An Investigation of the Effects of Increased Tidal Inundation, Competition, and Facilitation on Salt Marsh Systems

by

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DEDICATION

This dissertation is dedicated to my son, Christopher Maul, whose love, kind words, patience, and encouragement have made this possible.

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ABSTRACT

The low-lying topographic nature of salt marshes makes plants in these communities particularly vulnerable to increased salinity and inundation exposure associated with sea level rise. Both increased salinity and inundation have been cited as major causes of reduced plant performance and survival in marsh and areas fringing marsh. In addition to limitations imposed by physical stress, interspecific interactions have also been shown to mediate the performance and survival of salt marsh and salt marsh fringing species. The Stress Gradient Hypothesis (SGH) postulates that species interactions shift from competitive to facilitative as stress levels increase and predicts that (a) the frequency and intensity of facilitative interactions increase as conditions become more stressful for plants and (b) the strength of competitive interactions increases as abiotic stress levels diminish. The SGH has been rigorously tested to examine how both the frequency and intensity of species interactions change under varying physical stress levels. Studies conducted in salt marsh systems have shown facilitation to be as strong of a driving force as competition in influencing plant performance and survival and have shown that while competition appears to be the pervasive force in the less physically stressful terrestrial zones fringing salt marshes, facilitation influences the performance and survival of species in harsher marsh areas. Under conditions of sea level rise, it remains unclear if the nature of interspecific interactions would shift as stress levels change. This research endeavors to examine

the interplay between abiotic stresses and biotic interactions under conditions of increased salinity and inundation exposure.

The first study presented here investigated the effects of increased inundation and soil salinity associated with sea level rise on four salt marsh fringing species, and assesses how competition and facilitation impact survival of salt marsh fringing plant survival under these changing conditions. All plant species experienced reduced growth and photosynthetic inhibition below their current distributional positions, both in the presence and absence of neighboring above ground vegetation. The findings also signal a potential shift in the nature of interspecific interactions from competition to facilitation to neutral as plants begin to experience increased salt and inundation exposure.

The second study aimed to disentangle the effects of increased soil salinity and increased soil moisture on four salt marsh fringing species, and to examine the effects of plant neighbors. The results showed that fringe plants exposed to increased inundation experienced a two-fold reduction in performance and survival over 750 g pure salt addition, suggesting that inundation may be a more important limiting factor than salinity with rising sea levels. Landward transplants at the forest-fringe margin exposed to lower soil salinity and decreased inundation exhibited a three-fold increase in performance and survival when compared to controls. Neighbor manipulation studies, which consisted of trimming neighboring vegetation to ground level, again suggested that interspecific interactions in salt marsh fringing species may shift from competitive to facilitative with climate-induced sea level rise. Overall, our findings suggest that salt marsh fringing species may not be able to tolerate changing conditions associated with sea level rise and their survival may hinge on their ability to migrate towards higher elevations.

The final experiment tested the Stress Gradient Hypothesis and investigated the relative importance of facilitation and competition in a salt marsh system under varying stress levels. This study also ascertained whether salt or inundation exposure is the primary influence on salt marsh plant performance and survival. As in previous studies, our findings suggest that many salt marsh plants don't require, but merely tolerate harsher abiotic conditions. The results showed that plants at higher elevations were depressed by strong competitive pressure from neighboring fringe species while plants at lower elevations benefited from the presence of neighbors. Collectively, the results of these studies indicate that species interactions are an integral driver of plant distribution in salt marsh communities. Furthermore, our findings indicate that changing stress levels may not always result in a shift in the nature of interspecific interactions. These studies have endeavored to show that the interplay between competition and facilitation interacts with physical processes to determine the growth and performance of both fringe and marsh plant species. The paucity of studies examining the roles of species interactions and changing abiotic stress levels on multiple salt marsh and salt marsh fringing species warrants the need for additional research. The responses of salt marsh and salt marsh fringing species to sea level rise can not only serve as very valuable and sensitive indictors of climate change, but will also aid in predicting the future location of the marsh-fringe-forest ecotone, which is predicted to shift inland as sea levels continue to rise.

CHAPTER 1

INTRODUCTION

In temperate and sub-tropical areas, salt marshes occur in a zone between the highest tide of the year and mean sea-level (Titus et al. 2006), causing even the smallest increases in tidal influence to have profound effects. These low-lying communities typically experience episodic pulses of tidal inundation in varying magnitudes and frequency across harsh physical gradients. A conspicuous plant zonation often occurs between sea and forest, resulting from diminished soil salinity and moisture levels with increasing distance from the water source, creating a physical stress gradient (Bertness 1991). Differing physiological thresholds to abiotic conditions often influence the distribution or zonation of plants in these salt marsh areas. As a result, marshes comprise a mosaic of communities, defined in part by the environmental tolerance of plant species to abiotic stresses.

Abiotic Interactions

Evidence suggests a negative correlation exists between increased saltwater inundation and plant performance in salt marsh systems (Phleger 1971, Bowman and Strain 1987, DeLaune et al. 1987, Young et al. 1994, Broome et al. 1995, Miller et al. 2001). Williams et al. (1999a) cited salt exposure to be the major cause of death at higher elevations in coastal areas. Salinity concentrations are highly variable, varying in excess of 10ppt within a distance of a meter or within a matter of hours (Adam 1990, Moon and Stiling 2002a, 2002b) due to influxes of fresh and salt water into the system (periodic inundation, ebbing of tides, and precipitation events). An important regulator of salt marsh plant production, salinity levels in excess of 35ppt have the potential of altering plant reproduction, morphology and chemisty (Bowdish and Stiling 1998, Moon and Stiling 2000, 2002a, 2002b).

Other studies suggest that, although salt marsh species exhibit diminished growth and performance with increasing salinity, inundation plays a larger role in disrupting salt marsh plant distributions (Adams 1963, Gleason 1980, Mendelssohn et al. 1981, Howes et al. 1981, Williams et al. 1999a, Donnelly and Bertness 2001, Emery et al. 2001). The frequency and duration of inundation typically dictate the magnitude of plant response (Miller et al., 2001), and negative effects often include anoxia, increased assimilation of salts through tissues, increased production of soil sulfides, and augmented exposure to these aqueous toxins (Adam 1990). Decomposition of organic matter further depletes soil oxygen, exacerbating anoxic conditions.

Marsh Zonation

The low-lying topographic nature of salt marshes makes plants in these communities particularly vulnerable to impacts associated with sea level rise. In subtropical areas of the United States, inland marsh areas endure frequent submersion and are commonly inhabited by black mangrove (*Avicennia germinans*), saltwort (*Batis maritima)* and other extreme halophytes, while high marsh zones are dominated by black needlerush (*Juncus roemerianus*) and are prevalent in areas above the mean high water mark, experiencing occasional inundation for shorter durations of time. Progressing landward, the terrestrial fringe is vegetated by saltwater false willow (*Baccharis angustifolia*), eastern baccharis *(Baccharis halimifolia),* marsh elder (*Iva frutescens*), and the grass *Andropogon glomeratus*. Characterized by lower soil salinity, infrequent inundation, higher redox potentials, and lower soil sulfide levels, the terrestrial fringe serves as an ecotone between the marsh and terrestrial ecosystems (Bertness and Hacker 1994).

While most salt marsh plant species can tolerate salinity stress and inundation (Bertness and Hacker 1994; Donnelly and Bertness 2001; Emery et al. 2001), species in areas fringing salt marshes lack the physiological mechanisms to cope with such stresses and, under conditions of sea-level rise, may experience depressed plant metabolism (Nyman and DeLaune 1991; Miller et al. 2001), decline in gross production (Miller et al. 2001; Morris et al. 2002; Voss et al. 2013), and diminished growth, fitness, and survival (Adams 1963; Mendelssohn et al. 1981; Howes et al. 1981; Williams et al. 1999; Donnelly and Bertness 2001, Emery et al. 2001). It is therefore possible that the plants in these fringe areas will experience more serious impacts than salt marsh plants as rising sea levels encroach on the terrestrial margin. It remains unclear whether rising sea levels would result in enough tree deaths to increase border permeability at the forest margin and allow for the landward migration of these fringe species.

Biotic Interactions

Studies have shown that while salt marsh and salt marsh fringing zonation is defined by limitations imposed by physical stress at the lower limits, interspecific interactions also mediate the performance and survival of species (Bertness and Ellison 1987, Bertness 1991). For decades, ecologists have documented competition and more recently in the last two decades, facilitation in these systems. Numerous studies have tested the Stress Gradient Hypothesis (SGH) to examine how both the frequency and intensity of species interactions change along stress gradients. Coined by Bertness and Callaway (1994), the SGH predicts that (a) the frequency and intensity of facilitative interactions increase as conditions become more stressful for plants and (b) the strength of competitive interactions increases as abiotic stress levels diminish. Studies conducted in salt marsh systems have shown facilitation to be as strong of a driving force as competition in influencing salt marsh plant performance and survival and have shown that while competition appears to be the pervasive force in the less physically stressful terrestrial zones fringing salt marshes, facilitation influences the performance and survival of species in harsher marsh areas (Bertness et al. 1992; Pennings and Callaway 1992; Bertness and Shumway 1993; Bertness and Callaway 1994; Levine et al. 1998; Bertness and Ewanchuk 2002; Charles and Dukes 2009). Salt marsh plant species are equipped with the necessary metabolic and architectural adaptations to effectively tolerate moderate salt and inundation stresses, which afford them the ability to mitigate harsher physical conditions for neighboring species (Bertness and Hacker 1994; Callaway 1994; Donnelly and Bertness 2001; Emery et al. 2001; Ewanchuk and Bertness 2004; Richards et al. 2005; He and Bertness 2014). The presence of neighboring plant species can alleviate stress, permitting the survival of some species which, on their own, would not be able to persist (Pennings and Callaway 2000.

Sea-Level Rise

Under conditions of accelerated sea level rise, many predict the subsequent landward migration of salt marsh species (Morris et al. 2002; Gardner et al. 1992; Gardner and Porter 2001). As rising sea levels submerge low marsh areas, propagules from the species which inhabit these areas are predicted to invade fringe habitats at their landward border. While several studies have already documented landward migration of low marsh species at the expense of higher marsh species in response to sea-level rise (Donnelly and Bertness 2001; Raabe et al. 2012), others cite the need for the degredation of higher marsh species to increase border permeability and allow for the successful migration of lower marsh species (Peterson and Bell 2012). Fringe species at higher elevations are less stress tolerant, compared to lower marsh species, and allocate more of their resources to growth which enables them to competitively exclude the more stress tolerant low marsh species at the fringe-marsh border (Levine et al. 1998). As conditions become more stressful in areas fringing the marsh, however, it is predicted that the fringe species will experience reduced performance and survival. The subsequent degradation of the fringe community would in turn weaken competitive pressure and increase border permeability, allowing for the successful migration of low marsh species into fringe areas.

Some attribute the successful landward expansion and invasion of low marsh species into upland areas as the primary reason for diminished performance and survival of terrestrial fringe species (Alexander and Crook 1974, Gardner et al. 1992, Donnelly and Bertness 2001, Gardner and Porter 2001, Miller et al. 2001, Costa et al. 2003). Bertness and Ellison (1987) found that while salt marsh species typically perish when transplanted to lower elevations, they are fully capable of establishing at higher elevations. This was supported by Donnelly and Bertness (2001), who documented the landward migration of low marsh cordgrass (*Spartina alterniflora*) at the expense of marsh hay *(Spartina patens*) and other terrestrial species. Hence, low marsh vegetation will continue invading upland vegetation if relative sea level continues to rise.

Some authors argue that terrestrial fringe species may be capable of resisting invasion by salt marsh plant species. Brinson et al. (1995) demonstrated that forests were capable of precluding the transition from forest to high marsh community. Canopy cover is one mechanism by which some encroaching marsh species can be competitively excluded. This can be problematic for establishment in the terrestrial forest and may preclude species establishment. Similarly, other studies have inferred that high marsh vegetation may be capable of excluding low marsh plants (Bertness and Ellison 1987, Brinson et al. 1995). Bertness and Ellison (1987) found that dense monocultures of dominant perennials can reduce light penetration to the substrate, limiting invader seedling success. The above supports the hypothesis that competition is a major determinant of plant distribution and zonation pattern at higher elevations (Bertness and Ellison 1987, Bertness and Hacker 1994). Bertness and Ellison (1987) attribute this to differences in plant morphology, suggesting the competitive dominance of phalanx over guerilla growth form, and clonal over solitary plants. They and others also hypothesized that a trade-off may exist between stress tolerance and competitive ability (Bertness 1991, Levine et al. 1998, Costa et al. 2003). Stress intolerant species are capable of allocating resources to production, rather than to specialized adaptations, thereby enhancing competitive ability. Bertness (1991) demonstrated this by showing how *Juncus gerardi* competitively dominates high marsh areas, displacing and restricting the more salt tolerant *Spartina patens* to lower elevations.

While the effects of sea level rise on salt marshes (Orson et al. 1985; Brinson et al. 1995; Callaway et al. 1996; Miller et al. 2001; Morris et al. 2002; Reed 2002; Slocum et al. 2005; Charles and Dukes 2009; Craft at al. 2009; Kirwan et al. 2010; Kirwan and Guntenspergen 2012; Langley et al. 2013; Voss et al. 2013) and coastal forest stands (Williams et al. 1999a; Williams et al. 1999b; Desantis et al. 2007; Geselbracht et al. 2011) have been well studied along the US Atlantic and northern Gulf coasts, areas fringing salt marshes have received relatively little attention. When rising sea levels begin to encroach on the terrestrial boundary of marsh systems, fringe areas adjoining the forest could be the first to experience serious impacts. Fringe species have lower physiological thresholds and narrower tolerances to both salt and inundation stress than true marsh species and may therefore very responsive to changing environmental conditions associated with sea level rise.

Experimental Studies

The first study examined the interplay between abiotic stresses and biotic interactions. We moved four salt marsh fringing species, *Andropogon glomeratus* (bluestem grass), *Baccharis angustifolia* (saltwater false willow), *Baccharis halimifolia* (eastern baccharis), and *Iva frutescens* (marsh elder), from the terrestrial fringe into marsh areas both with neighbors and without neighboring above ground vegetation to (a) simulate the increased inundation and soil salinity associated with sea level rise and (b) assess the role of competition and facilitation in defining salt marsh fringing plant survival under these changing conditions. All plant species experienced reduced growth and photosynthetic inhibition below their current distributional positions, both in the presence and absence of neighboring above ground vegetation. Our neighbor manipulation studies showed strong competitive effects between species in the more benign conditions of the terrestrial fringe but facilitation in the more physically stressful marsh areas. Conditions in the lower marsh appeared to be so stressful that the presence of neighboring species did not facilitate any increases in growth. In line with He and Bertness's findings (2014), the results from our study signal a potential shift in the nature of interspecific interactions from competition to facilitation to neutral as plants begin to experience increased stress. Since fringing species have lower physiological thresholds and narrower tolerances to both salt and inundation stress than marsh species (Levine et al. 1998), these findings suggest that they may not be able to tolerate changing conditions associated with sea level rise.

In the second study, we aimed to disentangle the effects of increased soil salinity and increased soil moisture on four salt marsh fringing species, and to examine the effects of plant neighbors. We transplanted the fringe species seaward and landward of their original positions and salt pellets were added to plots in the fringe. Fringe plants exposed to increased inundation experienced a two-fold reduction in performance and survival over pure salt addition, suggesting that inundation may be a larger limiting factor than salinity with rising sea levels. These findings concur with other studies which have shown that while increasing salinity negatively impacts the growth of salt marsh species (Adams 1963), tidal influences are the primary determinant of salt marsh plant distribution and success (Adams 1963; Gleason and Zieman 1981; Mendelssohn et al. 1981; Howes et al. 1981; Bertness and Ellison 1987; Donnelly and Bertness 2001; Emery et al. 2001; Miller et al. 2001; Rasser et al. 2013; Wasson et al. 2013). Landward transplants exposed to lower soil salinity and decreased inundation exhibited an increase in performance and survival when compared to controls. Our neighbor manipulation studies suggest that interspecific interactions in salt marsh fringing species may shift from competitive to facilitative with climate-induced sea level rise as these species begin to experience marsh conditions. In this study, both performance and survival of all four marsh-fringing species were greatly impacted by increased inundation both with and without neighbors, which suggests that they may not be able to tolerate changing conditions associated with sea level rise. As sea levels rise and inch toward the forest margin, the survival of these species may hinge on their ability to migrate toward higher elevations.

The final experiment presented here tested the SGH in a salt marsh system and investigated the relative importance of facilitation and competition in these systems under varying stress levels. We transplanted three salt marsh species, *Avicennia germinans* (Black mangrove), *Borrichia frutescens* (seaside oxeye), *Batis maritima* (saltwort), into fringe areas, landward of salt marshes, both in the presence and absence of neighboring fringe species to determine whether salt marsh species require or merely tolerate frequent inundation and saline conditions present in their native low marsh habitat and to assess the role of biotic interactions on their performance and survival at higher elevations. Additionally, we added salt to transplants in decreased inundation plots to ascertain whether salt or inundation exposure is the primary influence on salt marsh plant performance and survival. These findings, like others, suggest that many salt marsh plants don't require, but merely tolerate harsher abiotic conditions. Additionally, all three species transplanted at higher elevations were depressed by strong competitive pressure from neighboring fringe species while plants in the more physically stressful marsh areas benefited from the presence of neighbors. Our data suggests facilitation is important in salt marsh environments as a result of neighbors buffering other species from potentially limiting physical stresses (Bertness and Hacker 1994).

These findings are in general agreement with our results from the first two experiments and suggest that salt marsh plants are competitively displaced seaward to low marsh areas by fringe species. Interestingly, adding salt stress to transplants in decreased inundation plots in the fringe weakened competitive interactions but did not precipitate a shift in the nature of interspecific interactions from competitive to facilitative, which suggests that increased stress may not result in a shift in the nature of interspecific interactions in all cases. The strong competitive pressure from neighboring fringe species at the fringe-marsh boundary suggests that salt marsh plants may not be able to successfully migrate landward to higher elevations as sea levels rise as long as neighboring species persist. Under conditions of sea level rise, these data suggest that salt marsh plants may only be able to successfully migrate landward if the strength of competitive interactions weakens at the fringe-marsh boundary. The responses of salt marsh species to sea level rise not only serve as valuable and sensitive indictors of climate change, but will also aid in predicting the future location of the marsh-fringe ecotone, which is predicted to migrate inland as sea levels continue to rise.

