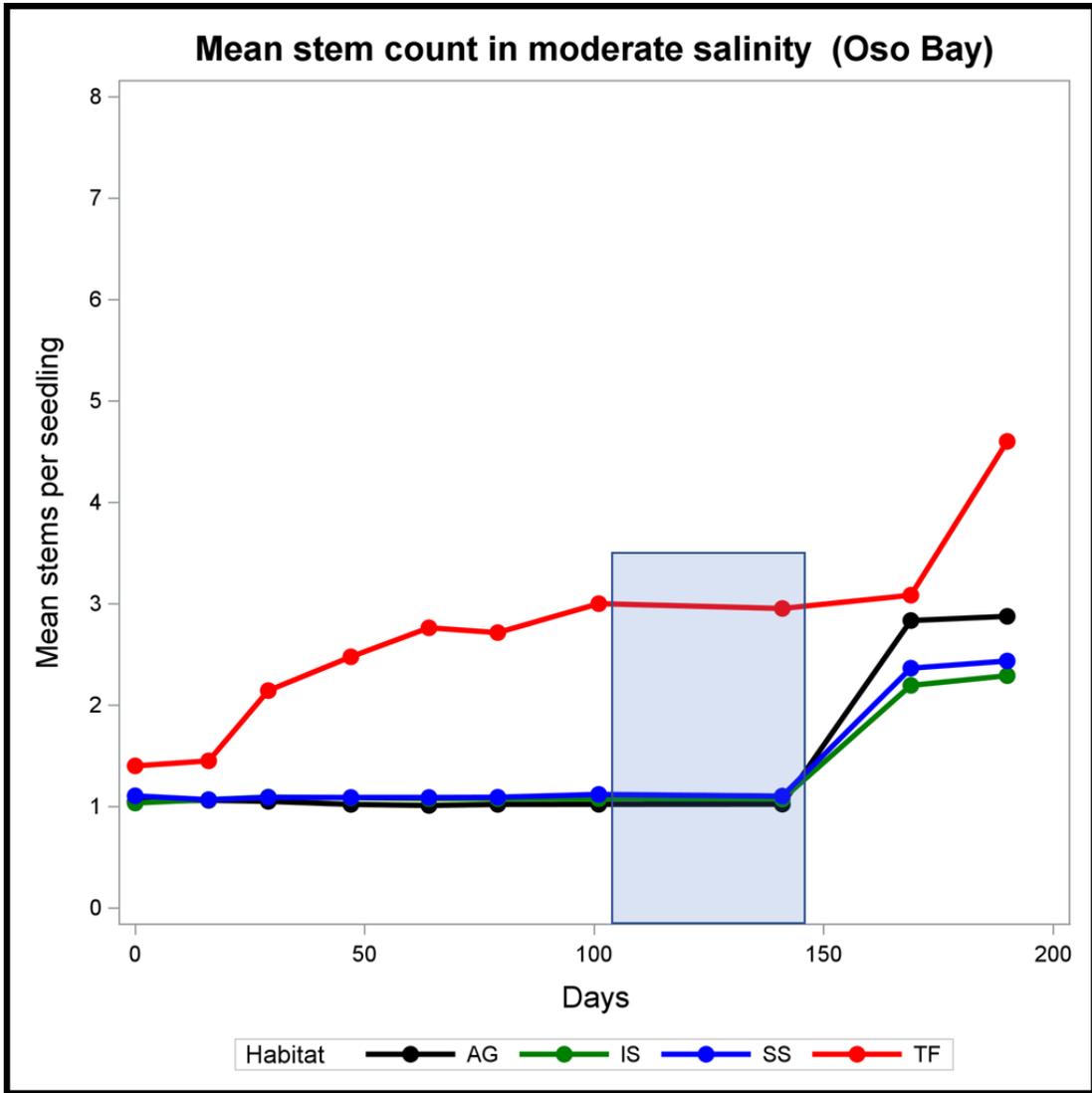


Figure 31: Mean seedling stem count for habitats in moderate salinity (Oso Bay). The blue box indicates the 5-week flooding period. (AG-*A. germinans* canopy cover, IS-inshore succulents, SS-shoreline succulents, TF-tidal flats).