Similar to other findings, the work presented here suggests that competition plays a role in mediating the growth and survival of both terrestrial fringe and salt marsh species at higher elevations, while facilitation influences plant performance in harsher marsh areas. While most studies cite the role local geomorphology and sediment accretion play in salt marsh sustainability relative to sea level rise (Patrick and DeLaune 1990; Morris et al. 2002; Reed 2002; Slocum et al. 2005; Day et al. 2008; Voss et al. 2013), the importance of species interactions in governing plant distribution in salt marsh communities has also been underscored. There is overwhelming evidence to suggest that species interactions are an integral driver of plant distribution in salt marsh communities. These studies have endeavored to show that the interplay between competition and facilitation interacts with physical processes to determine the growth and performance of both fringe and marsh plant species. Moreover, responses to this interplay may differ significantly among species. Only by studying the effects of increased tidal inundation on multiple species and by incorporating the effects of neighboring vegetation in future experiments are we likely to determine the true effects of tidal increases on salt marsh and terrestrial fringe plants. Additionally, ecologists need to appreciate how interspecific interactions can shift with changing environmental conditions to fully understand how physical stress and biotic factors interact to generate salt marsh structure.

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CHAPTER 2

THE EFFECTS OF INCREASED TIDAL INUNDATION, COMPETITION, AND FACILITATION ON SALT MARSH FRINGING PLANTS

Synopsis

While increased tidal inundation from sea level rise may impact salt marsh plants, the effects may be even greater for salt marsh fringing plants which lack many adaptations to salt stress and increased inundation. This study employs plant transplants of four salt marsh fringing species, *Andropogon glomeratus* (bluestem grass)*, Baccharis angustifolia* (saltwater false willow), *Baccharis halimifolia* (eastern baccharis*),* and *Iva frutescens* (marsh elder), to simulate the increased inundation and soil salinity associated with sea level rise. Individuals of each species were moved seaward across three distances, representing a 1, 2, or 3 cm sea level increase. The transplants were performed both in the presence and absence of neighboring above ground vegetation to assess the role of competition and facilitation in defining salt marsh fringing plant survival as sea level rises. Soils (salinity, moistre, redox, pH, sulfide), growth (height, circumference, leaf production), performance (fluorescence), and survival measurements were recorded for all plant individuals for one year. Soil salinity increased with decreasing elevation but was lower in the presence of neighbors

at all locations except 3cm below current levels. Soil redox potential was decreased with decreasing elevation but was elevated by the presence of neighbors at all locations except at 3cm below current levels. All plant species experienced reduced growth and photosynthetic inhibition even 1 vertical centimeter below their current distributional positions, both in the presence and absence of neighboring above ground vegetation. Survival and growth were even more impacted at 2 and 3 vertical centimeters lower. In our neighbor manipulation study, neighboring vegetation was clipped at ground level within 30 cm surrounding each plant for the entire duration of the experiment. In fringe areas, taller neighbors were also cut to ground level to eliminate canopy cover. Our neighbor manipulation studies showed increased plant growth and survival at the control and 1cm elevational decrease positions but decreased growth and survival at 2cm elevational decrease positions. At the 3 cm elevational decrease position, neighbor manipulation had no significant effect. The neighbor manipulation studies also showed strong competitive effects between species in the more benign conditions of the terrestrial fringe but facilitation in the high marsh area. Conditions in the lower marsh appeared to be so stressful that the presence of neighboring species did not facilitate any increases in growth. These findings signaled a potential shift in the nature of interspecific interactions from competition to facilitation to neutral as plants begin to experience increased stress. The interplay between physical stress and interspecific interactions, coupled with the physiological tolerance of species to changing environmental conditions, will likely be key determinants of plant response to sea level rise in salt marsh fringing communities.

Introduction

Bertness and Callaway's (1994) stress-gradient hypothesis (SGH) postulates that both the importance and frequency of competitive and facilitative interactions change as organisms experience more or less stressful conditions. This hypothesis has been supported in both marine and terrestrial plant studies across growth forms, climatic zones and abiotic stress types. Shifting interspecific interactions with changing abiotic conditions is considered by some to be a general phenomenon in communities such as salt marshes, which frequently experience harsh conditions (Callaway and Davis 1993; Bertness and Callaway 1994; He et al. 2013). While competition appears to play a large role in the less physically stressful terrestrial zones fringing salt marshes, facilitation is prevalent in more stressful marsh areas where elevated soil salinity and waterlogging are both evident (Bertness et al. 1992; Pennings and Callaway 1992; Bertness and Shumway 1993; Bertness and Callaway 1994; Levine et al. 1998; Bertness and Ewanchuk 2002; Charles and Dukes 2009). The presence of neighbors has been shown to elevate soil oxygen in waterlogged areas (Bertness and Hacker 1994; Ewanchuk and Bertness 2004) and ameliorate hypersaline conditions (Bertness and Hacker 1994; Callaway 1994). However, at the highest stress levels, even facilitation is not sufficient to ameliorate the effects of stress (He and Bertness 2014). Under conditions of sea level rise, it is therefore possible that a shift in the nature of interactions from competitive to facilitative to no effects could occur in the more benign terrestrial fringe areas as plants in these zones begin to experience more salt and inundation stress.

To our knowledge, few experimental studies have examined the roles of species interactions and increased abiotic stress on salt marsh fringing plant communities. While some studies have established that a few salt marshes have been successful in keeping pace with sea-level rise over the last several thousand years (Patrick and DeLaune 1990; Reed 2002), most concur that the rate of sea-level rise now exceeds vertical accretion rates in many regions, resulting in marsh submergence (DeLaune et al. 1983; Park et al. 1989; Titus et al. 1991; Titus and Narayanan 1995; Morris et al. 2002; Slocum et al. 2005). This is especially problematic along low-lying Florida coastlines, and models infer marsh submergence in these regions even for conservative projections of sea level rise (Kirwan et al. 2010; Kirwan and Guntenspergen 2012). Salt marsh acreage has declined by 40% over the past 100 years in the Tampa Bay region (DEP 2010), as a result of rapid metropolitan growth and extensive dredging. Hence, any increases in tidal influence in this area could cause additional impacts by further altering already diminished salt marsh communities.

The low topographic relief of Tampa Bay makes Florida west coast marshes susceptible to sea level rise (Williams et al. 1999) and an ideal location for studying its effects. To our knowledge, no experimental studies exist that quantify the effects of varying levels of tidal inundation and the presence of neighboring species on Florida west coast marsh-upland communities. This study had two main objectives. First, the effects of different amounts of sea level rise were simulated by transplanting four terrestrial fringe species, *Andropogon glomeratus, Baccharis angustifolia*, *Baccharis halimifolia,* and *Iva frutescens*, toward lower marsh at three distances. This helped to quantify the physiological stress responses of these four species to two effects:

increased salinity exposure and increased inundation due to sea level rise, to determine under what circumstances they would begin to be affected. The species spanned a range of growth forms from grasses to small shrubs and small trees. This is a unique approach because most studies only quantify the effects of a single variable on a limited number of species, failing to investigate the impact of covarying factors (Brinson et al. 1995; Walther 2007). One of the novel aims of our study was to also investigate the differential responses of all four fringe species to changing abiotic conditions. Second, the relative importance of facilitative and competitive interactions in affecting plant performance and survival were quantified by incorporating neighbor manipulation treatments to see if biotic interactions changed in response to different stress levels. This study poses two questions: 1) What levels of sea level rise negatively impact the performance and survival of terrestrial fringe species? 2) Is the performance and survival of salt marsh fringing species influenced more by facilitative or competitive pressure from existing plant species as conditions change?

While we expect that all four fringe species will experience reduced growth and survival with seaward transplantation, we predict some differential responses of the species to the increased tidal influence. *B. angustifolia* is anticipated to outperform *B. halimifolia* at all transplant positions. *B. angustifolia's* root system lies closer to the surface, which may allow this species to intercept more water and nutrients following short rain events. We also predict that both *Baccharis* species will perform better than *Iva frutescens* at all seaward transplant positions. *Iva* is similar to both *Baccharis* species in that it is fairly tolerant to saline conditions but it possesses a narrower pH tolerance between 5-5.7 and is relatively intolerant of anaerobic conditions.

Andropogon plant individuals are predicted to exhibit low survival rates when transplanted to any of the seaward positions due to their higher salt intolerance. The shading provided by neighbors is also expected to have a greater negative impact on this C_4 nonhalophytic species than the other species which are equipped with a C_3 photosynthetic pathway. Typically, C_3 species are favored under limited light conditions since they require less energy to fix CO_2.

Materials and Methods

Study System

All field work for this study was conducted at Upper Tampa Bay Park (28°00′48″N, 82°38′05″W), a 867 hectare park. Tampa Bay experiences an estimated mean tidal range of 0.52 m (http://tidesandcurrents.noaa.gov/ports/ports.shtml?stn=8726607+Old Port Tampa&port=tb). The region's average annual temperature is 23.0°C and average annual precipitation is approximately 127 cm (NOAA 2009; Yates et al. 2011). Mean monthly rainfall is approximately 17.8 cm during the rainy season and 5.8 cm during the dry months with approximately 60 percent of the annual rainfall occurring during the rainy season from June through September (NOAA 2009; Yates et al. 2011). Although annual and seasonal precipitation is variable from year to year, there were no significant storm events to report during 2011-2012 when this study was being conducted (NOAA 2012). Sea level rise at Upper Tampa Bay Park has been documented at approximately 30.48 cm every 100 years (http://www.hillsboroughcounty.org/parks). Marsh areas at the study site are bordered by a conspicuous tree-line, dominated by pine flatwoods forest (Fig. 2.1). Species prevalent in this area include *Serenoa repens* (saw palmetto), *Sabal palmetto* (cabbage palm), and *Pinus elliottii* (slash pine). The upper terrestrial fringe borders the forest and is dominated by target species *Andropogon glomeratus* (bluestem grass), *Baccharis angustifolia* (saltwater false willow), *Baccharis halimifolia* (eastern baccharis), and *Iva frutescens* (marsh elder). This zone served as the site for the first two sets of transplants moved a distance of 0 m (control) and 4.6m (equivalent to a 1 cm rise in sea level and at the lower limits of the fringe). The terrestrial fringe transitions to high marsh area, which is dominated by *Juncus roemerianus* (needlegrass rush) and *Frimbristylis cymosa* (hurricane grass). This zone extends approximately 7.5 meters seaward beyond the lower distributional limits of the terrestrial fringe and served as the site for the third set of transplants, moved a lateral distance of 9.3 meters (equivalent to a 2 cm rise in sea level). Areas of the lower marsh are inhabited by *Avicennia germinans* (Black mangrove), *Borrichia frutescens* (seaside oxeye), *Batis maritima* (saltwort), *Monanthochloe littoralis* (keygrass), *Sesuvium portulacastrum* (sea purslane), and *Sporobolus virginicus* (seashore dropseed). This area served as the site for transplants moved a distance of 14 meters (equivalent to a 3 cm rise in sea level).

A 50 m x 50 m study site was surveyed at one meter intervals using a TOPCON AT-G2 autolevel (TOPCON, Livermore, CA, USA) to determine the vertical grade from the lower marsh to the forest margin. This data established the four transplant distances, equivalent to 0 cm, 1 cm, 2 cm, and 3 cm changes in vertical elevation, at 0 m, 4.6 m, 9.3 m, and 14 m, respectively. The furthest seaward distance simulated a projected decadal increase in sea level if there was no accompanying substrate accretion. This estimate is based on the documented 3mm/year sea level rise over the past 100 years at Upper Tampa Bay Park and excludes any likelihood of accelerated rates in sea level rise (http://www.hillsboroughcounty.org/parks). The other two transplant distances approximated a 1 and 2 cm sea level increase, respectively.

Seaward Transplantation

We moved four terrestrial fringe species, *Andropogon glomeratus, Baccharis angustifolia*, *Baccharis halimifolia,* and *Iva frutescens*, distances 0 m, 4.6 m, 9.3 m, and 14 m, (approximates 0 cm, 1 cm, 2 cm, and 3 cm decreased in elevation, respectively), into lower fringe and marsh areas starting from their positions in the upper terrestrial fringe zone. All four study species were transplanted among *Iva frutescens* at the 4.6 m position (1 cm elevational decrease). All plants were transplanted among *Juncus roemerianus* (needlegrass rush) at the 9.3 m position (2 cm elevational decrease). Finally, all transplants at the 14 m position (3 cm elevational decrease) were neighbored by *Borrichia frutescens* (seaside oxeye), *Batis maritima* (saltwort), and *Monanthochloe littoralis* (keygrass). We selected plant individuals of approximately the same height for each species; 1.3 m to 1.5 m for *Andropogon*, and 1.5 m to 1.8 m for *Iva* and both *Baccharis* species. Three replicates of each the four species were assigned to 4 treatments with two levels of neighbor manipulation to yield 96 plots. In addition, 12 reference plants at the 0 m position (3 for each of the species) received no treatment and were not dug up. Our objective with these reference plants was to test for transplant effects.

We transplanted species by excising and placing root balls into size-matched holes at the desired distances. Any gaps along the edges of the holes were filled with substrate from the original plot. This is a well-proven transplant protocol with no obvious differential transplant effects (Bertness and Ellison 1987; Emery et al. 2001). Our transplant regime of moving species to lower elevations naturally simulates encroachment of saline conditions and increased inundation into a terrestrial fringe zone.

Neighbor Manipulation

We established neighbor manipulation plots around half of the transplants. An area of 0.50 m x 0.50 m around each transplant was flagged at each corner. In the neighbor manipulation treatment plots, neighboring vegetation was clipped at ground level within 30 cm surrounding each plant for the entire duration of the experiment in a manner similar to neighbor manipulation plots performed in New England salt marshes by Bertness et al. (1992). Removing neighbors in their entirety would have resulted in significant spikes in soil salinities, which would have potential adverse effects on the target plants. In fringe areas, taller neighbors were also cut to ground level to eliminate canopy cover.

Soil Characteristics

We measured a suite of substrate variables, (pH, salinity, moisture, redox potential, and sulfide concentration) monthly. Soil redox potential and pH were measured with a hand held Spectrum model 8601 pH/mV meter (Spectrum, Plainfield IL, USA) for 3 sub-samples taken at 5 cm depths. An average of subsamples for each plot was used for statistical analysis. Soluble sulfide concentrations were measured using a Hach DREL/2400 portable spectrophotometer (Hach, Loveland, CO, USA). Sulfate is a common anion in water and soil with a range of a few ppm to greater than 1,000 ppm. Concentrations in excess of 250 ppm have been shown to have a cathartic effect on plants. Soil moisture was measured by recording the mass (g) of collected soil samples taken at 5 cm depth, drying to a constant mass, then subtracting dry mass (g) from initial mass (g) and converting moisture to a percentage. Salinity was measured by rehydrating the dried soils in a known volume of deionized water and reading the salinity of the supernatant after 1 day with a Vista A366ATC refractometer.

Plant Performance and Survival

Plant performance in all plots was measured pre-treatment in June 2011 and monthly after treatments were performed in June 2011. Data were taken on all surviving plants for a year. Plant height was measured from ground height to apical meristem. At each census, we haphazardly selected five stems on *Iva frutescens, Baccharis halimifolia, and Baccharis angustifolia* and then measured stem lengths. Total leaf counts were also conducted on these same selected stems. For *Andropogon* *glomeratus,* basal coverage was determined by measuring the diameter of the clump 2 cm above the ground to calculate the circular area of the foliage. Plant circumference was recorded by measuring the diameter of the crown of foliage at its densest portion. Plant growth was determined by subtracting the initial measurements from measurements after 4 months.

To examine the effects of the treatments on plant physiological condition, fluorescence measurements were conducted monthly on young leaves of all target plants using an Underwater Fluorometer Diving-PAM, Submersable Photosynthesis Yield Analyzer (Heinze Walz GmbH, Germany). Three dark adapted measurements were averaged to produce a single value for each plant individual. The potential quantum yield (Φ_{PSII}), or how efficient a plant is in using available light energy to fix carbon dioxide, serves as a reliable indicator of photosystem II (PSII) efficiency. Since the efficiency of photosystem II photochemistry is correlated with linear electron transport rates, chlorophyll fluorescence measurements are also an indicator of overall photosynthetic performance (Maxwell and Johnson 2000). As plants become stressed or as irreversible damage to photosystem II apparatus occurs, quantum yield values decline. Optimal (Φ_{PSII}) range for most flowering plant species is 0.79 – 0.83, with values ranging from 0 to 1.0 (Maxwell and Johnson 2000). Collection of fluorescence data yields a more complete picture of the impact of stress on photosynthesis and physiological tolerance of a plant to changing environmental conditions than would growth data alone.

Treatment effects on plant height, circumference, branch length, leaf production, chlorophyll fluorescence yields, and soil characteristics were tested using Analysis of

Variance with transplant distance, neighbor manipulation, and plant species as main effects using data after 4 months, and for fluorescence 30 days and 4 months, after transplantation. After 4 months, there were too many plant deaths to be able to perform the ANOVAs. Plant survival was analyzed using ANOVA on mean plant longevity after 1 year. There were no significant three-way interactions and no two-way interactions except as noted.

Results

Pre-treatment Comparisons

All transplants at 0 m (0 cm elevational decrease) showed no effects of transplantation on plant growth, chlorophyll fluorescence, or survival when compared to the reference plots ($p > 0.05$ in all cases). There were also no significant differences between individuals of the same plant species in pre-treatment measurements in June 2011 ($p > 0.05$ in all cases).

Effects of Seaward Transplantation

Soil characteristics

Interstitial water salinities increased with seaward transplantation distance ($F_{1,64} = 6.114$, $p = 0.004$; Fig. 2.2a). Soil moisture was also significantly affected by transplant distance ($F_{1,64}$ = 5.422, p = 0.002), being highest at the most seaward marsh position. There were also sharp reductions in substrate redox potentials with seaward progression ($F_{1,64}$ = 5.325, p = 0.024; Fig. 2.2b). Variation in substrate pH was slight, but increased with distance from the upper terrestrial fringe, resulting in a significant transplant distance effect ($F_{1,64}$ = 4.314, p = 0.042). Lower pH at the terrestrial fringe may be attributed to the presence of increased leaf litter. There were no significant effects of plant species on soil salinity, soil moisture, redox potential, and pH ($p > 0.05$ in all cases). Soil characteristics showed very similar patterns after 1 year. The presence of hydrogen sulfide was undetectable.