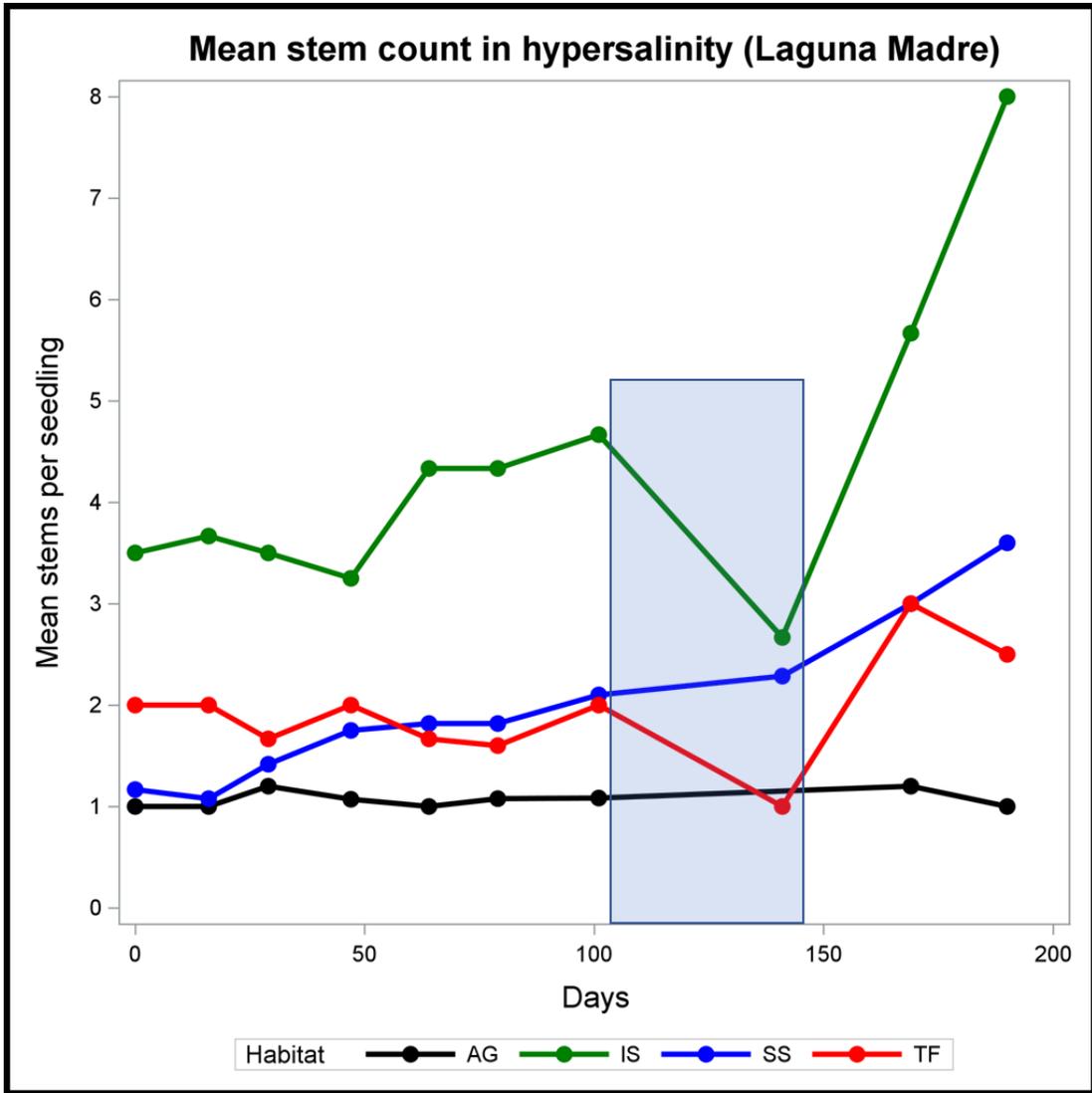


Figure 32: Mean seedling stem count for habitats in hypersalinity (upper Laguna Madre). The blue box indicates the 5-week flooding period. (AG-*A. germinans* canopy cover, IS-inshore succulents, SS-shoreline succulents, TF-tidal flats).

Study 3: Observational study of reproductive output

Overall, there was no significant difference in the total number of reproductive units or the dimensions (length in cm x width in cm) of propagules between the field sites. There also was no significant difference in the total number of buds, flowers, fruits, and propagules per branch between the field sites.

By total units produced

A separate MANOVA was conducted on the total number of reproductive units per branch; there was no significant difference in units per branch between the moderate salinity and hypersaline sites (Table 6). Branches at Oso Bay had practically the same number of reproductive units as branches at hypersaline Laguna Madre. Although the moderate salinity site had higher counts over time, the declining slopes were very similar (Figure 33).

Oso Bay had a peak number of buds and flowers in June with a mean of 31.7 buds and 0.14 flowers per branch, then a mean of 23.38 fruits per branch in August, a peak of propagules in September at a mean of 11.63 per branch, and a final mean of 3.98 propagules per branch in December. Laguna Madre peaked in June for bud and flower counts with a mean of 33.6 buds and 1.8 flowers per branch, then 16.2 fruits in August. Propagules peaked at the end of September with a mean of 5.2 per branch and a final count of 0.6 in December. It is likely that flower count was low compared to bud count because flowers are in bloom for just a day or two and become fruits within several days and data were taken in six-week increments. Propagules also could have declined from November to December due to maturing propagules falling from the parent tree for dispersal.

Source	DF	F-value	P-value
30 Jun	1	1.73	0.1904
04 Aug	1	0.86	0.3557
07 Sept	1	0.61	0.4369
28 Sept	1	0.13	0.7233
18 Nov	1	0.16	0.6888
10 Dec	1	1.24	0.2681
Wilk's Lambda	111	1.00	0.4318

Table 6: The Type III results for the mean reproductive units per branch between the two field sites, Oso Bay and Laguna Madre.

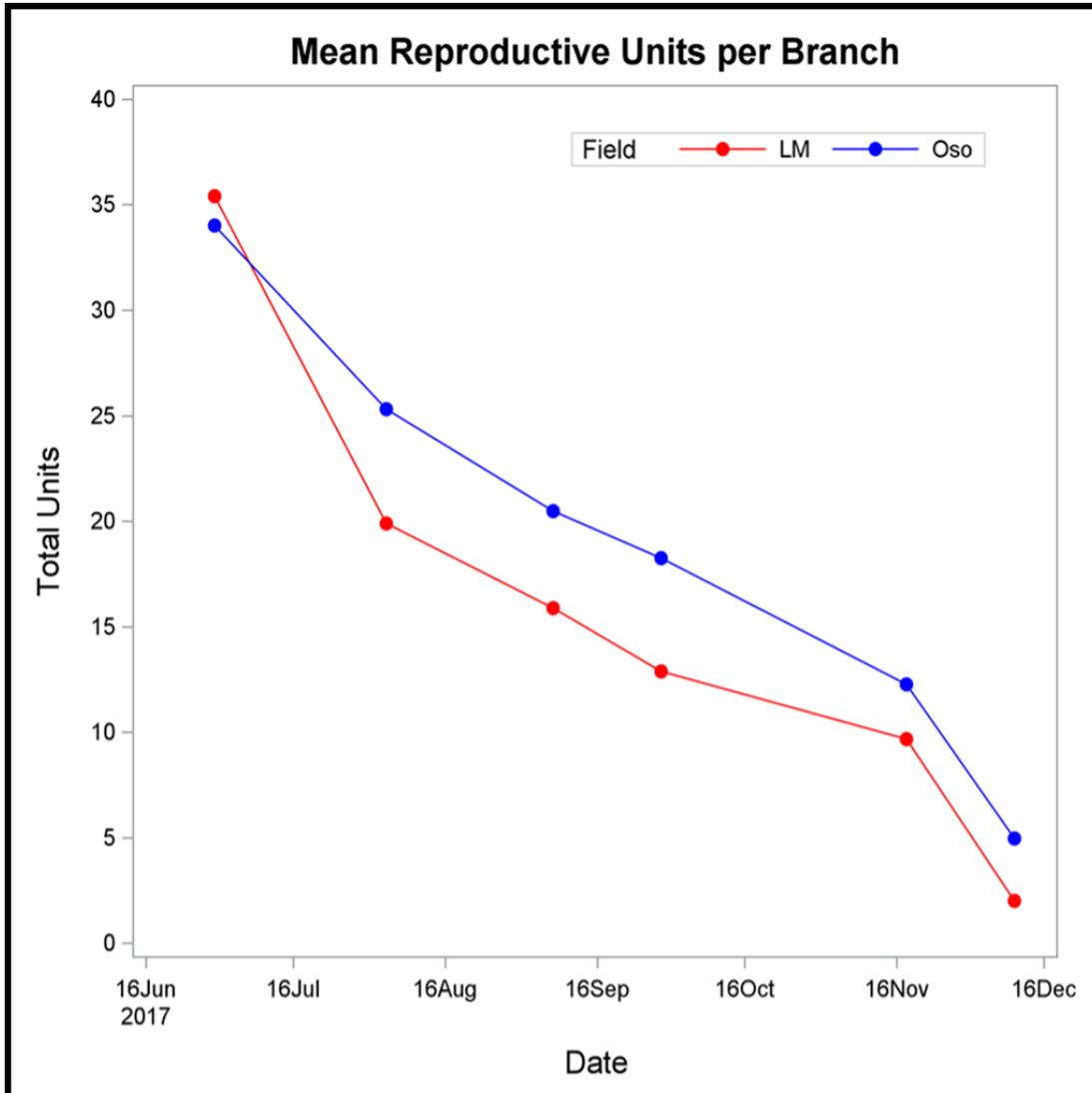


Figure 33: Mean total count of reproductive units per branch between the moderate salinity site (Oso Bay-blue) and the hypersaline site (Laguna Madre-red).

By reproductive stages

There was not a significant difference in mean bud count per branch of mature *A. germinans* in moderate salinity and hypersaline conditions (Table 7). Mean bud count per branch was initially slightly lower at the moderate salinity site in late June 2017, with 31 buds per branch and 33 buds respectively (Figure 34). Over time, bud count decreased at nearly the

same rate over a 5-week period, with a mean of 1.7 and 1.8 buds by August 2017, then no buds present at either field site by September 2017.

There was not a significant difference in mean flower count per branch in moderate salinity and hypersaline conditions (Table 8). Mean flower count per branch was slightly higher at Oso Bay than in Laguna Madre in June 2017, with 2.3 and 1.8 flowers respectively (Figure 35). Flower count decreased at nearly the same rate and were not statistically different (Table 8), but flowers were present for slightly longer time, until late-September 2017, at Oso Bay. Field notes indicate that pollinators were present in high numbers at both field sites during this time.

There was not a significant difference in mean fruit count per branch of mature *A. germinans* in moderate salinity and hypersaline conditions (Table 9). Fruits were first noted in beginning of August, with Oso Bay having slightly higher fruit counts than Laguna Madre, (23.3 and 18 fruits respectively). Fruits declined at a similar rate between time points, resulting in 19.6 and 15.8 fruits in September and then were no longer present at the end of November (Figure 36).

Fruits mature into propagules, the final developmental stage of the embryo on the parent tree. Although there was a slight lag in the timing of propagule maturation at Laguna Madre, there was not a significant difference in mean propagule count per branch in moderate salinity and hypersaline conditions (Table 10). A few propagules were first noted at the moderate salinity site in August, while the first at Laguna Madre appeared in late September (Figure 37). September was the peak for propagule count at Oso Bay (mean 12 propagules per branch) while November was the peak for Laguna Madre (mean 9 propagules per branch). Propagule count per branch increased at similar rates in September and declined in December.

Source	DF	F-value	P-value
30 June	1	0.58	0.4478
04 Aug	1	0.05	0.8249
07 Sept	1	0.92	0.3382
Wilks Lambda	129	0.61	0.6110

Table 7: The Type III results for the mean bud count per branch for the time points in which buds were present.

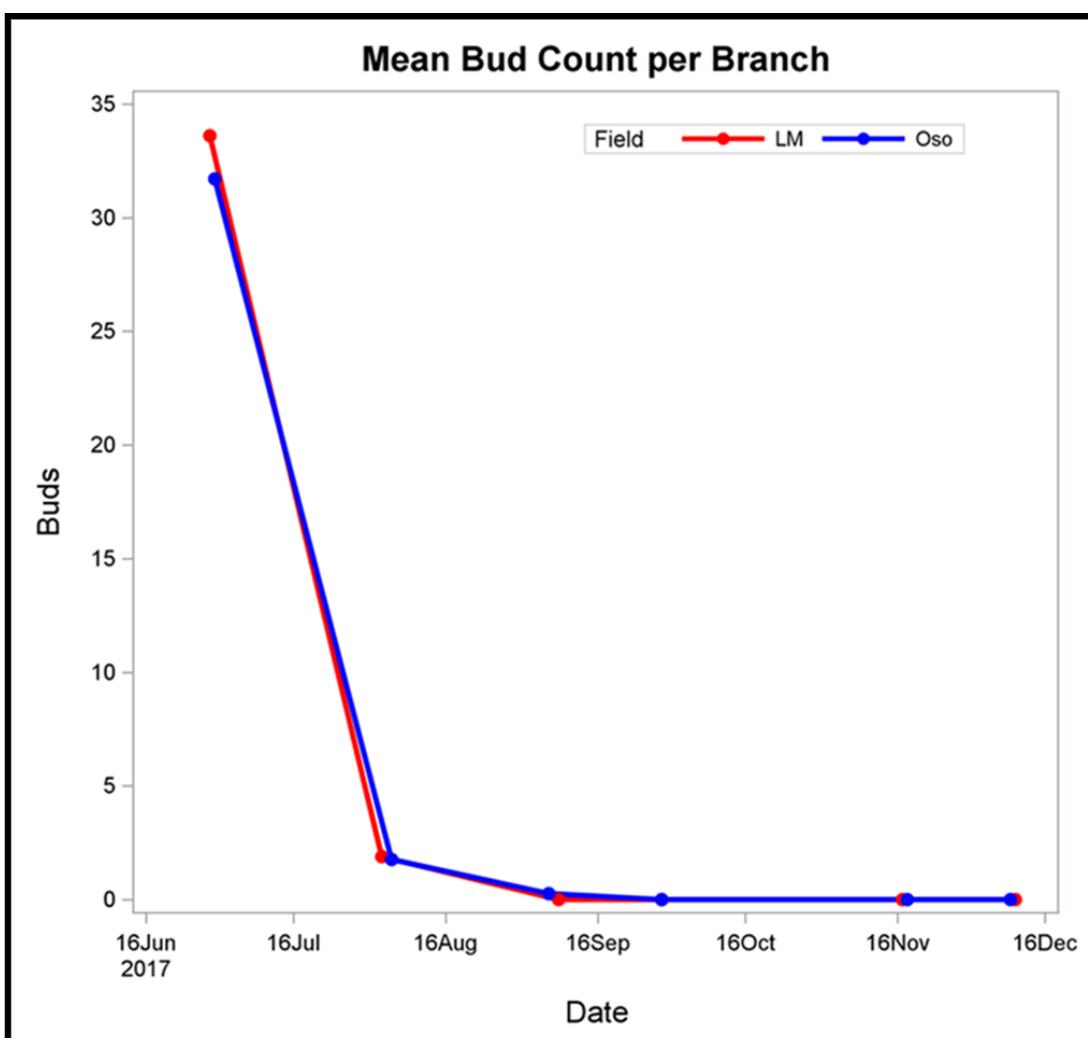


Figure 34: Mean bud count per branch between the moderate salinity site (Oso Bay-blue) and the hypersaline site (Laguna Madre-red).

Source	DF	F-value	P-value
30 June	1	0.06	0.7999
04 Aug	1	0.30	0.5855
07 Sept	1	0.06	0.8014
Wilks Lambda	129	0.15	0.9320

Table 8: The Type III results for the mean flower count per branch for the time points in which flowers were present.