Plant performance and survival

After 4 months, moving plants seaward had a significant effect on plant height, circumference, branch length, and leaf production for all plant species ($F_{1,64}$ = 6.962, $p <$ 0.001; $F_{1,64}$ = 9.831, $p < 0.001$; $F_{1,48}$ = 2.873, p = 0.018; $F_{1,48}$ = 6.112, p = 0.004, respectively; Fig. 2.3). Plant growth decreased with seaward transplant distance, with plants transplanted 14 m into the marsh (3 cm elevational decrease) exhibiting the most reduced growth. There was also an interaction of plant species and transplant distance on height growth, circumference growth, and leaf production ($F_{1,64}$ = 6.750, p = 0.012; $F_{1,64}$ = 2.315, p = 0.025; $F_{1,48}$ = 2.393 , p = 0.076, respectively), since transplantation had less impact on *B. halimifolia*'s growth than for the other species.

Potential quantum yield was impacted by seaward transplant distance for all four species after both 30 days and 4 months ($F_{1, 64}$ = 2.312, p = 0.026; $F_{1, 64}$ = 6.115, p = 0.004, respectively; Fig. 2.4). However, fluorescence yield after 30 days for all species was greater than after 4 months, reflecting an ability of all species to maintain photosynthesis better under short-term stress than long-term stress (Fig. 2.4). Plants transplanted only 4.6 m beyond their current positions (1cm elevational decrease) experienced less photosynthetic inhibition than species transplanted 9.3 m and 14 m. Distant transplants showed photosynthetic inhibition even after 30 days, and even greater inhibition after 4 months. *I. frutescens, A. glomeratus* and *B. angustifolia* exhibited lower potential quantum yields than *B. halimifolia*, yielding an interaction of species and transplant distance on potential quantum yield at both 30 days and 4 months ($F_{1,64} = 2.067$, $p = 0.045$; $F_{1,64} = 2.309$, $p = 0.027$, respectively).

Seaward transplantation reduced plant survival after 1 year, with plants at the most seaward transplant position experiencing the greatest number of plant deaths ($F_{1,64} = 4.775$, $p < 0.001$; Fig. 2.5). *B. halimifolia* persisted better at all transplant distances than *I. frutescens, B. angustifolia* and *A. glomeratus*, yielding a marginally significant interaction of plant species and transplant distance on survival ($F_{1,64} = 2.042$, $p = 0.055$.

Effects of Neighbor Manipulation

Soil characteristics

The clipping of neighboring vegetation resulted in higher soil salinity levels and lower redox potentials at all transplant positions, yielding a significant effect on mean soil salinities ($F_{1,64} = 6.960$, $p < 0.001$). and soil redox potentials ($F_{1,64} = 2.581$, p =

0.012; Fig. 2.2). Neighbor manipulation but did not result in any change in soil moisture ($F_{1,64}$ = 1.168, p = 0.329), or pH ($F_{1,64}$ = 0.807, p = 0.372). Clipping of neighboring vegetation resulted in higher soil salinity levels and lower redox potentials at all transplant positions. This effect was greatest in the high marsh zone (2 cm elevational decrease), but barely noticeable in the low marsh zone (3 cm elevational decrease) resulting in an interaction of neighbor manipulation and treatment on both soil salinity and redox ($F_{1,64}$ = 6.874, p < 0.001; $F_{1,64}$ = 6.683, p < 0.001, respectively).

Plant performance and survival

The effect of neighbor manipulation on plant performance and survival differed with seaward transplant distance (Fig. 2.3). All species performed better without neighboring above ground vegetation in the terrestrial fringe (0 cm elevational decrease and 1 cm elevational decrease zones), but better with neighbors in the high marsh zone (2 cm elevational decrease) (significant neighbor manipulation x transplant distance effects, ($F_{1,64}$ = 7.841, p < 0.001; $F_{1,64}$ = 6.326, p < 0.001; $F_{1,64}$ = 7.589, p < 0.001, respectively), for height, circumference, leaf production). Our data showed little effect of neighbors in the low marsh zone (3 cm elevational decrease). Neighbors had no effect on branch length ($F_{1,48}$ = 0.432, p = 0.652).

Neighbor manipulation had significant effects on potential quantum yield for all species during the first 30 days ($F_{1,64}$ = 5.426, p = 0.002), and after 4 months ($F_{1,64}$ = 4.528, p < 0.001). After 30 days and at 4 months, transplants in the 0 cm and 1 cm elevational decrease plots experienced greater photosynthetic inhibition with neighbors (Fig. 2.4). Conversely, plants in the upper marsh position (2 cm elevational decrease) were more inhibited without neighboring above ground vegetation both after 30 days and 4 months. In the lower marsh, potential quantum yield was unaffected by neighbors. These findings show an interaction of neighbor manipulation with transplant distance on potential quantum yield at both 30 days and 4 months ($F_{1,64} = 3.803$, $p = 0.015$; $F_{1,64} = 7.378$, $p < 0.001$, respectively).

Neighbor manipulation also impacted plant survival ($F_{1,64} = 2.402$, $p < 0.001$; Fig. 2.5). Neighbor manipulation increased survival in the fringe zone at both the upper and lower transplant locations (0 cm, 1 cm elevational decrease), had the opposite effect in the upper marsh plots (2 cm elevational decrease), but no effect in the lower marsh plots (3 cm elevational decrease) ($F_{1,64} = 4.119$, $p < 0.001$; Fig. 2.5), yielding a significant interaction of neighbor manipulation and transplant distance on survival.

Discussion

Effects of Seaward Transplantation

Our results revealed that all species at the marsh-terrestrial interface are negatively impacted by additional inundation and saline conditions that would result from rising sea levels. After four months, all plant species experienced reduced growth and performance, (plant height, circumference, branch length, leaf production, and chlorophyll fluorescence yield), even 1 vertical centimeter below their current positions. Growth and fluorescence yield were even more impacted at 2 and 3 vertical centimeters lower.

Contrary to our predictions, all four fringe species responded similarly to increased tidal influence. As expected, all species experienced reduced survival with seaward transplantation after one year. Although all four fringe species exhibited slight differences in growth, performance, and survival, these differences did not yield a main species effect. Species identity was only important under certain conditions as *B. halimifolia* experienced less morbidity than the other species and outperformed the other species under conditions of increased abiotic stress. We did not anticipate *B. halimifolia* to outperform *B. angustifolia* since both perennial shrubs are characterized by similar growth rates, as well as comparable anaerobic and salinity tolerance. We also predicted that both *Baccharis* species would perform better than *Iva frutescens* at all seaward transplant positions. *Iva* is similar to both *Baccharis* species in that it is fairly tolerant to saline conditions but it possesses a narrower pH tolerance between 5-5.7 and is relatively intolerant of anaerobic conditions. Interestingly, *Iva* experienced slightly more growth and higher survival than *Baccharhis angustifolia*, though these findings were not statistically significant. *Iva* possesses a deeper root depth (40.6 cm.) than *Baccharsis angustifolia* (30.5 cm.) and may be more capable of garnering accumulated sub-surface waters, especially during drier periods. We also expected all *Andropogon* plant individuals to die when transplanted to any of the seaward positions due to their higher salt intolerance. Interestingly, *Andropogon* performed similarly to the other three fringe species at all seaward transplant positions and in our neighbor manipulation studies. *Andropogon* exhibited slightly less growth and survival than *Iva* and both *Baccharis* species but persisted longer than expected. *A. glomeratus* has been shown to exhibit genetic differentiation for tolerance to varying levels of salt and inundation exposure (Bowman and Strain 1988). Bowman and Strain (1988) showed that two populations of *Andropogon* (inland and marsh) differed in survival following short-term inundation exposure. Plant individuals from the marsh population exhibited more rapid recovery of photosynthetic capacity following the inundation exposure, affording these plant individuals a higher capacity to survive inundation events. In this study, it is possible that *Andropogon* individuals representative of the more stress tolerant marsh population were selected. The lack of main species effect and lack of high variance for growth and performance suggest that the environment may have a stronger effect than genotype on these species growth, performance, and survival.

Overall, our results suggest that many terrestrial fringe species may not be capable of tolerating changing abiotic conditions associated with moderate sea level rise. Similar findings were reported by Bertness et al. (1992), who found that *I. frutescens* experienced reduced survival with seaward transplantation, suggesting an intolerance of this species to flooded and saline conditions, compared to marsh species. As sea levels rise, the frequency and duration of inundation and saline conditions are expected to increase, both of which have been shown to directly influence plant growth and survival in other salt marsh systems (Donnelly and Bertness 2001; Emery et al. 2001; Miller et al. 2001; Desantis et al. 2007; Chaves et al. 2009; Rasser et al. 2013; Wasson et al. 2013). Most of the transplants were able to survive the four months from transplantation in June through October, but after the rainy season ended, the effects of more stressful conditions likely caused increased plant death. Langley et al. (2013) reported similar findings in their experiments where plants were placed on sloping terraces and exposed to different levels of inundation by sea water. All plants exposed to the high levels of tidal inundation died within 2 years.

Effects of Neighbor Manipulation

In this study, biotic interactions were found to be important in mediating plant growth, photosynthetic capacity, and survival under conditions of stress. All four plant species at 0 cm and 1 cm elevational decrease transplant distances experienced more growth in the absence of neighbors, while transplants at the 2 cm elevational decrease positions exhibited the greatest increase in growth with neighbors. Transplants at the 3 cm elevational decrease positions appeared unaffected by neighbors. These findings suggest that at higher elevations, interspecific competitive interactions influence plant performance and survival. Stunted growth in the presence of tall neighboring *Baccharis angustifolia*, *Baccharis halimifolia,* and *Iva frutescens* in the terrestrial fringe (at the 0 cm and 1 cm elevational decrease transplant positions) may have resulted from reduced light infiltration, competition for space, or altered nutrient status. Even though neighbors can alleviate salt stress and oxygenate the soil, in the more benign conditions of the terrestrial fringe, where salinity is generally low and redox high, such effects may not be important. The competitive effects of neighbors on light availability, moisture, or nutrients are stronger than the facilitative effects at higher elevations than in marsh areas because the taller fringe species likely cast more shade on their neighbors and intercept more water and nutrients than smaller marsh species. Furthermore, a trade-off may exist between stress tolerance and competitive ability (Bertness 1991; Levine et al. 1998; Costa et al. 2003). The more stress intolerant species in terrestrial fringe zones may be more capable of allocating resources to production, rather than to specialized adaptations to stress, which would in turn enhance their competitive ability.

At the more seaward positions (2 cm elevational decrease), all four plant species appeared to benefit from the presence of neighbors, providing compelling evidence that the enhanced growth was the result of facilitative interactions. Marsh zones are typically characterized by higher soil salinities, and plant shading provided by neighbors can limit surface evaporation and substrate salt accumulation, benefiting the less salt tolerant terrestrial plants. While there still may be competition for space, water, minerals, and nutrients among neighbors at this transplant position, the lower height of the vegetation in the high marsh (*Juncus roemerianus* (needlegrass rush) and *Frimbristylis cymosa* (hurricane grass) makes competition for light much less likely with the taller *Baccharis angustifolia*, *Baccharis halimifolia,* and *Iva frutescens.* Additionally, marsh plants possess more arenchyma to effectively oxygenate their rhizosphere, which, in turn has been shown to ameliorate soil conditions at these lower elevations by effectively raising soil redox potentials (Bertness and Hacker 1994). Clipping of neighbors in this high marsh zone subsequently has the potential to create more reducing conditions, which, in turn drives down soil redox potentials below critical values. Bertness and Shumway (1993) reported similar findings, suggesting that facilitative interactions are prevalent under harsh environmental conditions of the upper marsh where neighbors can act as buffers, moderating physical stress. Our results support others that have found facilitation to be pervasive in areas which experience more physical stress until conditions become too stressful, suggesting that species interactions tend to shift from competitive to facilitative as plants begin to experience harsher environmental conditions (Bertness and Shumway 1993; Bertness and Hacker 1994; Bertness and Ewanchuk 2002) Interestingly, transplants in the low marsh zone (3 cm elevational decrease) experienced little increased growth with neighbors, suggesting that the benefits of neighbors are less able to overcome the impact of physical stress under more harsh environmental conditions. In the more highly saline areas of the lower marsh, where inundation is more frequent, even the presence of neighboring salt marsh species cannot compensate for the stressful nature of the environment. Thus, our results firmly support the ideas of He and Bertness (2014) that species interactions shift from competitive to facilitative with increased stress but such facilitation collapses in areas of high stress outside of species realized niches.

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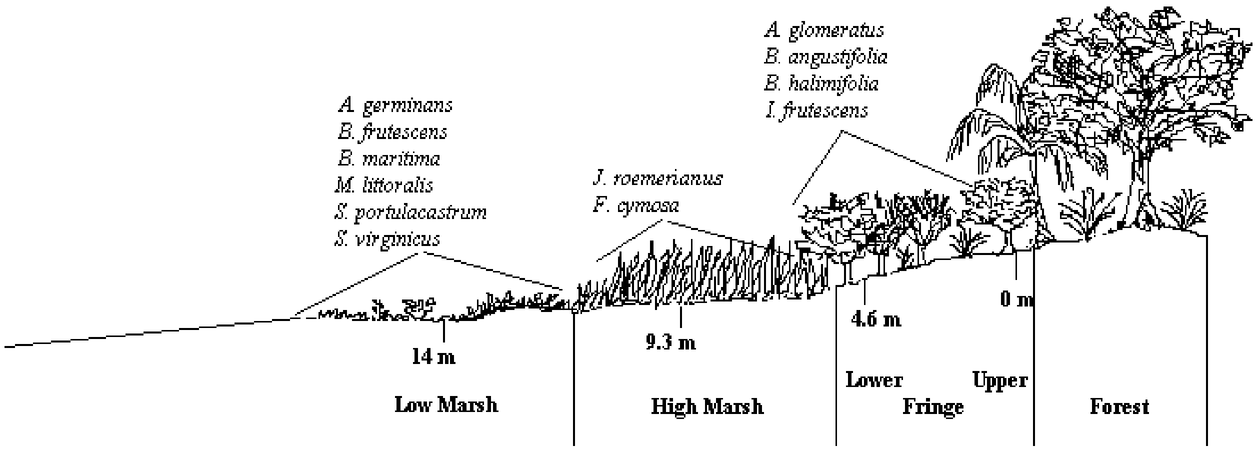
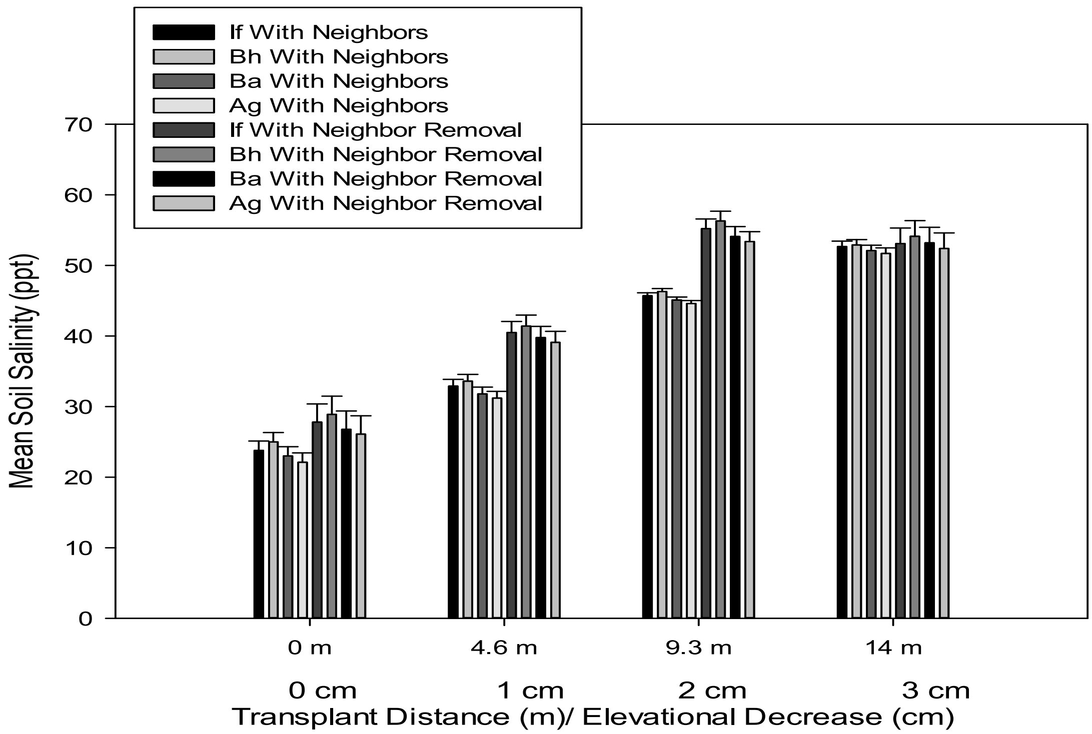


Figure 2.1: Schematic diagram of the study site illustrating the vegetation zones and transplant design. Distances represent transplant sites.