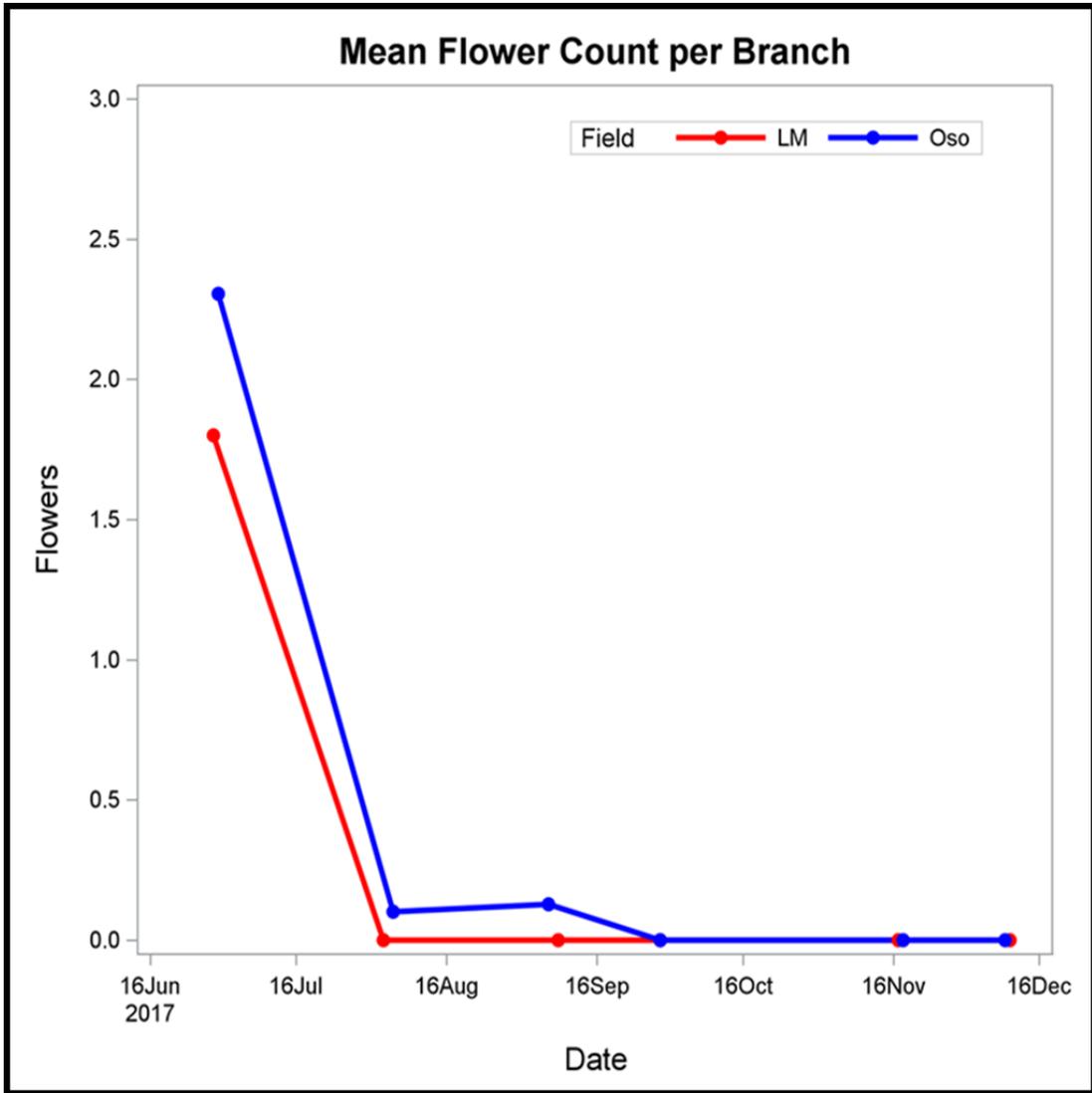


Figure 35: Mean flower count per branch between the moderate salinity site (Oso Bay-blue) and the hypersaline site (Laguna Madre-red).

Source	DF	F-value	P-value
04 Aug	1	1.02	0.3150
07 Sept	1	0.91	0.3433
29 Sept	1	0.65	0.4222
18 Nov	1	0.06	0.8105
10 Dec	1	0.39	0.5339
Wilk's Lambda	112	0.52	0.7627

Table 9: The Type III results for the mean fruit count per branch for the time points in which fruits were present.

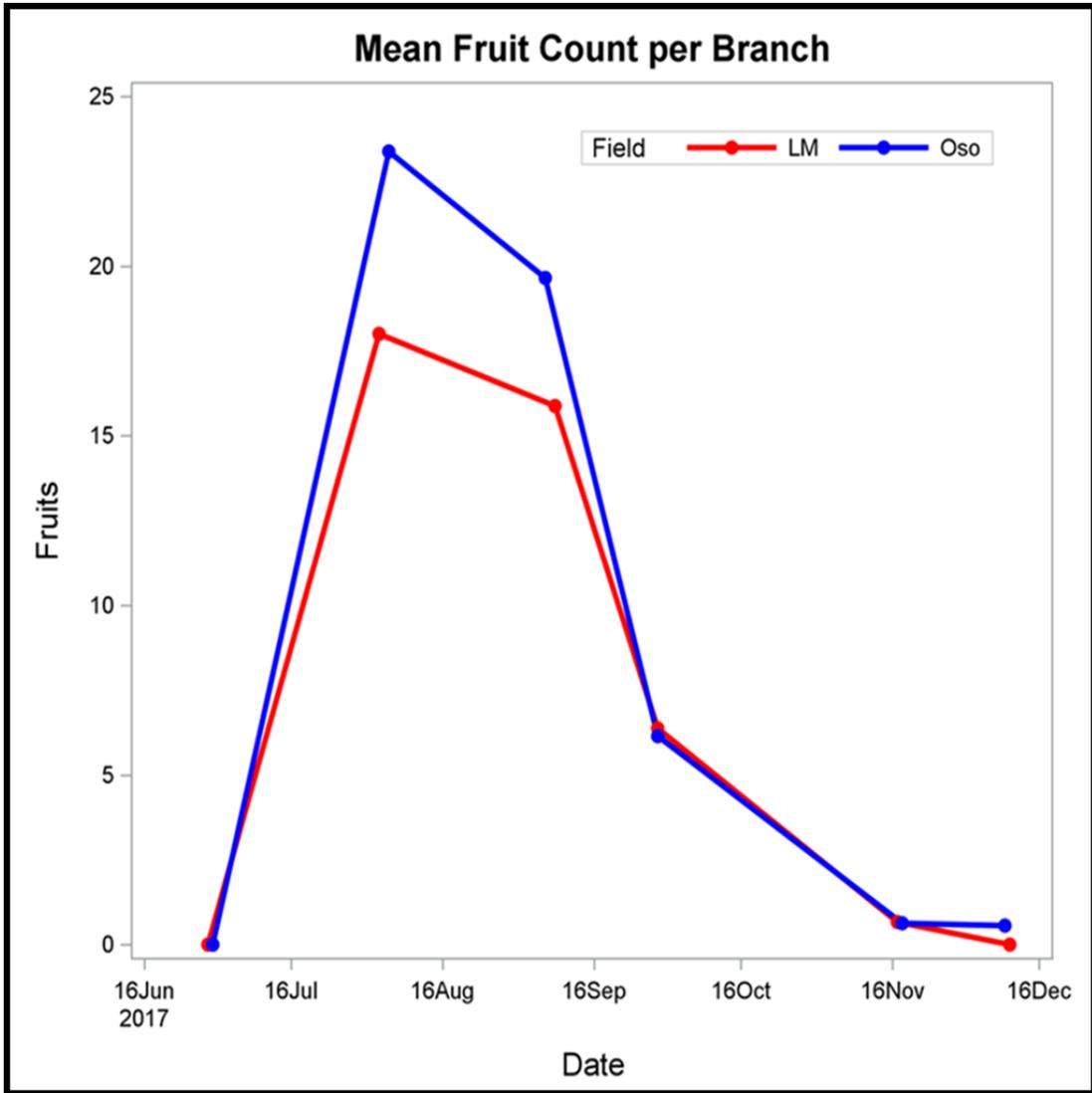


Figure 36: Mean fruit count per branch between the moderate salinity site (Oso Bay-blue) and the hypersaline site (Laguna Madre-red).

Source	DF	F-value	P-value
04 Aug	1	0.03	0.8725
07 Sept	1	0.16	0.6922
29 Sept	1	0.08	0.7797
18 Nov	1	0.12	0.7349
10 Dec	1	0.86	0.3556
Wilk's Lambda	112	0.22	0.9513

Table 10: The Type III results for the mean propagule count per branch for the time points in which propagules were present.

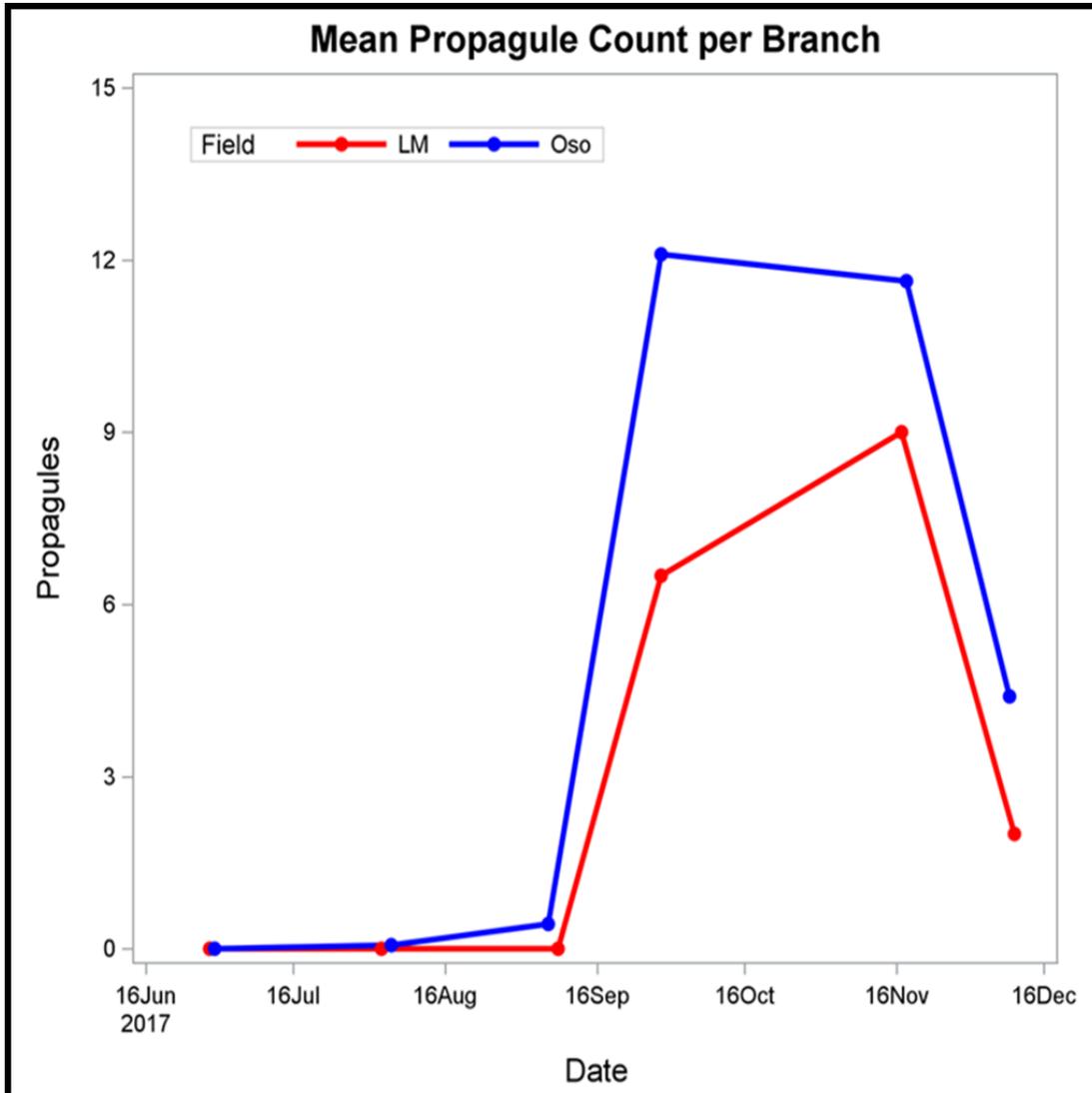


Figure 37: Mean propagule count per branch between the moderate salinity site (Oso Bay-blue) and the hypersaline site (Laguna Madre-red).

Propagule size

A MANOVA of propagule dimensions (length in cm x width in cm) showed no significant difference in propagule size between moderate salinity and hypersalinity sites (Table 11). Propagules from Oso Bay were slightly larger than the Laguna Madre propagules in November, at 2.2 cm² and 1.5 cm² respectively (Figure 38). By December, propagules from

Laguna Madre had grown slightly larger while propagules from Oso Bay had relatively no change in size, at 2.16 cm² and 2.3 cm² respectively.

Source	DF	F-value	P-value
18 Nov	1	0.19	0.6626
10 Dec	1	0.05	0.8224
Wilk's Lambda	57	0.24	0.7860

Table 11: The Type III results for mean propagule dimensions (length in cm x width in cm) per branch for the time points in which propagules were present.