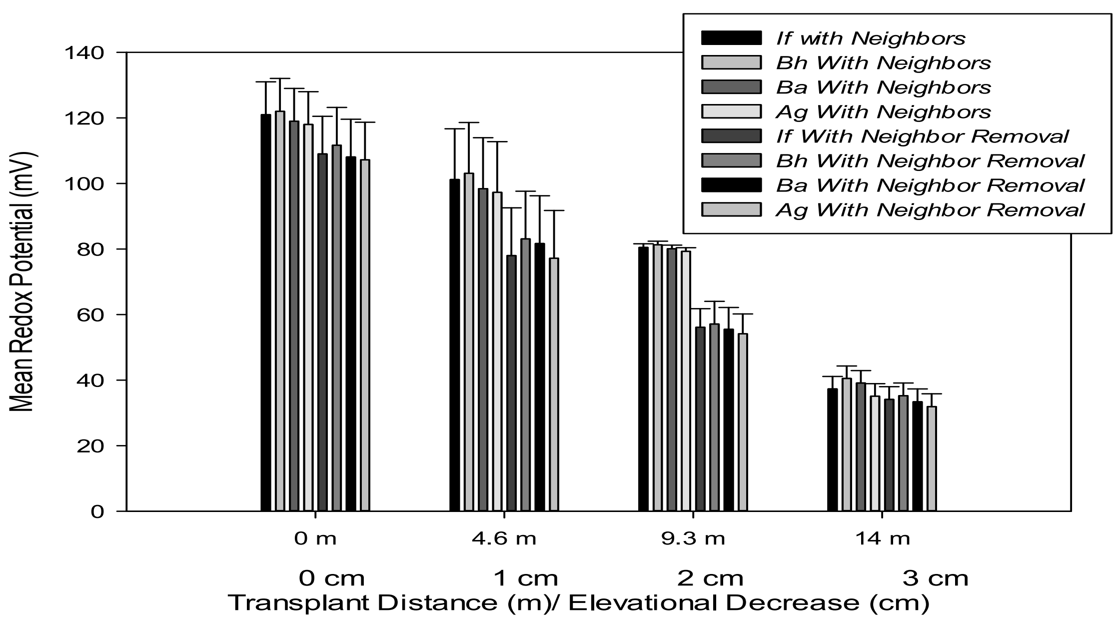


Figure 2.2: Mean (a) interstitial soil salinity (ppt), (b) redox potential (mV) for *Iva frutescens (If) Baccharis halimifolia (Bh), Baccharis angustifolia (Ba), and Andropogon glomeratus (Ag),* at different transplant positions with and without neighboring above ground vegetation after 4 months. Bars represent ± 1 SE. n = 3

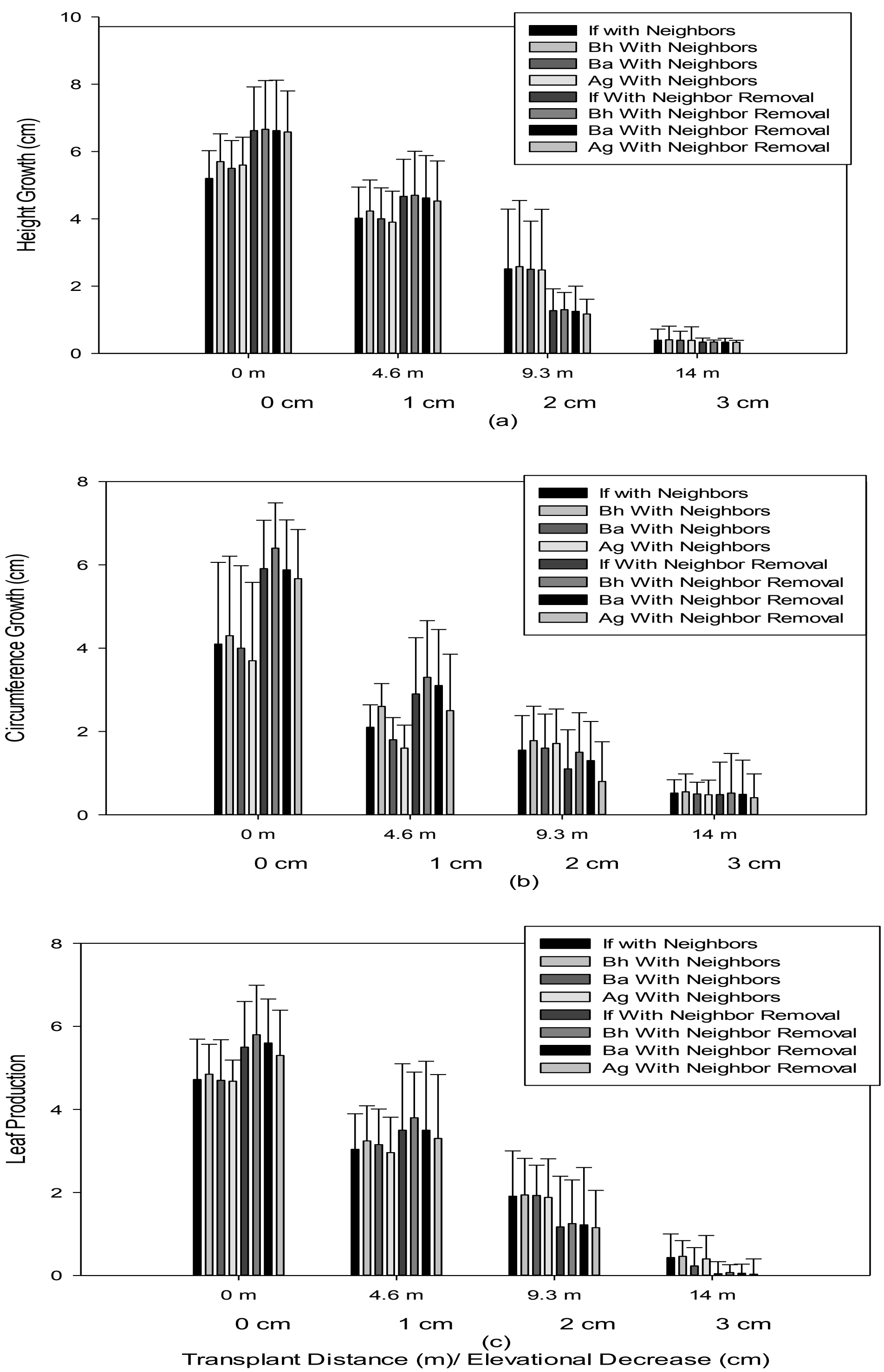


Figure 2.3: Average (a) height growth, (b) circumference growth, and (c) leaf production for *Iva frutescens (If), Baccharis halimifolia (Bh), Baccharis angustifolia (Ba), and Andropogon glomeratus (Ag*) at different transplant positions with and without neighboring above ground vegetation after 4 months. Plant growth was determined by subtracting the initial measurements from measurements after 4 months. Bars represent ± 1 SE. n=3

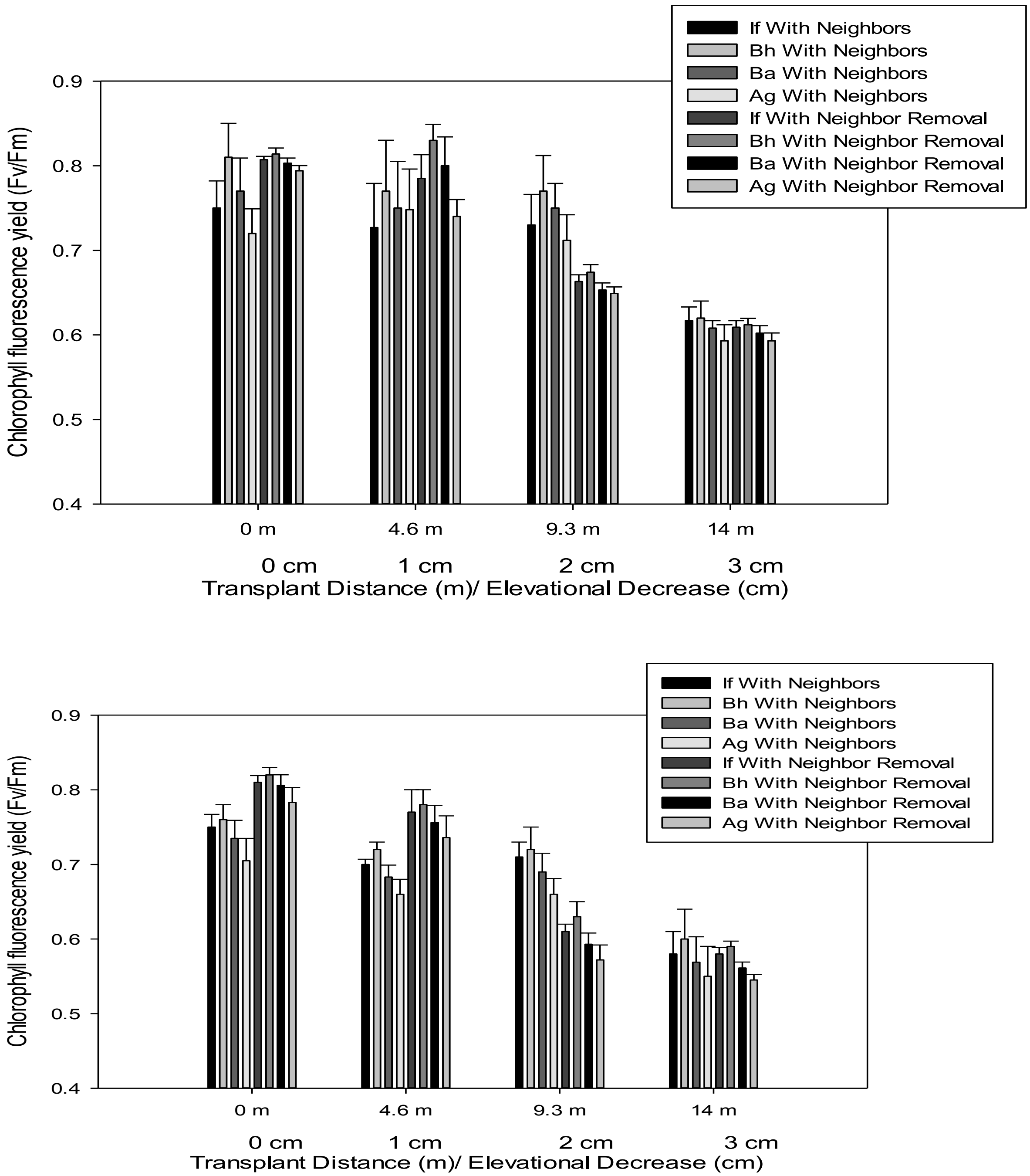


Figure 2.4: Average potential quantum yield (Fv/Fm) for *Iva frutescens (If), Baccharis halimifolia (Bh), Baccharis angustifolia (Ba), and Andropogon glomeratus (Ag*), at different transplant positions with and without neighboring above ground vegetation after 30 days and 4 months. Bars represent ± 1 SE. n=3

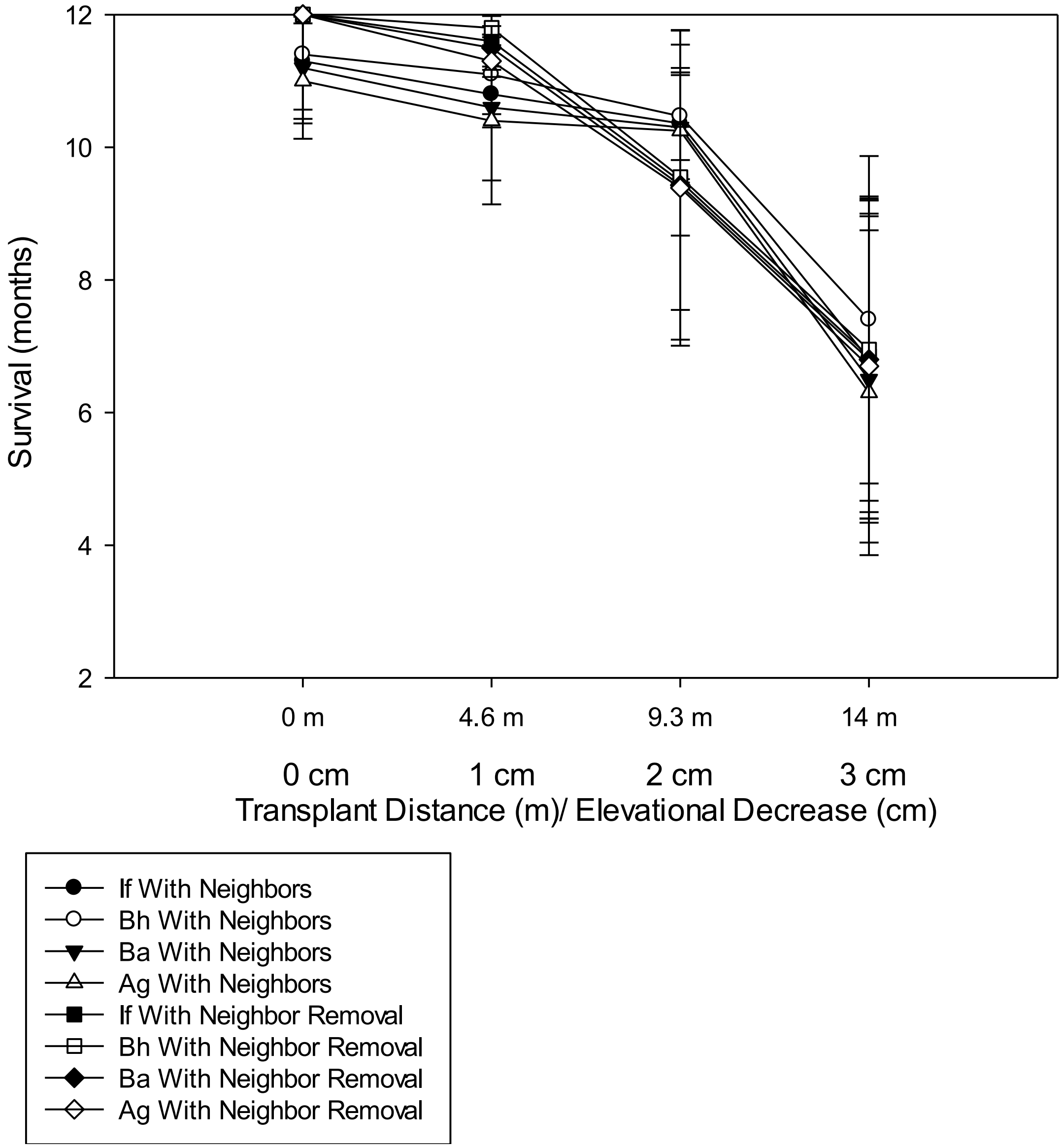


Figure 2.5: Mean survivorship of *Iva frutescens (If), Baccharis halimifolia (Bh), Baccharis angustifolia (Ba), and Andropogon glomeratus (Ag)*, at different transplant positions with and without neighboring above ground vegetation after 1 year. Bars represent ± 1 SE. n=3

Table 2.1: ANOVA *F* statistics and significance are presented for the effects of species, transplant distance, and neighbor manipulation on soil characteristics, performance, and survival of four salt marsh fringing species using data 4 months, and for fluorescence 30 days and 4 months, after transplantation. Plant survival was analyzed on mean plant longevity after 1 year. There were no significant species effects or three-way interactions to report. *P<0.05; **P<0.01; ***P<0.001; NS P>0.05

	Soil Salinity	Soil Moisture	Soil Redox	Soil pH
Source of variation	F	F	F	F
Transplant Distance	6.114**	5.422**	5.325*	4.314*
Neighbor Manipulation	6.960***	1.168 NS	2.581*	0.807 NS
Species	0.972 NS	1.039 NS	0.851 NS	0.468 NS
Species x Transplant Distance	1.431 NS	1.437 NS	1.654 NS	0.583 NS
Species x Neighbor Manipulation	0.891 NS	0.873 NS	0.907 NS	0.061 NS
Transplant Distance x Neighbor Manipulation	6.874***	0.163 NS	6.683***	0.653 NS

	Height	Circumference	Branch Length	Leaf Production	Chlorophyll Fluorescence Yield		Survival
					30 days	4 months	
Source of variation	F	F	F	F	F	F	F
Transplant Distance	6.962***	9.831***	2.873*	6.112**	2.312*	6.115**	4.775***
Neighbor Manipulation	5.422 **	5.334 *	0.489 NS	0.531 NS	5.426**	4.528***	2.402***
Species	1.083 NS	2.034 NS	0.431 NS	1.187 NS	1.352 NS	0.978 NS	1.461 NS
Species x Transplant Distance	6.750*	2.315*	1.270 NS	2.393NS	2.067*	2.309*	2.042 NS
Species x Neighbor Manipulation	3.114 NS	2.396 NS	0.432 NS	0.323 NS	1.079 NS	1.289 NS	1.738 NS
Transplant Distance x Neighbor Manipulation	7.841***	6.326***	0.823 NS	7.589***	3.803*	7.378***	4.119***

CHAPTER 3

INUNDATION AND SOIL SALINITY INFLUENCE THE IMPORTANCE OF FACILITATION AND COMPETITION IN SALT MARSH FRINGING SPECIES

Synopsis

As rising sea levels flood salt marshes and increase soil salinity, fringe species at the marsh-upland interface may be more impacted than salt marsh plants because fringe species lack the physiological mechanisms to cope with increasing soil salinity and water levels. Such impacts may or may not be ameliorated by the presence of neighboring plant species. To disentangle the effects of increased soil salinity and increased soil moisture on four salt marsh fringing species, *Andropogon glomeratus* (bluestem grass)*, Baccharis angustifolia* (saltwater false willow, *Baccharis halimifolia* (eastern baccharis*),* and *Iva frutescens* (marsh elder), and to examine the effects of plant neighbors, we employed plant transplants seaward and landward of their original positions and the addition of salt pellets. Soils (salinity, moistre, redox, pH, sulfide), growth (height, circumference, leaf production), performance (fluorescence), and survival measurements were recorded for all plant individuals for one year. For all species, seaward-transplanted plants exposed to increased inundation and salinity experienced a 50% reduction in performance over those in their original positions

receiving just pure salt addition. Those plants receiving just salt addition experienced less of a reduction in performance and survival over controls, which suggests that inundation may influence marsh fringing plants more than increased soil salinity. Landward transplants exposed to lower soil salinity and decreased inundation exhibited a three-fold increase in performance and survival. The neighbor manipulation studies revealed that neighbor manipulation in the more benign landward transplant locations fringing the marsh resulted in increased vegetative growth for all four species but had the opposite effect on seaward transplants that experienced higher salinity and increased soil inundation. These results suggest that interspecific interactions in salt marsh fringing species may shift from competitive to facilitative with climate-induced sea level rise.