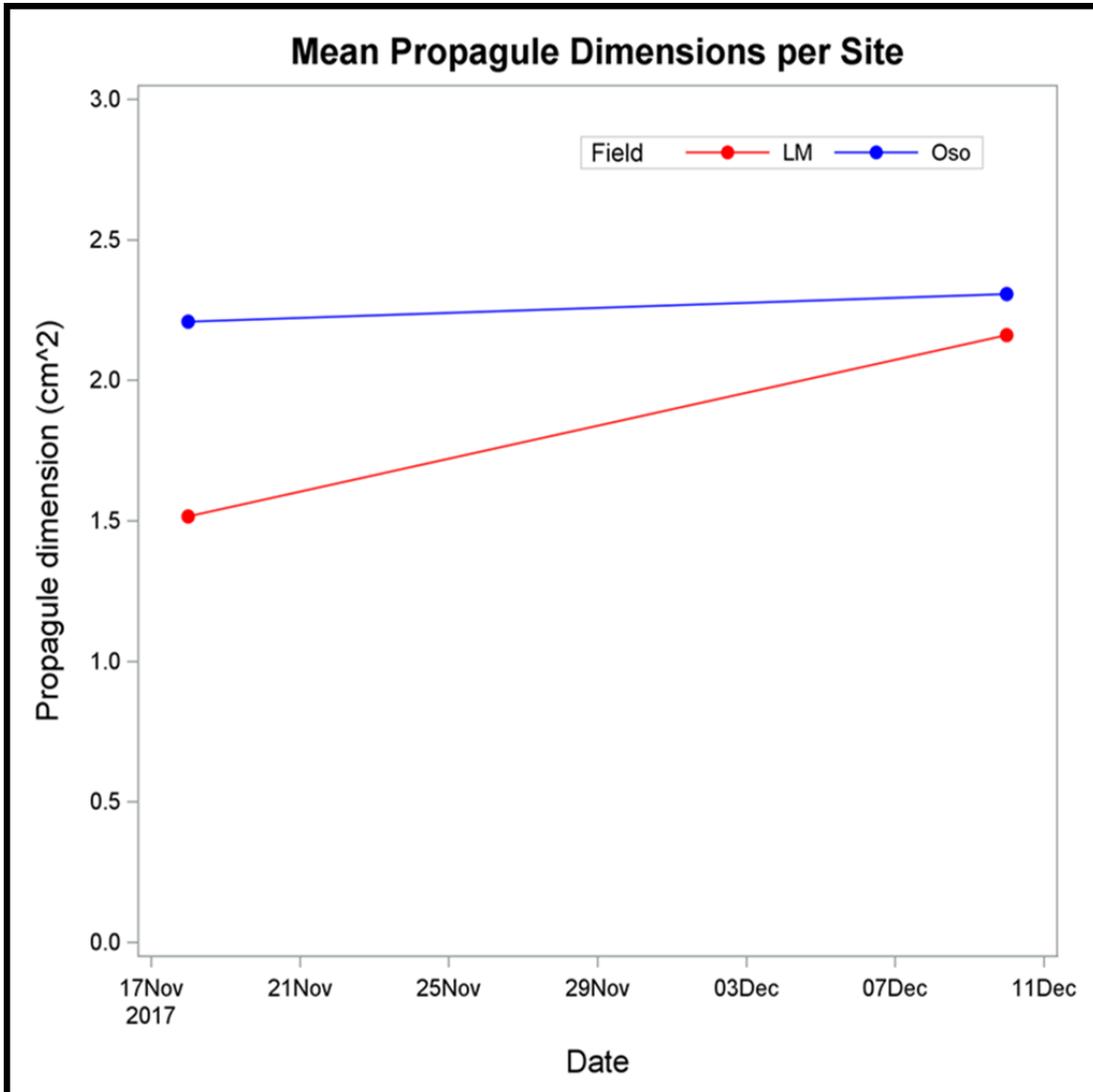


Figure 38: Mean propagule dimensions (length x width in cm) per branch between the moderate salinity site (Oso Bay-blue) and the hypersaline site (Laguna Madre-red).

CHAPTER IV: DISCUSSION

The Stress Gradient Hypothesis (SGH) was partially validated by results from this research project and facilitation was found to be an important factor in *A. germinans* seedling survival and growth in hypersaline conditions. In the transplant experiment, vegetation was found to be facilitative to seedlings along a salinity gradient as seedlings did best in succulent marsh forbs and under *A. germinans* canopy at both moderate and hypersalinity; no competition was noted. In the observational study of naturally occurring seedlings, shading from *A. germinans* had competitive effects on seedling growth at moderate salinity, but facilitative effects at hypersalinity. Overall, vegetation was facilitative to seedling recruitment at both field sites. Facilitative effects and interactions have previously not been highlighted or incorporated into ecological theory as strongly as competition has been and that the SGH can be refined by considering the type of stress and its magnitude (Brooker & Callaghan 1998, Bruno et al. 2003, Maestre et al. 2009, He et al. 2013). This research project supports that facilitative interactions can play an integral role in plant community dynamics.

Study 1: Reciprocal transplant experiment

Overall, vegetation was facilitative to seedling survival at both planting sites. Seedlings from Oso Bay had higher survival rates at both moderate and hypersalinity, suggesting *A. germinans* in lower Laguna Madre are not locally adapted to hypersalinity. While survival for this experiment was very low, this study also demonstrates that the propagule stage acts as an environmental filter for potential colonizers. On a regional scale, a <1% survival rate may translate to hundreds of propagules establishing and surviving during each reproductive cycle, contributing to the creation of new stands of *A. germinans* in Laguna Madre.

By natal site

Opposite to what was hypothesized, propagules from Oso Bay survived better than those from lower Laguna Madre at both moderate salinity and hypersaline planting sites. Salinities in the lower Laguna Madre near South Padre Island, Texas typically remain under 40 PSU, which is lower than salinities in the upper Laguna Madre, typically ranging from 45-60 PSU (Tunnell & Judd 2002) and were 37-57 PSU in this study (M Ziegler, unpublished data). Oso Bay is a shallow water body that receives marine tidal flow from Corpus Christi Bay and freshwater input from Oso Creek. Salinities here vary 15-25 PSU and can reach above seawater strength in high summer heat or during drought conditions (Nicolau 2001). It is possible that *A. germinans* stands in Oso Bay may experience an overlap in salinity regime with *A. germinans* in lower Laguna Madre, meaning that propagules from lower Laguna Madre would not necessarily receive sufficient selection pressure to develop local adaptations to hypersaline conditions.

In addition to salinity, it is possible that *A. germinans* stands in Oso Bay (Corpus Christi, TX) have adaptations in vessel structures due to exposure to cold-stress and these adaptations also are beneficial in hypersaline conditions (Madrid et al. 2014). On a 70-year average, Corpus Christi, Texas experiences lower winter temperatures than South Padre Island near Brownsville, Texas (Tunnell & Judd 2002, NOAA) Snow flurries, while uncommon in south Texas, have occurred more times in Corpus Christi, Texas (2005, 2011, 2017) than in Brownsville, Texas (2004) in this century (NOAA) with the last deep freeze occurring in the 1980s (Tunnell & Judd 2002). *A. germinans* stands in Louisiana and Texas are the most cold-tolerant compared to stands from elsewhere in the Gulf of Mexico (McMillan 1975, Markley et al. 1982, McMillan & Sherrod 1986, Osland et al. 2013, Cavanaugh et al. 2014).

By field site and habitat

Seedlings transplanted to Oso Bay had lower survival rates than their counterparts transplanted to hypersaline Laguna Madre. Crab burrows were higher at Oso Bay and likely decreased seedling survival. Some seedlings were noted to be partially covered or buried by in pseudofeces and tethering lines that anchored seedlings were cut apparently by crabs. In other studies, crab activity and predation can vary with light and temperature conditions, many crabs preferring shaded areas for cooler soil temperatures (Krauss et al. 2008). In a field experiment on the Caribbean and Pacific coast of Panama, Dangremond (2015) found that crabs consumed up to 90% of mangrove propagules in mangrove forests and altered survival between forest types; when crab excluders were placed, survival did not vary between forests. In this study, crabs may have had an indirect effect on seedling survival through burrowing activity, which smothered some propagules with sediment or may have cause established seedlings to topple over.

Study 2: Observational study of naturally occurring seedlings

Salt marsh forb habitats under conditions of moderate salinity had the greatest *A. germinans* seedling densities and means heights, which suggests that this habitat has facilitative effects on seedlings and is more vulnerable to mangrove encroachment. Seedlings under *A. germinans* canopy did not perform as well in moderate salinity, suggesting that shading may have competitive effects on seedlings. But in hypersaline conditions, *A. germinans* canopy had the highest seedling recruitment and growth rates compared to salt marsh forbs and unvegetated tidal flats, transitioning from competitive to facilitative interactions as salinity stress increased which validates predictions made by the SGH. Facilitative interactions can play a key role in mangrove stand expansion in hypersaline conditions, such as the Laguna Madre.

Seedling survival

Overall, hypersaline conditions negatively affected seedling recruitment as density was near eight times lower in Laguna Madre than at Oso Bay. The Laguna Madre system has fewer *A. germinans* than Oso Bay, likely due to salinity stress, and therefore a lower supply of propagules. At the moderate salinity site, succulent marsh forbs had higher seedling densities due to trapping propagules in a matrix of vegetation and providing partial shading, which may reduce soil salinity and increase soil moisture, all of which are favorable conditions for seedlings (Peterson & Bell 2012). But, succulent marsh forbs at lower elevations did not have similar seedling densities; propagules can establish and be successful in this zone, but increased frequency of tidal inundation may wash away propagules before they have a chance to establish. Predation can cause tissue damage to cotyledons, leaving the propagule with fewer reserves and more vulnerable to infections and decay; all leading to reduced seedling densities over time (Patterson et al. 1997). Some plots in this study contained *S. alterniflora*, which can be highly competitive with *A. germinans* seedlings at low-marsh elevations (McKee & Rooth 2008, Guo et al. 2013), but Patterson et al. (1997) found that seedlings in this zone in a Louisiana marsh were taller and could compete with surrounding vegetation for resources; similar trends in seedling density and height were seen in this study in the 'Shoreline succulent' habitat. *S. alterniflora* was not present in any plots at Laguna Madre, and so effects of this species could not be evaluated here. Tidal flats had the lowest recruitment at both field sites, which also suggests that marsh vegetation can be facilitative to mangrove colonization. The frequency of tidal inundation and depressions in the sediment can deliver and strand seedlings, but without surrounding vegetation to trap them, seedlings may be washed away. An inundation-free period can be a 'window of

opportunity' for seedlings to quickly grow roots and anchor themselves before washing away in the next high energy tide (Balke et al. 2011).

At Laguna Madre, seedling density was highest under *A. germinans* canopy, near double of all other habitats combined. Canopy shade likely reduces soil salinities and increases soil moisture, making conditions more hospitable for seedlings compared to other habitats (Devaney et al. 2017). An alternative explanation is that propagules fall from the parental trees and establish before being dispersed by tidal activity, causing higher seedling densities.

The extended period of flooding from Hurricane Harvey reduced seedling densities at both sites, but at a much higher magnitude at the moderate salinity site. The highest mortality rate by habitat was under *A. germinans* canopy, and at a higher magnitude at the moderate site. Shading coupled with inundation likely reduced gas exchange and photosynthetic ability. Inundation reduces the availability of oxygen and alters soil chemistry, thus creating anoxic conditions. Adult *Avicennia spp.* rely on pneumatophores for aerial gas exchange during flooding, yet seedlings in this study were too young to have pneumatophores. McKee and Mendelsohn (1987) found that while seedlings cannot maintain aerobic respiration through flooding, there are exchanges in metabolites between the roots, sediment and with unsubmerged parts of the seedling. In this study, mortality was highest for shorter seedlings that were mostly or completely submerged. Taller seedlings with more stem and leaf tissue above the waterline may have been able to maintain their metabolic needs until floods receded. Seedlings at the hypersaline site likely had higher survival rates due to having already been exposed to a long-term stress (salinity) and so were acclimated to some degree to handle stressful conditions. Moreover, the flooding event lowered open water salinity by 10-12 PSU and flushed sediments which reduced soil salinities by half compared to previous measurements (Table 12). This

essentially changed the type of stress seedlings were exposed to, salinity stress to inundation stress. Whereas for the moderate salinity site, the inundation levels became the main stressor for seedlings and altered marsh-mangroves interactions and caused higher mortality rates compared to Laguna Madre.

Oso Bay									
Habitat	June 16	June 30	July 18	Aug 5	Aug 19	Sept 6	Oct 27	Nov 18	Dec 11
Shoreline succulents	64	19	86	64	104	66	NA	41	30
Mangrove canopy	88	50	137	81	218	144	45	55	47
Inshore succulents	75	53	119	70	87	78	42	39	41
Tidal flats	89	62	127	68	154	111	46	37	44
Laguna Madre									
Habitat	June 16	June 30	July 18	Aug 5	Aug 19	Sept 6	Oct 27	Nov 18	Dec 11
Shoreline succulents	168	42	203	NA	132	87	63	37	44
Mangrove canopy	167	51	90	NA	107	192	57	39	51
Inshore succulents	204	120	221	NA	362	126	94	53	51
Tidal flats	162	61	224	NA	205	260	123	79	69

Table 12: Soil salinity data for all habitats at Oso Bay and Laguna Madre from June-December 2017, following protocol from Richards & Pennings 2006. Units in PSU.

Sediment composition at each field were not measured in this study but may be a factor in seedling survival rates during the flooding period. The moderate salinity site has primarily fine, clay-based sediment while the hypersaline site has a sandy texture. Clay and sand have different porosities, which affects water retention, the movement of nutrients and overall soil chemistry. During long periods of inundation, clay soils become water-logged and anoxic, which causes a rise in toxic hydrogen sulfide. Adult *Avicennia spp.* rely on pneumatophores and aerenchyma tissues as oxygen sources (McKee et al. 1988). Young seedlings in this study do not

yet have these structures and tissues to withstand changes in soil chemistry, which may in part explain higher mortality at the moderate salinity site.

McMillan (1975b) studied how soil texture interacts with hypersaline conditions and how this affects the survival of *A. germinans* seedlings. Seedlings were transplanted in a gradient of sandy soils with increasing clay content; seedlings survived high salinities when planted in soils with the highest clay content but died in sandy soils. Therefore, sandy soils at the Laguna Madre site, but not at the moderate salinity Oso Bay site, may be another factor for low seedling densities under hypersaline conditions.