Introduction

There is general consensus that rising sea levels will spawn numerous changes to salt marshes and their adjoining terrestrial communities. If sea-levels continue to rise, as predicted, some studies have suggested that the fringe areas at the marsh-upland interface will experience more profound impacts than species in marsh areas (Orson et al. 1985; Raabe et al. 2012; Wasson et al. 2013). Many salt marsh plant species are equipped with the necessary metabolic and architectural adaptations to tolerate some salt and inundation stresses, which afford them a better chance of persisting with increases in sea level (Bertness and Hacker 1994; Donnelly and Bertness 2001; Emery et al. 2001). Terrestrial fringe species, however, lack these physiological mechanisms and, under conditions of sea-level rise, may experience a decline in gross production (Olff et al. 1997; Miller et al. 2001; Morris et al. 2002; Keammerer and Hacker 2013; Voss et al. 2013), depressed plant metabolism (Nyman and DeLaune 1991; Miller et al. 2001), and diminished survival (Adams 1963; Mendelssohn et al. 1981; Howes et al. 1981; Williams et al. 1999a; Donnelly and Bertness 2001; Emery et al. 2001). As such, any increased tidal influence at the marsh-upland margin could precipitate more drastic changes to plants in this zone than to plants in the marsh itself.

As sea levels rise, reductions in fringe plant performance and survival could result from increases in soil salinity, from increases in inundation, or from both. Some studies have shown increased salt exposure to be the primary determinant of reduced plant performance and survival as sea levels rise (Pennings and Callaway 1992; Young et al. 1994; Broome et al. 1995; Williams et al. 1999a; Desantis et al. 2007; Chaves et al. 2009). Reduced plant growth under saline conditions may be attributable to lowered plant turgor, ion toxicity, or lowered photosynthesis (Bowman and Strain 1987) and salinity levels in excess of 35ppt have been shown to also alter plant morphology, chemistry, and herbivory levels (Bowdish and Stiling 1998; Moon and Stiling 2000, 2002a, 2002b). Other authors suggest that although marsh plants and adjoining species may exhibit diminished performance and survival with increasing salinity, inundation has larger effects on these communities (Bertness and Ellison 1987; Donnelly and Bertness 2001; Emery et al. 2001; Miller et al. 2001; Rasser et al. 2013; Wasson et al. 2013). Plants under inundation conditions have been shown to experience increased loss of salts, nutrient limitation, and increased exposure to soil sulfides and phytotoxins (Adam 1990; Reed 2002; Stiling and Moon 2005). Inundation also promotes the decomposition of organic matter which may further deplete soil oxygen and exacerbate anoxic soil conditions. To our knowledge, no experimental studies have been conducted to ascertain whether salt exposure or inundation due to sea level rise is the primary influence of plant performance and survival in communities fringing the marsh.

It is possible that the presence of neighboring plant species may be able to moderate the impact of changing environmental conditions, facilitating the survival of some fringing species. The stress-gradient hypothesis (SGH), coined by Bertness and Callaway (1994), predicts that the frequency and importance of facilitative interactions increase as conditions become more stressful for plants. This hypothesis has been repeatedly supported in both intertidal and terrestrial studies and across growth forms, climatic zones and stress types (Callaway and Davis 1993; Bertness and Callaway 1994; He et al. 2013; He and Bertness 2014). Studies of salt marsh systems have shown that while competition appears to be the pervasive force in the less physically stressful terrestrial zones fringing salt marshes, facilitation influences the performance and survival of species in harsher marsh areas (Bertness et al. 1992; Pennings and Callaway 1992; Bertness and Shumway 1993; Bertness and Callaway 1994; Levine et al. 1998; Bertness and Ewanchuk 2002; Charles and Dukes 2009). The presence of neighbors has been shown to elevate soil oxygen in waterlogged areas (Bertness and Hacker 1994; Ewanchuk and Bertness 2004) and ameliorate hypersaline conditions for less stress tolerant species (Bertness and Hacker 1994; Callaway 1994). So, under conditions of sea level rise, a shift in the nature of interactions from competitive to facilitative could occur in the more benign terrestrial fringe, though this has not yet been investigated. Here, we quantified the performance and survival of species in terrestrial fringe zones to changing soil salinity and soil moisture and assessed how increased stress interplays with biotic interactions.

This study had four main objectives. First, we simulated the effects of sea level rise by transplanting four terrestrial fringe species, *Andropogon glomeratus, Baccharis angustifolia*, *Baccharis halimifolia,* and *Iva frutescens*, seaward into marsh areas. Seaward plant transplantation helped to quantify the physiological responses of these four species to increased soil salinity and inundation. Second, to disentangle the effects of salinity and inundation, we applied salt treatments to the four terrestrial fringe species in their natural salt marsh fringing habitat. Soil salinities in salt addition plots approximated soil salinities at the seaward transplant position. Any difference in plant performance and survival between the transplanted plants and the salt-addition plants would be mainly due to the effects of increased water inundation. Third, we transplanted all four species landward from the fringe closer to the forest margin to examine the effects of decreased soil salinity and inundation on fringe species. Finally, to quantify the relative importance of facilitative and competitive interactions in affecting plant performance and survival, we incorporated neighbor manipulation treatments, where neighboring plants were trimmed in half the plots in all four sets of experiments. This study poses three questions: 1) To what extent will sea-level rise negatively impact the performance and survival of species in salt marsh fringing communities? 2) Will reduced plant performance and survival be mainly attributable to increased soil salinity or water inundation? and 3) Will fringe plant performance and survival be influenced more by competitive or facilitative interactions when sea level rise occurs?

We predict that all four fringe species will experience reduced performance under conditions of both increased salt and increased salt and flooding but predict some differential responses of the species to these conditions. *B. angustifolia* is anticipated to outperform *B. halimifolia* across all treatments. *B. angustifolia's* root system lies closer to the surface, which may allow this species to intercept more water and nutrients following short rain events. We also predict that both *Baccharis* species will perform better than *Iva frutescens* in increased salt and increased salt and flooding plots. *Iva* is similar to both *Baccharis* species in that it is fairly tolerant to saline conditions but it possesses a narrower pH tolerance between 5-5.7 and is relatively intolerant of anaerobic conditions. *Andropogon* plant individuals are predicted to exhibit the lowest survival rates in both increased salt and increased salt and flooding plots due to their higher salt intolerance. The shading provided by neighbors in decreased salt and flooding plots at the forest margin is also expected to have a greater negative impact on this C_4 nonhalophytic species than the other species which are equipped with a C_3 photosynthetic pathway. Typically, C_3 species are favored under limited light conditions since they require less energy to fix CO_2. When compared to the controls, all four species are predicted to exhibit more growth under conditions of decreased salt and flooding.

Materials and Methods

Study System

All field work for this study was conducted at Upper Tampa Bay Park (28°00′48″N, 82°38′05″W)**,** Oldsmar, Florida, USA. The site is bordered by Tampa Bay, which has an average depth of 4 m at mid-tide and spans 896 km^2 (Raabe et al. 2012). The Tampa Bay estuary, which is Florida's largest, consists of 1,030 square kilometers at high tide and supports extensive marshy areas (Terrell 1979; Yates et al. 2011). Studies have documented sea-level rise in the Tampa Bay area at a rate of 2.4 mm/year, compared to the current global rate of 1.8mm/year (TBRPC 2006; Titus and Narayanan 1995; NOAA 2001; Raabe et al. 2012). The region's average annual temperature is 73.4°F and average annual precipitation is approximately 127 cm (NOAA 2009; Yates et al. 2011). Approximately 60 percent of the annual rainfall occurs during the rainy season from June through September (NOAA 2009; Yates et al. 2011). Mean monthly rainfall is approximately 17.8 cm during the rainy months and 5.8 cm during the dry season. Although annual and seasonal precipitation is variable from year to year, there are no significant storm events to report during 2011-2012 when this study was being conducted (NOAA 2012).

The park's highest elevation is approximately 1.83 m above sea level, so much of the study site is exposed to frequent inundation and saline conditions. The northern boundary of the study site consists of pine flatwoods forest and is inhabited by *Serenoa repens* (saw palmetto), *Sabal palmetto* (cabbage palm), and *Pinus elliottii* (slash pine). The forest - fringe margin served as the site for the transplants receiving the decreased salt & inundation treatment. The terrestrial fringe is a narrow area between the pine flatwoods forest and the salt marsh dominated by target species *Andropogon glomeratus* (bluestem grass)*, Baccharis angustifolia* (saltwater false willow), *Baccharis halimifolia* (eastern baccharis*),* and *Iva frutescens* (marsh elder), and inundated primarily by spring tides. The fringe served as the site for the control and salt addition treatments. The terrestrial fringe transitions to marsh area, which is inundated approximately 8 days per month and more frequently during spring tides (J. Hyder, *personal observation*). The marsh area is inhabited by *Frimbristylis cymosa* (hurricane grass), and *Juncus roemerianus* (needlegrass rush) and extends approximately 7.5 meters seaward beyond the lower distributional limits of the terrestrial fringe. This area served as the site for the set of seaward transplants (equivalent to a 2 cm rise in sea level as measured by survey equipment, Hyder and Stiling unpublished data).

Experimental Plots

We conducted three sets of experiments, (effects of increased salt, effects of increased salt and inundation, and effects of decreased salt and inundation), in this study. A total of 96 0.50 m x 0.50 m experimental plots were randomly assigned to one of four treatments: (1) control; (2) increased salt; (3) increased salt & inundation; or (4) decreased salt & inundation. Six individuals, including root balls, of each of the four species, *Andropogon glomeratus, Baccharis angustifolia, Baccharis halimifolia,* and *Iva frutescens,* were collected from the upper terrestrial fringe and transplanted to each treatment. Any gaps along the edges of the holes were filled with substrate from the original plots. This transplant protocol has shown no obvious differential transplant effects between plant species (Bertness and Ellison 1987; Emery et al. 2001). In addition, 12 reference plants in the terrestrial fringe (3 for each of the species) received no treatment and were not dug up. The objective with these reference plots was to test for effects of transplantation. We selected plant individuals of approximately the same size for each of the species; 1.3 m to 1.5 m for *Andropogon*, and 1.5 m to 1.8 m for *Iva* and both *Baccharis* species. The three sets of experiments (effects of increased salt, effects of increased salt and flooding, effects of decreased salt and flooding), began in June 2011, after data from reference plots were collected.

Increased Salt

Plants in the control and salt plots were dug up and transplanted back into their original locations in their fringe habitat. To test for the effect of salt on plant performance and survival, we added 750 g of Morton's Solar Salt Pellets (Morton, Chicago, Illinois, USA) to each of the designated salt addition plots bi-weekly. Soil salinity measurements were recorded immediately before the first application, and then one week following each application to test that soil salinities approximated those for the seaward transplants. Up to 100 g more salt was added if soil salinities needed to be increased. Any difference in plant performance and survival between the control and increased salt plots would then be due to increased salinity.

Increased Salt and Inundation

We transplanted species seaward to locations which were subject to increased inundation and increased salinity by moving plants 9.3 m distant from the terrestrial fringe into the marsh, a vertical distance of 2 cm. All transplants at the 9.3 m position (2 cm elevational decrease) were neighbored by *Juncus roemerianus* (needlegrass rush). All plots were arranged in a single line, parallel to Tampa Bay, to minimize differential tidal input among the plots. Our transplant regime of moving species to a lower elevation naturally simulated increased salinity and inundation associated with less than a decade of tidal increase. Any change in plant performance and survival between the salt addition and increased inundation plots would then be due to the effects of inundation. To disentangle the effects of inundation (salt and inundation) from salt, soil salinities in the salt addition treatment (increased salt plots in the fringe) approximated soil salinities at the seaward transplant positions (increased salt and inundation plots in marsh).

Decreased Salt and Inundation

We transplanted species landward to locations which were subject to decreased inundation and decreased salinity by moving plants from the terrestrial fringe into the forest-fringe margin. These transplants were neighbored by *Serenoa repens* (saw palmetto), *Sabal palmetto* (cabbage palm), and *Pinus elliottii* (slash pine). All plots were arranged in a single line, parallel to the forest margin, to minimize differential tidal input among the plots. We examined the effects of decreased salt & inundation on fringe plant performance and survival by comparing the landward transplants to the controls.

Neighbor Manipulation

In the neighbor manipulation treatment plots, surrounding vegetation was clipped and maintained at ground level within 30 cm of each plant for the entire duration of the experiment in a manner similar to the neighbor manipulation performed in New England salt marshes by Bertness et al. (1992). Removing neighbors in their entirety would have resulted in significant spikes in soil salinities, which would have potential adverse effects on the target plants. In fringe areas, taller neighbors were also cut to ground level to eliminate canopy cover. Neighbor manipulation treatments were applied to three individuals of each species for each of the control, increased salt, increased salt and inundation, and decreased salt and inundation plots. This methodology allowed us to assess the facilitative or competitive impacts of neighboring vegetation on the performance of four terrestrial fringe species (Bertness 1991; Pennings and Callaway 1992; Emery et al. 2001; Pennings and Moore 2001; Pennings et al. 2004).

Soil Characteristics

We measured a suite of substrate variables, (salinity, moisture, redox potential, pH, and sulfide concentration) in each plot monthly. Salinity was measured by collecting soil core samples, rehydrating the dried soils in a known volume of deionized water and recording the salinity of the supernatant with a Vista A366ATC refractometer. Soil moisture was measured by recording the initial mass (g) of collected samples, drying to a constant mass, then subtracting dry mass (g) from initial mass (g) and converting moisture to a percentage. Soil redox potential and pH were measured at 5 cm depths using a hand held Spectrum model 8601 pH/mV meter (Spectrum, Plainfield

IL, USA). Three measurements were averaged for each plot to produce a single measurement for statistical analysis. Total soluble sulfide concentrations were recorded using a Hach DREL/2400 portable spectrophotometer (Hach, Loveland, CO, USA).

Plant Growth and Survival

Plant performance in all plots was measured pre-treatment in June 2011 and then monthly for one growing season. Plant height was measured from ground to apical meristem for all species. At each census, five stems on *Iva frutescens, Baccharis halimifolia, and Baccharis angustifolia* were half haphazardly selected and the lengths were then measured. Total leaf counts were also recorded for these stems. Plant circumference was recorded for these species by measuring the diameter of the crown of foliage at its densest portion. For *Andropogon glomeratus,* basal coverage was determined by measuring the diameter of the clump 2 cm above the ground to calculate the circular area of the foliage. Plant growth was determined by subtracting the initial measurements from measurements after 6 months. Plant survivorship was determined by using data a year after the transplants.

Chlorophyll Fluorescence

To further quantify plant response to increased and decreased salinity and inundation, we conducted fluorescence measurements monthly on young leaves of all plants between 12 – 2 pm using an Underwater Fluorometer Diving-PAM, Submersable Photosynthesis Yield Analyzer (Heinze Walz GmbH, Germany). Three measurements were averaged to produce a single value for each plant individual. The potential quantum yield (Φ_{PSII}), or how efficient a plant is in using available light energy to fix carbon dioxide, serves as a reliable indicator of photosystem II (PSII) efficiency (Maxwell and Johnson 2000). Quantum yield values decrease as plants experience more stress or as irreversible damage to photosystem II apparatus occurs (Nainanayake 2007). Optimal (Φ_{PSII}) range for most flowering plant species is 0.79 – 0.83, with values ranging from 0 to 1.0 (Maxwell and Johnson 2000). Since photosystem II photochemistry efficiency is correlated with linear electron transport rates, quantum yield measurements are also a reliable indicator of overall photosynthetic capacity (Genty et al. 1989; Bilger et al. 1995; Maxwell and Johnson 2000). Fluorescence data helps to quantify the physiological tolerance of plant species to changing environmental conditions and the impact of this stress on photosynthesis.

Analysis

The three sets of experiments (effects of increased salt, effects of increased salt and flooding, and effects of decreased salt and flooding), were analyzed separately but the results of all three mini experiments are presented together on each figure. We tested the effects of salt, inundation and neighbors on plant height, circumference, branch length, leaf production, chlorophyll fluorescence yields, and soil characteristics separately using three-way Analysis of Variance with salt or inundation, neighbor manipulation, and plant species as the three main effects. The effects of salt addition were investigated by comparing the salt addition plots to the controls. The effects of increased inundation were examined by comparing the seaward transplants to the salt addition plots. Finally, to examine the effects of decreased salt & inundation, we compared the landward transplants to the controls. Growth, fluorescence, and soils data 6 months after transplantation were used in our analyses. After 6 months, there were too many plant deaths to be able to perform the ANOVAs for plant growth though similar trends were evident after one year. Plant survival was analyzed using ANOVA on mean plant longevity (in months) after 1 year. There were no significant three-way interactions and no two-way interactions except as noted.

Results

Pre-treatment Comparisons

All transplants in the control plots at 0 m showed no effects of transplantation on plant growth, chlorophyll fluorescence, or survival when compared to the reference plots ($p > 0.05$ in all cases). There were also no differences in height and circumference between individuals of the same plant species selected for transplantation in June 2011 pre-treatment measurements ($p > 0.05$ in all cases).

Effects of Increased Salt

Soil characteristics

Our study showed a significant increase in interstitial soil salinities following salt addition ($F_{1,32} = 4.838$, $p = 0.007$; Fig. 3.1a), but little impact on soil moisture, redox potential, or pH ($p > 0.05$ in all cases). Soil salinities were higher in salt treatment plots than in control plots but were not statistically different from salinity levels at the seaward transplants (Fig. 3.1). Our study revealed no significant effects of plant species on soil salinities, redox potential, soil moisture, or pH ($p > 0.05$ in all cases) and the presence of hydrogen sulfide was undetectable. All soil characteristics showed very similar trends for the duration of the experiment.

Plant performance and survival

Adding salt to plants significantly reduced plant height growth, circumference growth, and leaf production ($F_{1,32} = 10.274$, $p = 0.003$; $F_{1,32} = 9.633$, $p = 0.004$; $F_{1,24} = 8.163$, $p = 0.002$, respectively; Fig. 3.2a, b, c), but did not impact branch length ($p > 0.05$). All species experienced less growth in salt treatment plots after 6 months when compared to plants in control plots, but *B. halimifolia* suffered less growth reduction than the other three species, resulting in a significant interaction of treatment x species on plant growth (($p < 0.001$) for all parameters except branch length, which was not significant, $p > 0.05$). These findings are indicative of species effects as abiotic conditions became more stressful. Salt addition to plots reduced plant chlorophyll fluorescence for all four species ($F_{1,32} = 3.911$, $p = 0.017$; Fig. 3.3). There was a significant effect of increased salt on plant survival after 1 year ($F_{1,32} = 10.281$, $p = 0.003$; Fig. 3.4).

Effects of Increased Inundation

Soil characteristics

Our study showed no significant effects of inundation on substrate salinities when compared to the salt addition plots ($p > 0.05$; Fig. 3.1a). Mean soil redox potential and soil moisture were both significantly impacted by inundation in the seaward transplants ($p < 0.001$ in both cases; Fig. 3.1b, c). Inundation in marsh plots resulted in lower redox potential and higher moisture when compared to salt treatment plots at control positions. Substrate pH was also lower in flooded plots, although variation across zones was minimal, resulting in a marginally significant treatment effect ($F_{1,32} = 2.768$, $p = 0.055$). Our study revealed no significant effects of plant species on substrate salinities, redox potential, soil moisture or pH ($p > 0.05$ in all cases) and the presence of hydrogen sulfide was undetectable. All soil characteristics showed very similar trends for the duration of the experiment.

Plant performance and survival

After 6 months, plants transplanted seaward into marsh exhibited reduced growth when compared to the salt addition plots, as evidenced by a significant effect of inundation on plant height growth, circumference growth, and leaf production (($p < 0.001$) in all cases; Fig. 3.2). Inundation had less of an impact on *B. halimifolia's* height growth, circumference growth, and leaf production, when compared to the other species, resulting in an interaction of plant species and treatment on growth ($p < 0.001$ for all parameters. When compared to plants in salt treatment plots, those exposed to both salt and inundation experienced more than a 50% reduction in height growth, circumference growth and leaf production. Plants in flooded plots also experienced a sharp decline in chlorophyll fluorescence yield when compared to plants receiving salt treatment ($F_{1,32} = 13.446$, $p = 0.001$; Fig. 3.3). *B. halimifolia* experienced less photosynthetic inhibition than the other species, resulting in an interaction of species and treatment on chlorophyll fluorescence yield ($F_{1,32} = 4.597$, $p = 0.009$).

Plants exposed to increased inundation experienced reductions in survival after 1 year ($F_{1,32} = 10.358$, $p = 0.003$; Fig. 3.4). *B. halimifolia* persisted better than the other species under inundation conditions, yielding in an interaction of plant species and treatment on survival ($F_{1,32} = 4.199$, $p = 0.013$). Most plant deaths for the other three species occurred 5-6 months after transplantation, on entering the dry season.

Effects of Decreased Salt and Inundation

Soil characteristics

Our study revealed significant differences in soil salinities between transplant plots at the forest margin when compared to the control plots in the fringe. ($F_{1,32} = 14.41$, $p = 0.001$; Fig. 3.1). Decreased salt and inundation in forest margin plots resulted in a sharp decrease in interstitial soil salinities. Mean redox potential and soil moisture were both significantly impacted by decreased salt & inundation ($F_{1,32} = 3.057$, $p = 0.042$; $F_{1,32} =3.315$, $p = 0.032$, respectively; Fig. 3.1). Lower duration and frequency of inundation exposure in landward transplant plots at the forest margin resulted in significantly higher redox potential and lower moisture when compared to control plots in the fringe. Substrate pH was also higher in plots exposed to less salt & inundation, although variation across zones was minimal, resulting in a marginally significant treatment effect ($F_{1,32}$ = 2.729, p = 0.059). Our study showed no significant effects of plant species on substrate salinities, soil moisture, redox potential, or pH ($p > 0.05$ in all cases) and all soil characteristics showed very similar trends for the duration of the one year experiment.

Plant performance and survival

When compared to plants in control plots, those exposed to decreased salt & inundation experienced more than a three-fold increase in height growth ($F_{1,32}$ = 13.657, p = 0.001), and more than a two-fold increase in circumference growth and leaf production ($F_{1,32}$ = 4.840, p = 0.007; $F_{1,24}$ = 5.194, p = 0.13, respectively; Fig. 3.2). Additionally, all four species in decreased salt & inundation plots experienced a slight increase in chlorophyll fluorescence yield when compared to control plots. However, the difference in fluorescence yield is not statistically significant ($F_{1,32}$ = 2.195, p = 0.108; Fig. 3.3). Reductions in salt and inundation had a marginal effect on survival after 1 year with all plants in decreased salt and inundation plots surviving ($F_{1,32}$ = 2.759, p = 0.058; Fig. 3.4).

Effects of Neighbor Manipulation

Soil characteristics

Neighbor manipulation caused a significant increase in mean substrate salinities ($p < 0.001$; Fig. 3.1a), and decrease in soil redox potentials ($p < 0.001$; Fig. 3.1b) across all plots, when comparisons between decreased salt & inundation vs. control, control vs. increased salt, and increased salt vs. increased salt & inundation were made. Effects of neighbor manipulation were greatest in the increased salt and increased salt & inundation plots. Neighbor manipulation had no impact on pH or soil moisture in any comparisons ($p > 0.05$ in all cases).

Plant performance and survival

Neighbor manipulation had significant effects on plant height growth, circumference growth, and leaf production ($p < 0.001$ in all three comparisons; Fig. 3.2a, b, c), but there was a shift in the nature of this effect with seaward progression. Neighbor manipulation resulted in increased height growth, circumference growth, and leaf production for all species in the decreased salt and inundation plots at the forest margin, and in the control plots and increased salt plots in the terrestrial fringe, but had the opposite effect in the increased salt & inundation plots at the seaward transplant position in the marsh. These findings yielded a significant interaction of neighbor manipulation and treatment in the increased salt vs. increased salt & inundation comparison plots for all plant growth parameters ($p < 0.001$ in all cases). Although neighbor manipulation had a positive effect on plant growth in both control and salt treatment plots at the fringe, this benefit was less for plants experiencing added salt, yielding a neighbor manipulation x treatment interaction in the control vs. increased salt comparison for height growth, circumference growth, and leaf production ($F_{1,32}$ = 3.752, p = 0.020; $F_{1,32}$ = 3.625, p = 0.066; $F_{1,24}$ = 3.522, p = 0.059, respectively). Our study showed no significant effect of neighbor manipulation on branch length (p > 0.05). Neighbor manipulation also had significant effects on effective quantum yield in all treatments for all species in both the control vs. increased salt and increased salt vs. increased salt & inundation comparisons ($F_{1,32}$ = 3.069, p = 0.040; $F_{1,32}$ = 3.521, p = 0.026, respectively; Fig. 3.3). Quantum yield in control and salt treatment plants responded similarly to neighbor manipulation, but there was an interaction of neighbor manipulation with treatment in the increased salt vs. inundation comparison ($F_{1,32}$ = 5.259, p = 0.005) because plants in the increased salt plots experienced less photosynthetic inhibition when neighbors were removed while plants in flooded plots were more inhibited with this treatment.

Neighbor manipulation also impacted plant survival in the control vs. increased salt and increased salt vs. increased salt & inundation comparisons ($F_{1,32}$ = 13.889, p = 0.001; $F_{1,32}$ = 14.212, p < 0.001, respectively; Fig. 3.4). Plants in control and salt addition plots in the terrestrial fringe survived better in the absence of neighboring vegetation while those in high marsh experienced decreased survival without neighboring above ground vegetation, resulting in a significant neighbor manipulation x treatment interaction on survival in the increased salt vs. increased inundation comparison ($F_{1,32}$ = 4.592, p = 0.009).

Discussion

Effects of Abiotic Stress

Our results revealed that salt marsh fringing species are negatively impacted by both increased salt and increased inundation, although inundation appears to have a greater effect on their performance and survival. The control vs. increased salt comparisons show that all four plant species receiving salt treatment experienced a notable reduction in performance (plant height growth, circumference growth, leaf production, and chlorophyll fluorescence yield) after 6 months, although *B. halimifolia* suffered less growth reduction and photosynthetic inhibition than the other species. After one year, all species in increased salt plots, with the exception of *B. halimifolia*, experienced increased plant mortality. These findings are consistent with others which have shown that salinity plays a role in influencing the performance and survival of salt marsh species (Cooper 1982; Levine et. al 1998; Rasser et al. 2013). Bowman and Strain (1987) cite rapid osmotic adjustment as one mechanism that allows many plants lacking adaptations to effectively tolerate short-term salt stress. A predicted increase in climate induced precipitation and storm events might help to moderate higher soil salinities resulting from rising sea levels, allowing plants some respite from salt stress, although this is by no means certain.

The increased salt vs. increased salt and inundation comparisons revealed that all plant species exposed to increased salt and inundation experienced a two-fold reduction in performance and survival over pure salt addition, which suggests that inundation may be a more important limiting factor than salinity under conditions of sea level rise. Bertness et al. (1992) reported similar findings in their field study where *I. frutescens* individuals were transplanted to lower elevations and exposed to inundation conditions. In their experiments, all plant individuals died within a year, both in the presence and absence of neighbors. As sea levels rise, the frequency and duration of inundation are expected to increase, both of which have been shown to directly influence plant performance and survival in other salt marsh systems (Miller et al. 2001). As in our previous study, we predicted all four fringe species would respond very differently to increased salt and inundation exposure. All four fringe species did exhibit slight differences in growth, performance, and survival but these differences did not yield a main species effect. Our study revealed that *B. halimifolia* experienced less morbidity than the other species and outperformed the other species under conditions of increased abiotic stress, yielding a species x treatment effect under higher abiotic stress levels. We did not anticipate *B. halimifolia* to outperform *B. angustifolia* since both perennial shrubs are characterized by similar growth rates, as well as comparable anaerobic and salinity tolerance. We had also predicted that both *Baccharis* species would perform better than *Iva frutescens* at the seaward transplant position. *Iva* is similar to both *Baccharis* species in that it is fairly tolerant to saline conditions but it possesses a narrower pH tolerance between 5-5.7 and is relatively intolerant of anaerobic conditions. Interestingly, *Iva* experienced slightly more growth and higher survival than *Baccharhis angustifolia*, although not statistically significant. *Iva* possesses a deeper root depth (40.6 cm.) than *Baccharsis angustifolia* (30.5 cm.) and may be more capable of garnering accumulated sub-surface waters, especially during drier periods. We had also expected all *Andropogon* plant individuals to die when transplanted to the seaward positions due to their higher salt intolerance. Interestingly, *Andropogon* performed similarly to the other three fringe species at all seaward transplant positions. *Andropogon* exhibited slightly less growth and survival than *Iva* and both *Baccharis* species but persisted longer than predicted. *A. glomeratus* has been shown to exhibit genetic differentiation for tolerance to varying levels of salt and inundation exposure (Bowman and Strain 1988). Bowman and Strain (1988) showed that two populations of *Andropogon* (inland and marsh) differed in survival following short-term inundation exposure. Plant individuals from the marsh population exhibited more rapid recovery of photosynthetic capacity following the inundation exposure, affording these plant individuals a higher capacity to survive inundation events. In our study, it is possible that we selected *Andropogon* individuals representative of the more stress tolerant marsh population.

The decreased salt & inundation vs. control comparison revealed that landward transplants exposed to less salt and inundation stress exhibited more than a two-fold increase in height growth and increase in both circumference growth and leaf production in the absence of neighbors. All species performed similarly, as expected, to conditions of decreased salt and inundation. These findings suggest that fringe species merely tolerate harsher conditions and are competitively displaced seaward to fringe areas by terrestrial species in the forest. There were no obvious differences in plant performance and survival in the landward transplants in the presence of neighbors, which suggests that the benefits of reduced salt and inundation may not counter any competitive effects from neighboring tree species at higher elevations. Light intercepted by the taller tree species at the forest-fringe margin creates a shaded understory that is not suitable for the establishment and survival of smaller fringe species.

Overall, all four fringe species performed similarly under conditions of increased salt, increased salt and inundation and decreased salt and inundation. The lack of main species effect and lack of high variance for growth and performance suggest that the environment may have a stronger effect than genotype on these species growth, performance, and survival.

Effects of Biotic Interactions

Our findings show that species interactions mediated the performance and survival of the fringe species in all treatment plots. In the forest transplants, controls, and increased salt plots located in the terrestrial fringe, the presence of neighbors negatively impacted the growth, photosynthetic capacity, and survival of all four species. Other studies have shown that plant species at higher marsh elevations appear to be better competitors, restricting the competitively subordinate plants to the more physically stressful areas of the marsh (Bertness and Ellison 1987; Emery et al. 2001; Pennings and Bertness 2001). The areas fringing the marsh are dominated by taller species, which grow rapidly and are more capable of competitively excluding others by limiting light, space, and nutrient supply. At the same time, the shading provided by these taller species can help to moderate water evaporation and salt stress, but the strength of competitive interactions appears to exceed any benefits of neighbors at higher elevations in the terrestrial fringe.

The increased salt vs. inundation comparison showed that the plants in flooded plots, in the more physically stressful marsh areas, benefited from the presence of neighbors, signaling a change in the direction of interspecific interactions from competitive to facilitative. Although some studies have reported competitive interactions to be more common than positive interactions in marsh areas (Pennings et al. 2003, Maestre et al. 2009; Guo and Pennings 2012; Keammerer and Hacker 2013), our results support others that have found facilitation to be pervasive in areas which experience more physical stress, suggesting that species interactions tend to shift from competitive to facilitative as plants begin to experience harsher environmental conditions (Bertness and Shumway 1993; Bertness and Hacker 1994; Bertness and Ewanchuk 2002). In our field experiment, fringe plants in flooded plots with marsh neighbors experienced a two-fold increase in height growth, circumference growth, and leaf production, when compared to their counterparts in neighbor manipulation plots. Marsh species endure frequent water logging and, as a result, allocate much of their energy to maintaining architectural and metabolic adaptations necessary to help alleviate inundation stress. Many such species possess adventitious roots and well-developed arenchyma tissue to facilitate root oxygenation. As oxygen is funneled to the root zone, soil redox potentials increase, lessening the effect of the anoxic conditions on neighboring plants, as evidenced in this study.

Overall, our results show that facilitative interactions became more influential as salt and inundation stress increased, lending strong support for the stress-gradient hypothesis. These findings are consistent with studies of Bertness and Callaway (1994) and others who have found that as plants begin to experience more stress, highly competitive plants have less of a competitive effect and the competitively subordinate, but more stress tolerant plants have stronger facilitative effects. In this system, both the direction and strength of plant interactions appear to be dependent upon the severity of salt and inundation exposure and the physiological tolerance of species to these stresses. These results support the hypothesis that a trade-off may exist between competitive ability and physical stress tolerance (Grime 1977, 1979; Bertness 1991; Levine et al. 1998; Costa et al. 2003). Regional climate may also influence the nature and strength of the interactions at this site. During the sub-tropical rainy season, from June through November, marsh plants endure more frequent rainfall. After the rainy season ends, these plants then experience more saline soil conditions as the hot, dry weather results in increased surface evaporation and substrate salt accumulation. Hence, annual conditions allow plants in sub-tropical marshes no respite from salt or flooding stress.

In the increased salt plots, we had expected to see evidence of facilitation. Since salt addition to plants did not appear to trigger a shift in the nature of interspecific interactions from competitive to facilitative, the impact of the salt stress on the plants may have been too low for these plants to benefit from any facilitative effects of neighbors. These findings suggest that increased levels of stress may not always lessen competitive effects and strengthen facilitative interactions. Rather, a knowledge of the number of stressors, types of stress, or strength of stresses coupled with the physiological tolerance of species to those stressors may be required to predict potential shifts in the nature of interactions and the strength of these interactions in salt marsh fringing systems.

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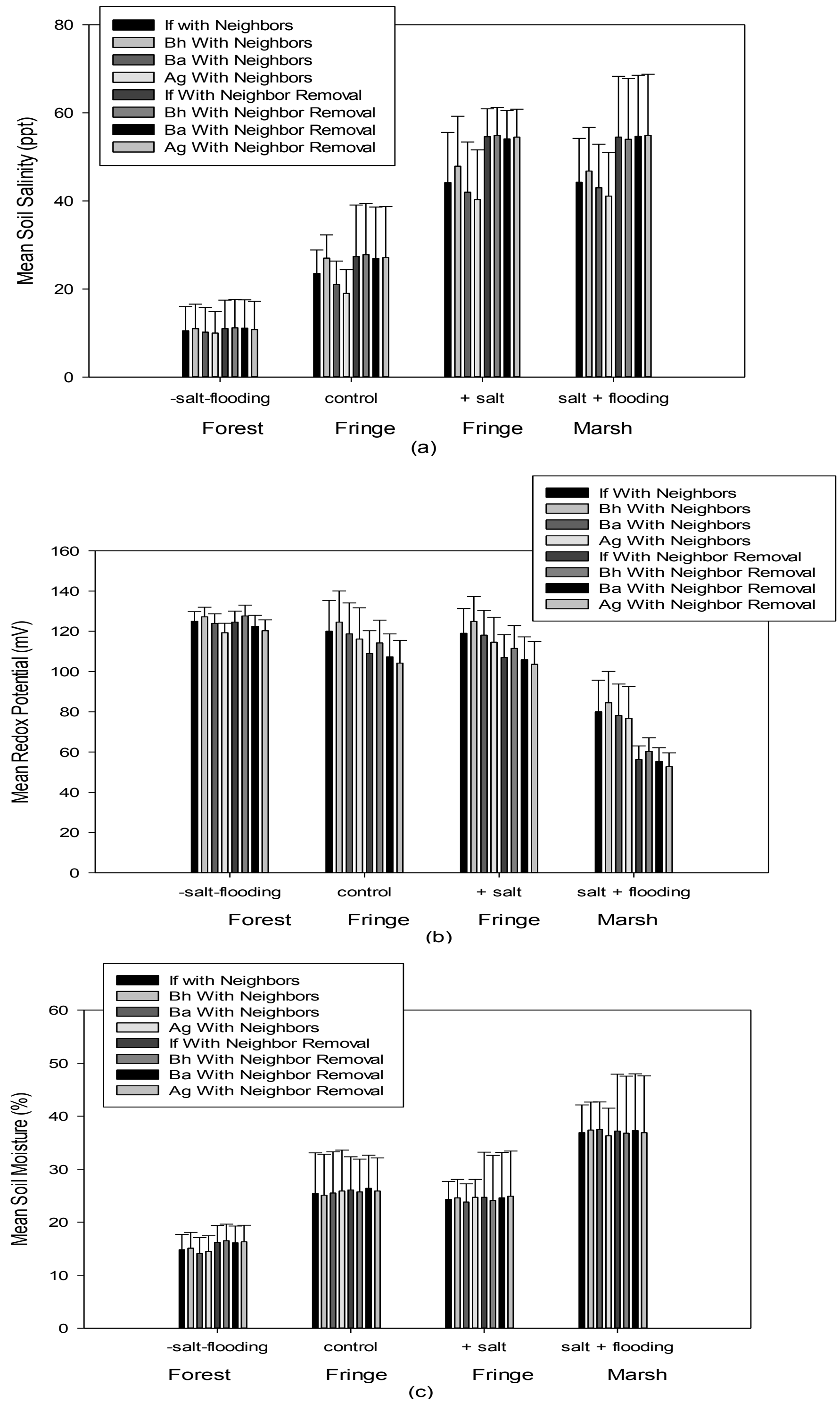