Seedling growth

Competitive and facilitative plant interactions can differ by habitat type depending upon the presence of vegetation, frequency of tidal inundation, and the amount of shading provided to seedlings. At the moderate salinity site, seedlings in all habitats had positive growth rates for height over time and maintained low numbers of stems and therefore leaves, except for seedlings in the ‘Tidal Flats’ habitat which were shorter but had more stems and leaves. The vegetated habitats (a mixture of salt marsh forbs and adult *A. germinans* canopy) are nearer the waterline. While abiotic stresses, such as high soil salinity and low soil moisture, are low in these habitats, competition from surrounding vegetation appears to be higher compared to the tidal flats. Seedlings here may allocate more resources to increasing height to compete with surrounding vegetation for space and light availability. Shading from surrounding vegetation can be facilitative in some circumstances as partial shading, such as a mixture of succulents, can protect seedlings from UV damage and heat stress as well as producing lower soil salinities and higher soil moisture. Seedlings in the ‘Shoreline succulent’ habitat were on the waterline and had the

greatest mean heights but low seedling density, showing that recruitment and retention rates may be low due to increased tidal flow and inundation; but seedlings can still prosper here despite occasional presence of *S. alterniflora* in some plots at Oso Bay. Even within the same mixture of succulent forb species, plant interactions may change from competitive in the 'Shoreline succulents' to facilitative in the 'Inshore succulents' possibly due to a decreased frequency of tidal inundation, causing lower soil moisture and higher accumulation of salts in the sediment. Tidal flats were further from the waterline and most times had up to 20% higher soil salinities than the 'Inshore succulent' habitat, particularly towards the end of summer (Table 12). Prior to flooding from Hurricane Harvey, seedlings under *A. germinans* canopy had the greatest maximum heights compared to other habitats, suggesting that seedlings are taller to compete for light or that propagule dropping from the parent tree recruit first in this nearest habitat and thus have more time to establish and develop here than in other habitats that require longer dispersal. After flooding however, seedlings in the three remaining habitats greatly increased in height, with seedlings in succulent marsh forbs exceeding those under canopy cover. Seedlings in tidal flats were shortest with little to no surrounding vegetation. High abiotic stress and low biotic alters seedling morphology; seedlings are shorter but have more leaves and branches. To regulate salinity, mangrove excrete salts through specialized glands on their leaves. Having more leaves will aid in salt regulation but comes at the cost of growth (Sobrado 2001). Overall, competition for resources such as nutrients, light and space is generally highest near the waterline but is reversed with increasing distance from the water line, where facilitation is more frequent with high abiotic stress. Following the Stress Gradient Hypothesis, plants experience high biotic stress (competition) when abiotic needs are met and low biotic stress (facilitation) when abiotic needs are not met.

At Laguna Madre, seedlings have variable growth rates across habitat types, and overall had greater numbers of leaves and stems, compared to the moderate salinity site. Seedlings are likely shorter here due to salinity stress and may have more leaves for salt regulation. Madrid et al. (2014) found that vessel structure was more narrow and shorter in *A. germinans* exposed to cold stress or hypersaline conditions; narrow vessel structures reduce the risk of embolisms, which can be fatal, but also restrict the flow of water and nutrients, thus causing trees to be shorter in stature. It is likely that seedling here are exhibiting a similar response to hypersaline conditions and allocating resources to leaf production and salt regulation.

Flooding had various effects on seedling heights, and leaf and stem count. Maximum heights show that flooding induced growth at the moderate salinity site in both succulent forb habitats and the tidal flats, but not under *A. germinans* canopy cover, which remained unchanged through the flooding event with a small lag in growth afterward. About half of the seedlings did not survive the flooding event at this site, taller seedlings may have benefited from nutrients brought in by flood waters or from reduced competition with surrounding vegetation. At Laguna Madre, maximum heights were relatively unchanged, except for the 'Shoreline succulent' habitat. Being on the waterline, it is possible that flood waters provided nutrients and flushed soils more thoroughly than other habitats. Many seedlings at Oso Bay were defoliated from the flooding and had black or brown apical tips and some had broken stems (M Ziegler, personal observation). At Laguna Madre, seedlings were not defoliated to the magnitude of the moderate salinity site, but had an increase in leaf count and height, suggesting that flood waters reduced salinities and may have brought nutrients, allowing seedlings to allocate resources to growth instead of salt regulation.

Study 3: Observational study of reproductive output

This observational field study demonstrated that hypersalinity did not reduce reproductive output per reproductive stem of sexually mature *A. germinans*. Moderate salinity estuaries, such as Oso Bay, have larger size mangrove stands and likely have more apical stems per tree than stands in hypersalinity. Small groups of *A. germinans* in Laguna Madre are scattered throughout the system, but reproductive branches of *A. germinans* in upper Laguna Madre can produce the same number of offspring. Results of the transplant experiment and observational seedling study in this research project indicate that propagules and seedlings were most successful under canopy cover when in hypersaline conditions, likely because of shade reducing abiotic stresses. In the transplant experiment, Oso Bay had significantly more crab burrows, which likely had a negative effect on seedlings at the moderate salinity site. As mature *A. germinans* in hypersalinity continue to reproduce and propagules are successful on canopy edges due to shading and less faunal interactions, current mangrove stands will likely expand in size and new stands may develop elsewhere in Laguna Madre.

Stress and disturbance can influence how trees invest energy to maintenance, growth and reproduction. In Louisiana, Alleman and Hester (2011) measured canopy dimensions and propagule production after hurricanes in 2005 and 2008; propagule count increased each year in a 3-year period while canopy growth varied, demonstrating that mature trees may trade-off energy investments between individual growth and reproduction following a disturbance. Crypto-vivipary in *A. germinans* provides advantages to offspring in high-stress estuaries as propagules can germinate on the parent tree then immediately establish or survive long dispersal periods. This reproductive strategy is costly and it's likely that individuals would trade-off investments to reproduction and maintenance over multiple years (Alleman & Hester 2011).

Under the pro-longed stress of hypersalinity, it's highly probable that *A. germinans* in this study follow a similar strategy. Only two trees were tagged at the hypersaline site while 33 trees were tagged at the moderate salinity site. After Hurricane Harvey, pedicles on the smaller of the two trees at the hypersaline site were broken or bare, most likely due to heavy winds and rains. In November 2017, the peak of propagule production for this study, the larger tree had 54 propagules while the smaller tree had 2. The mean propagule count per tree for the moderate salinity site was 41.9 propagules, while the mean is 54 at the hypersaline site, excluding the smaller tree since most pedicles were damaged during the hurricane. Although this study is limited by the number of mature trees present at the hypersaline site, large *A. germinans* have been noted elsewhere in upper Laguna Madre, such as Bird Island (M. Ziegler, personal observation). Trees here are of similar size or larger (and likely older) than those in the moderate salinity site. Propagules were seen in October 2017 and thought to be similar size and quantity to those observed in Oso Bay. Studying *A. germinans* on other spoil island in the upper Laguna Madre and over multiple years would provide a more detailed assessment of reproduction of *A. germinans* in hypersaline conditions, and specifically in the Laguna Madre.

With warming climate and variable rainfall, these facilitative interactions may create a positive feedback loop in hypersaline systems. As seedlings are successful under canopy cover, stand size will increase, providing more coverage for seedlings to recruit under. Areas with current *A. germinans* stands are most vulnerable to marsh encroachment. At moderate salinities, areas with salt marsh forbs are most vulnerable to mangrove expansion due to high seedling recruitment and densities found in this study, as well as resilience to disturbances such as flooding.

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