Figure 3.1: Mean (a) interstitial soil salinity (ppt), (b) redox potential (mV) and (c) soil moisture (%)for *Iva frutescens (If), Baccharis halimifolia (Bh), Baccharis angustifolia (Ba), and Andropogon glomeratus (Ag*) in decreased salt & flooding, control, increased salt and increased salt & flooding plots after 6 months. Bars represent ± 1 SE. n=3

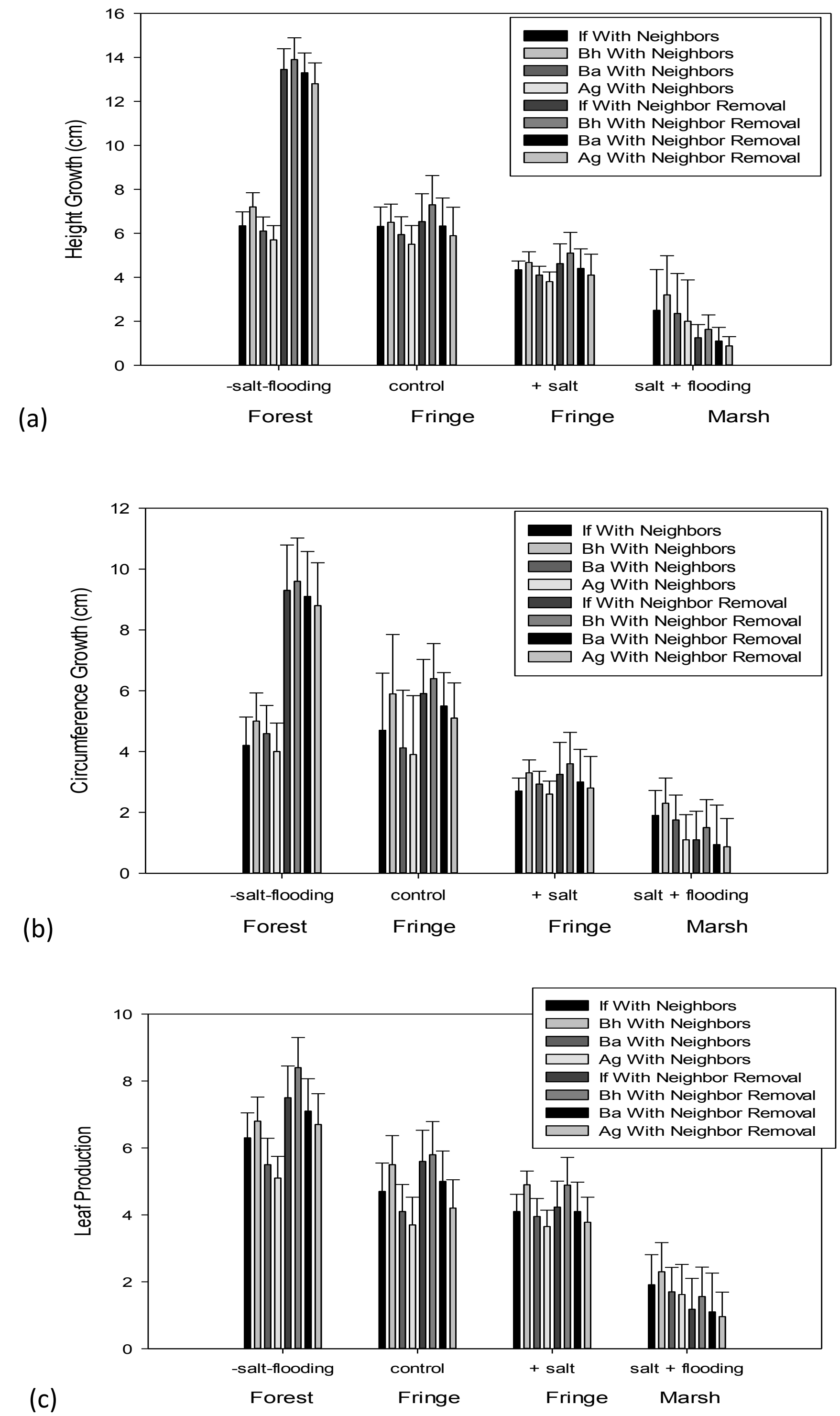

Figure 3.2: Average (a) height growth, (b) circumference growth, and (c) leaf production of *Iva frutescens (If), Baccharis halimifolia (Bh), Baccharis angustifolia (Ba), and Andropogon glomeratus (Ag*), in decreased salt & flooding, control, increased salt and increased salt & flooding plots with and without neighboring above ground vegetation after 6 months. Bars represent ± 1 SE. n=3

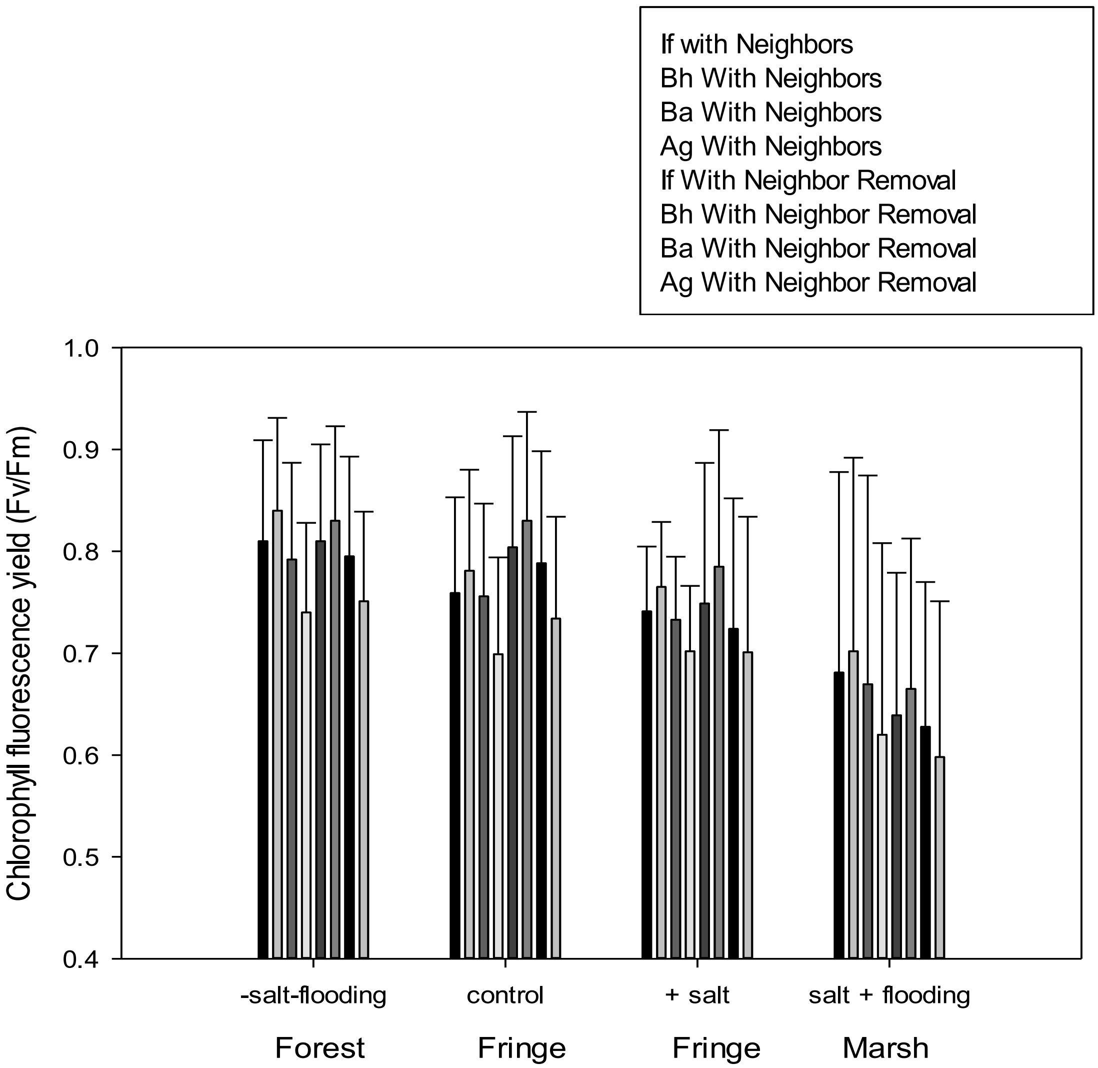

Figure 3.3: Average plant chlorophyll fluorescence yield (Fv/Fm) for *Iva frutescens (If), Baccharis halimifolia (Bh), Baccharis angustifolia (Ba), and Andropogon glomeratus (Ag*), in decreased salt & inundation, control, increased salt and increased salt & inundation plots with and without neighboring above ground vegetation after 6 months. Bars represent ± 1 SE. n=3

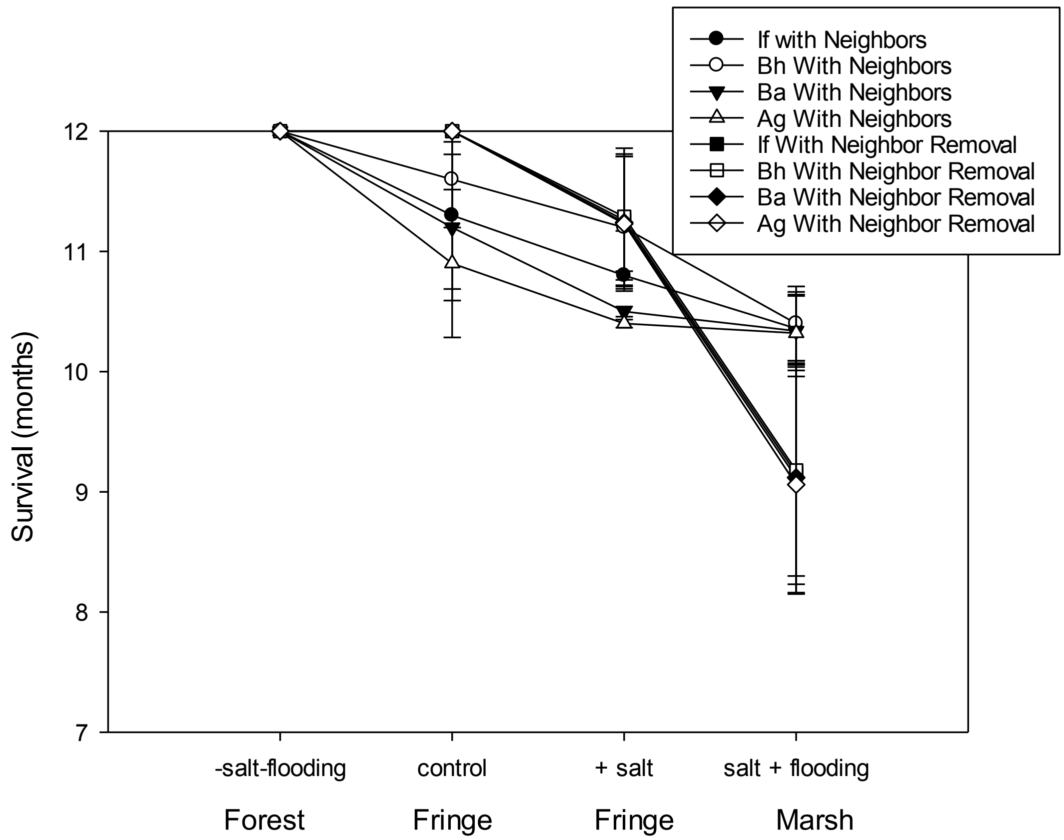

Figure 3.4: Mean survivorship of *Iva frutescens (If), Baccharis halimifolia (Bh), Baccharis angustifolia (Ba), and Andropogon glomeratus (Ag*), in decreased salt & inundation, control, increased salt and increased salt & inundation plots with and without neighboring above ground vegetation after 1 year. Bars represent ± 1 SE. n=3

Table 3.1: Three-way ANOVA *F* statistics and significance are presented for the effects of species, increased salt, and neighbor manipulation on soil characteristics, performance, and survival of four salt marsh fringing species. Growth, fluorescence, and soil characteristics were analyzed after 6 months. Plant survival was analyzed on mean plant longevity after 1 year. There were no significant three-way interactions to report.
*P<0.05; **P<0.01; ***P<0.001; NS P>0.05

	Soil Salinity	Soil Moisture	Soil Redox	Soil pH
Source of variation	F	F	F	F
Salt	4.838**	0.329 NS	0.477 NS	0.689 NS
Neighbor Manipulation	10.874 ***	0.264 NS	8.467***	0.477 NS
Species	1.365 NS	1.679 NS	0.361 NS	0.873 NS
Species x Salt	1.467 NS	0.521 NS	0.144 NS	0.313 NS
Species x Neighbor Manipulation	2.352 NS	0.387 NS	0.975 NS	0.073 NS
Salt x Neighbor Manipulation	1.879 NS	0.293NS	1.829 NS	0.112 NS

	Height	Circumference	Branch Length	Leaf Production	Chlorophyll Fluorescence Yield	Survival
Source of variation	F	F	F	F	F	F
Salt	10.274**	9.633**	1.109 NS	8.163**	3.911*	10.281**
Neighbor Manipulation	12.492* **	11.826** *	2.352 NS	16.026***	3.069*	13.889***
Species	1.247 NS	0.789 NS	0.564 NS	2.159 NS	0.823 NS	1.049 NS
Species x Salt	11.374***	12.241***	1.673 NS	12.349***	1.374NS	1.026 NS
Species x Neighbor Manipulation	0.541 NS	2.844 NS	2.167 NS	2.459 NS	0.848 NS	0.538 NS
Salt x Neighbor Manipulation	3.752*	3.625 NS	1.893 NS	3.522 NS	1.523 NS	0.729 NS

Table 3.2: Three-way ANOVA *F* statistics and significance are presented for the effects of species, increased inundation, and neighbor manipulation on soil characteristics, performance, and survival of four salt marsh fringing species. Growth, fluorescence, and soil characteristics were analyzed after 6 months. Plant survival was analyzed on mean plant longevity after 1 year. There were no significant three-way interactions to report.
*P<0.05; **P<0.01; ***P<0.001; NS P>0.05

	Soil Salinity	Soil Moisture	Soil Redox	Soil pH
Source of variation	F	F	F	F
Inundation	1.146 NS	13.598***	12.873***	2.768 NS
Neighbor Manipulation	12.394***	1.728 NS	11.581***	1.283 NS
Species	1.292 NS	2.437 NS	1.741 NS	1.394 NS
Species x Inundation	1.583 NS	1.489 NS	1.382NS	0.687 NS
Species x Neighbor Manipulation	1.629 NS	1.543 NS	1.264NS	1.596 NS
Inundation x Neighbor Manipulation	1.467 NS	1.361 NS	1.519NS	0.894 NS

	Height	Circumference	Branch Length	Leaf Production	Chlorophyll Fluorescence Yield	Survival
Source of variation	F	F	F	F	F	F
Inundation	7.958***	11.684***	0.535 NS	12.889***	13.446**	10.358**
Neighbor Manipulation	18.463***	10.487***	0.176 NS	10.742***	3.521*	14.212***
Species	0.862 NS	1.948 NS	0.741 NS	1.632 NS	1.983 NS	1.167 NS
Species x Inundation	12.294***	10.892***	0.242 NS	13.541***	4.597**	4.199*
Species x Neighbor Manipulation	0.293 NS	0.094 NS	0.379 NS	0.133 NS	0.039 NS	0.827 NS
Inundation x Neighbor Manipulation	11.859***	11.389***	0.184 NS	11.587***	5.259**	4.592**

Table 3.3: Three-way ANOVA *F* statistics and significance are presented for the effects of species, decreased salt & inundation, and neighbor manipulation on soil characteristics, performance, and survival of four salt marsh fringing species. Growth, fluorescence, and soil characteristics were analyzed after 6 months. Plant survival was analyzed on mean plant longevity after 1 year. There were no significant two-way or three-way interactions to report. *P<0.05; **P<0.01; ***P<0.001; NS P>0.05

	Soil Salinity	Soil Moisture	Soil Redox	Soil pH
Source of variation	F	F	F	F
Decreased Salt & Inundation	14.41**	3.315*	3.057*	2.729NS
Neighbor Manipulation	13.254***	1.117 NS	11.874***	NS
Species	1.142 NS	0.672 NS	0.256 NS	0.713 NS
Species x Decreased Salt & Inundation	0.839 NS	0.758 NS	0.481 NS	1.201 NS
Species x Neighbor Manipulation	1.036 NS	0.943 NS	0.836 NS	0.948 NS
Decreased Salt & Inundation x Neighbor Manipulation	0.954 NS	0.108 NS	0.637 NS	0.231 NS

	Height	Circumference	Branch Length	Leaf Production	Chlorophyll Fluorescence Yield	Survival
Source of variation	F	F	F	F	F	F
Decreased Salt & Inundation	13.657**	4.840**	0.329 NS	5.194 NS	2.195 NS	2.759 NS
Neighbor Manipulation	11.859***	10.954***	0.271 NS	11.286***	0.981 NS	1.157 NS
Species	0.872 NS	1.164 NS	0.182 NS	1.851 NS	1.159 NS	0.732 NS
Species x Decreased Salt & Inundation	0.846 NS	0.879 NS	0.364 NS	2.018 NS	1.326 NS	0.573 NS
Species x Neighbor Manipulation	1.15 NS	0.684 NS	0.297 NS	1.643 NS	0.847 NS	0.936 NS
Decreased Salt & Inundation x Neighbor Manipulation	1.627 NS	0.791 NS	0.651 NS	1.296 NS	0.624 NS	1.254 NS

CHAPTER 4

ABIOTIC STRESS AND INTERSPECIFIC INTERACTIONS INFLUENCE SURVIVAL OF SALT MARSH PLANTS IN SALT MARSH FRINGING HABITAT

Synopsis

As sea levels continue to rise, salt marsh plants are expected to be impacted by increased inundation and salt exposure and some authors predict a subsequent landward migration of these species to higher elevations. To examine survival rates of salt marsh species under such conditions, we transplanted three salt marsh species, *Avicennia germinans*, *Borrichia frutescens*, *Batis maritima,* into fringe areas, landward of salt marshes, both in the presence of neighboring fringe species and in areas where neighbors had been trimmed to ground level. This allowed us to determine whether salt marsh species require or merely tolerate frequent inundation and saline conditions present in their native low marsh habitat and to assess the role of biotic interactions on their performance and survival at higher elevations. Additionally, we added salt to transplants in some plots to ascertain whether salt or inundation exposure is the primary influence on salt marsh plant performance and survival. Soils (salinity, moisture, redox, pH, sulfide), growth (height, percent cover, leaf production), performance (fluorescence), and survival measurements were recorded for all plant individuals for

one year. Overall, plants transplanted to higher elevations performed better than their counterparts in the more physically stressful low marsh zone, which suggests that many salt marsh plants don't require, but merely tolerate harsher conditions. When compared to controls in the marsh, plants moved to the fringe and receiving salt but less inundation exhibited increased performance (plant height growth, percent cover, leaf production, and chlorophyll fluorescence yield). Thus, inundation appears to have a greater negative impact on salt marsh plant performance than salt. The control vs. transplant comparisons also revealed that the plants at higher elevations were depressed by strong competitive pressure from neighboring fringe species while plants in the more physically stressful marsh areas benefited from the presence of neighbors. These findings suggest that salt marsh plants are competitively displaced seaward to low marsh areas by fringe species. Interestingly, plants receiving salt treatment at higher elevations were less depressed by competition imposed from neighboring fringe species than plants in plots with no salt addition. Our findings suggest that salt stress alone does not precipitate a shift in the nature of interspecific interactions from competitive to facilitative.

Introduction

Over the past two decades, ecologists have tested the Stress Gradient Hypothesis (SGH) by examining how both the frequency and intensity of species interactions change along stress gradients (Callaway and Davis 1993; Bertness and Callaway 1994; He et al. 2013; He and Bertness 2014). Coined by Bertness and

Callaway (1994), the SGH predicts that (a) the frequency and intensity of facilitative interactions increase as conditions become more stressful for plants and (b) the strength of competitive interactions increases as stress levels diminish.

Despite strong evidence documenting the SGH across ecosystems, some ecologists have challenged whether the SGH applies to extreme environments, where facilitation is of insufficient strength to boost performance, and many have called for revisions of the SGH (Maestre et al. 2009; Malkinson and Tielbörger 2010; Michalet et al. 2014). In addition, few studies of the SGH have tested the interplay between competition and facilitation across gradients of multiple, co-occurring stresses. For example, as sea levels rise, it remains unclear as to how increases in multiple stresses might shape the nature of interspecific interactions in salt marsh systems.

Studies conducted in salt marsh systems have shown facilitation to be as strong of a driving force as competition in influencing plant performance and survival and have shown that while competition appears to be the pervasive force in the less physically stressful terrestrial zones fringing salt marshes, facilitation influences the performance and survival of species in harsher marsh areas (Bertness et al. 1992; Pennings and Callaway 1992; Bertness and Shumway 1993; Bertness and Callaway 1994; Levine et al. 1998; Bertness and Ewanchuk 2002; Charles and Dukes 2009). Salt marsh plant species are equipped with the necessary metabolic and architectural adaptations to effectively tolerate moderate salt and inundation stresses, which afford them the ability to mitigate harsher physical conditions for neighboring species (Bertness and Hacker 1994; Callaway 1994; Donnelly and Bertness 2001; Emery et al. 2001; Ewanchuk and Bertness 2004; He and Bertness 2014).

Under conditions of accelerated sea level rise, many authors predict a subsequent landward migration of salt marsh species to salt marsh fringing areas (Morris et al. 2002; Gardner et al. 1992; Gardner and Porter 2001). While several studies have already documented landward migration of marsh species at the expense of higher marsh species in response to sea-level rise (Donnelly and Bertness 2001; Raabe et al. 2012), others cite the need for the degredation of higher marsh species to increase border permeability and allow for the successful migration of lower marsh species. As rising sea levels submerge low marsh areas, propagules from the species which inhabit these areas, such as mangroves, are more likely to invade fringe habitats at their landward border where fringing species are absent (Peterson and Bell 2012). However, the germination of these propagules and their survival as adults is not well known. It is hypothesized that the interplay between competition and facilitation could also impact plant distributional shifts as sea levels rise. This warrants the need for more rigorous tests of the SGH in coastal Florida salt marsh systems, which are predicted to experience increased abiotic stress under conditions of sea level rise.

To date, there is a paucity of studies investigating the relative ‘importance’ of facilitation and competition in Florida marsh systems. Fringe species at higher elevations are less stress tolerant, compared to marsh species, and allocate more of their resources to growth which enables them to competitively exclude the smaller, but more stress tolerant marsh species at the fringe-marsh border (Levine et al. 1998). As conditions become more stressful in areas fringing the marsh, however, it is possible that fringe species will experience reduced performance and survival. The subsequent degradation of the fringe community could in turn weaken competitive pressure and increase border permeability, allowing for the successful migration of marsh species into fringe areas. This outcome would significantly impact Florida salt marsh systems, dominated by extensive mangrove assemblages which are very vulnerable to rising sea levels. In accordance with the SGH, as stress levels increase, we would expect to see a shift in the nature of interspecific interactions from competitive to facilitative in areas typically governed by strong competition.

To date, few studies have examined the interplay between multiple co-varying abiotic stresses and biotic interactions in sub-tropical salt marsh systems. Our study is novel in that it investigated these effects on multiple marsh species to ascertain whether these species respond similarly under conditions of changing abiotic stresses both in the presence and absence of neighboring above-ground vegetation. This study had three main objectives. First, three salt marsh species, *Avicennia germinans* (Black mangrove), *Borrichia frutescens* (seaside oxeye), *Batis maritima* (saltwort)were transplanted landward into fringe areas. Landward plant transplantation tested whether salt marsh plants require or merely tolerate inundation and salt exposure. Second, to disentangle the effects of salinity and inundation, we applied salt treatments to some of the transplants. Soil salinities in salt addition plots approximated soil salinities at the seaward transplant position. Any difference in plant performance and survival between the transplanted salt addition plants in the fringe and the untreated transplants in the fringe would be mainly due to the effects of salt. Any difference in plant performance and survival between the transplanted salt addition plants and those in control plots (transplants in original holes) would be mainly due to the effects of inundation. Finally, to quantify the relative importance of facilitative and competitive interactions in affecting salt marsh plant performance and survival, we incorporated neighbor manipulation treatments, where neighboring plants were clipped to ground level, in half the plots in all three treatments. This study poses three questions: 1) As rising sea levels further inundate low marsh areas, will increased salt or inundation have a greater negative impact on salt marsh plant performance and survival? 2) To what extent will fringe species at the fringe-marsh border impact the performance of salt marsh species as sea levels rise? and 3) Under conditions of sea level rise, will increased abiotic stress in fringe areas change the nature of interspecific interactions from competitive to facilitative?

We predict that the plant individuals of all three species exposed to both decreased salt and flooding stress should perform better than those exposed to only decreased flooding. Further, we expect all plants transplanted into less physically stressful fringe areas typically governed by competition, (decreased salt and decreased salt and flooding experiments), to perform better in the absence of above-ground neighboring vegetation. In plots with neighbors in both decreased salt and decreased salt and flooding treatments, we predict that *B. maritima* and *B. frutescens* will be more negatively impacted than *A. germinans* by the reduced light infiltration imposed by its taller fringe neighbors. Both *A. germinans* and *B. frutescens* are taller species, capable of intercepting more light.

Materials and Methods

Study System

All field work for this study was conducted at Upper Tampa Bay Park (28°00′48″N, 82°38′05″W), Oldsmar, Florida, USA. The area's flat topography and microtidal coastline, make this region very vulnerable to fluctuations in sea level. (Stout 1984; Williams et al. 1999a, 1999b; Desantis et al. 2007; Geselbracht et al. 2011; Yates et al. 2011; Raabe et al. 2012). The region's average annual temperature is 23.0°C and average annual precipitation is approximately 127 cm (NOAA 2009; Yates et al. 2011). Mean monthly rainfall is approximately 17.8 cm during the tropical season and 5.8 cm during the dry months with approximately 60 percent of the annual rainfall occurring during the rainy season months June through September (NOAA 2009; Yates et al. 2011). Although annual and seasonal precipitation are variable from year to year, there are no significant storm events to report during 2011-2012 when this study was being conducted (NOAA 2012). Studies have documented sea-level rise in the Tampa Bay area at a rate of 2.4 mm/year, compared to the current global rate of 1.8mm/year (TBRPC 2006; Titus and Narayanan 1995; NOAA 2001; Raabe et al. 2012).

The landward boundary of the study site consists of pine flatwoods forest and is inhabited by *Serenoa repens* (saw palmetto), *Sabal palmetto* (cabbage palm), and *Pinus elliottii* (slash pine). The upper terrestrial fringe is a narrow area dominated by *Andropogon glomeratus* (bluestem grass), *Baccharis angustifolia* (saltwater false willow), *Baccharis halimifolia* (eastern baccharis), and *Iva frutescens* (marsh elder), and inundated primarily by spring tides. The fringe acts as an ecotone between marsh and forest and served as the site for transplantation of marsh species. The terrestrial fringe transitions to marsh area, which is inundated approximately 8 days per month and more frequently during spring tides (J. Hyder, *personal observation*). The upper marsh area is inhabited by *Frimbristylis cymosa* (hurricane grass), and *Juncus roemerianus* (needlegrass rush) while lower areas of the marsh are inhabited by *Avicennia germinans* (Black mangrove), *Borrichia frutescens* (seaside oxeye), *Batis maritima* (saltwort), *Monanthochloe littoralis* (keygrass), *Sesuvium portulacastrum* (sea purslane), and *Sporobolus virginicus* (seashore dropseed).

We transplanted eighteen individuals of each of the three species, *Avicennia germinans, Batis maritima*, and *Borrichia frutescens,* into the marsh or upper fringe area. Each individual was transplanted by excising and placing root balls into size-matched holes. Any gaps along the edges of the holes were filled with substrate from the original plots. This transplant protocol has shown no obvious differential transplant effects between plant species (Bertness and Ellison 1987; Emery et al. 2001). As described next, we randomly assigned a total of 54 0.50 x 0.50 experimental plots to one of three treatments: (1) control or (2) decreased salt and inundation stress; or (3) decreased inundation stress. Treatments also consisted of two levels of neighboring vegetation. Control plots consisted of excising and transplanting each plant back into in its original location in the low marsh. Additionally, 9 reference plants in the low marsh (3 for each of the species) received no treatment and were not dug up. The objective with these reference plots was to test for effects of transplantation. We selected plant individuals of approximately the same size for each species. Treatments began in June 2011, after data from reference plots were collected.

Decreased Salt and Inundation

We transplanted species landward 14 m distant from the low marsh into the terrestrial fringe. All three study species were transplanted among *Iva frutescens* in the fringe area. All plots were arranged in a single line, parallel to Tampa Bay, to minimize any differential tidal input among the plots. The transplant regime of moving low marsh species to a higher elevation naturally simulated both decreased inundation and salinity stress. Any difference in plant growth and survival between the decreased salt and inundation plots and decreased inundation plots (see below) would then be due to salt stress.

Decreased Inundation

We transplanted species 14m distant from the low marsh into the terrestrial fringe. Again, all three study species were transplanted among *Iva frutescens* in the fringe area. To test for the effect of inundation on plant growth and survival, we added 750 g of Morton's Solar Salt Pellets (Morton, Chicago, Illinois, USA) to each of the designated salt addition plots in the terrestrial fringe bi-weekly. Soil salinity measurements were recorded before the first application, and then one week following each application to test that soil salinities approximated those in the plants' original low marsh locations. Up to 150 g more salt was added if soil salinities needed to be increased to approximate soil salinities at the seaward transplant position. Any difference in plant growth and survival between the control plots and decreased inundation plots would then be due to the effects of inundation. To disentangle the effects of inundation (salt and inundation) from salt, soil salinities in the salt addition treatment (decreased inundation plots) approximated soil salinities in control plots.

Neighbor Manipulation

In plots receiving a neighbor manipulation treatment, surrounding vegetation was clipped and maintained at ground level within 30 cm surrounding each plant for the entire duration of the experiment in a manner similar to the neighbor manipulation performed in New England salt marshes by Bertness et al. (1992). Removing neighbors in their entirety would have resulted in significant spikes in soil salinities, which would have potential adverse effects on the target plants. In fringe areas, taller neighbors were also cut to ground level to eliminate canopy cover. We applied neighbor manipulation treatments to nine individuals of each species assigned to the control, decreased salt and inundation, and decreased inundation plots. This methodology allowed us to assess the competitive or facilitative impact of neighboring vegetation on each of the three low marsh species (Bertness 1991; Pennings and Callaway 1992; Emery et al. 2001; Pennings and Moore 2001; Pennings et al. 2004).

Soil Characteristics

We measured several substrate variables, (salinity, moisture, redox potential, pH, and sulfide concentration) monthly. Salinity was measured by extracting pore water from soil core samples, rehydrating the dried soils in a known volume of deionized water and recording the salinity of the supernatant with a Vista A366ATC refractometer. Soil moisture was measured by recording the initial mass (g) of collected samples, drying to a constant mass, then subtracting dry mass (g) from initial mass (g) and converting moisture to a percentage. Soil redox potential and pH were measured at 5 cm depths using a hand held Spectrum model 8601 pH/mV meter (Spectrum, Plainfield IL, USA). Three measurements were averaged for each plot to produce a single measurement for statistical analysis. Total soluble sulfide concentrations were recorded using a Hach DREL/2400 portable spectrophotometer (Hach, Loveland, CO, USA).

Plant Growth and Survival

We measured plant performance in all plots pre-treatment in June 2011 and then monthly for one year. At each census, plant height was measured from ground to apical meristem for both *Avicennia germinans and Borrichia frutescens*. Total leaf counts on 5 haphazardly selected stems were also recorded for these species. Height and leaf growth were determined by subtracting the initial measurements from maximum growth measurements after 1 year. Percent cover of *Borrichia frutescens and Batis maritima* was estimated by placing a 0.5 x 0.5 m quadrat with a 5 cm^2 grid over each plot and counting the number of squares containing the respective species. Percent cover of *Avicennia germinans* was determined by converting circumference to percent cover. Plant survivorship was determined by using data a year after the transplantation.

Chlorophyll Fluorescence

To further quantify plant response to decreased salinity and inundation stress, fluorescence measurements were conducted monthly on young leaves of all plants between 12 – 2 pm using an Underwater Fluorometer Diving-PAM, Submersable

Photosynthesis Yield Analyzer (Heinze Walz GmbH, Germany). Five measurements were averaged to produce a single value for each plant individual. The potential quantum yield (Φ_{PSII}), or how efficient a plant is in using available light energy to fix carbon dioxide, serves as a reliable indicator of photosystem II (PSII) efficiency (Maxwell and Johnson 2000). Quantum yield values decrease as plants experience more stress or as irreversible damage to photosystem II apparatus occurs (Nainanayake 2007). Optimal (Φ_{PSII}) range for most flowering plant species is 0.79 – 0.83, with values ranging from 0 to 1.0 (Maxwell and Johnson 2000). Since photosystem II photochemistry efficiency is correlated with linear electron transport rates, quantum yield measurements are also a reliable indicator of overall photosynthetic capacity (Genty et al. 1989; Bilger et al. 1995; Maxwell and Johnson 2000). Fluorescence data helps to quantify the physiological tolerance of plant species to changing environmental conditions and the impact of this stress on photosynthesis.

Analysis

The effects of decreased salt and decreased inundation on plant height, percent cover, leaf production, chlorophyll fluorescence yields, and soil characteristics were tested separately using three-way Analysis of Variance. We investigated the effects of decreased salt by comparing the decreased salt and inundation plots to the decreased inundation plots. We examined the effects of inundation stress by comparing the decreased inundation plots to the control plots. We examined the effects of neighbors by comparing the control to the clipped vegetation plots. We used growth, fluorescence, and soils data 1 year after transplantation. Plant survival was analyzed using ANOVA on mean plant longevity (in months) after 1 year. There were no significant three-way interactions to report and no two-way interactions except as noted.

Results

Pre-treatment Comparisons

All transplants in the control plots showed no significant effects of transplantation on plant growth, chlorophyll fluorescence, or survival when compared to the reference plots ($p > 0.05$ in all cases). We report no differences in height and % cover between individuals of the same plant species selected for transplantation in June 2011 pre-treatment measurements ($p > 0.05$ in all cases).

Effects of Salt

Soil characteristics

Salt addition in decreased inundation plots resulted in a sharp increase in interstitial soil salinities as compared to decreased salt and inundation plots ($F_{1,24}$= 6.050, p = 0.021; Fig. 4.1). Mean soil salinities were not statistically different from salinity levels in lower marsh control plots ($F_{1, 24}$= 1.055, p = 0.315; Fig. 4.1). Substrate moisture, redox potentials, and pH were not significantly impacted by salt addition in decreased inundation plots, when compared to decreased salt & inundation plots ($F_{1,24}$ = 2.793, p = 0.108; $F_{1, 24}$ = 1.541, p = 0.238 $F_{1,24}$ = 0.122, p = 0.735, respectively). Our study revealed no significant effects of plant species on substrate salinities, soil moisture, redox potential, or pH ($p > 0.05$ in all cases). All soil characteristics showed very similar trends for the duration of the experiment.

Plant performance and survival

Overall, adding salt to plants in decreased inundation plots increased plant height growth, % cover, and leaf production, when compared to plants in decreased salt & inundation plots ($F_{1,16} = 11.250$, $p = 0.004$; $F_{1,24} = 11.252$, $p = 0.003$; $F_{1,16} = 6.325$, $p = 0.017$, respectively; Fig. 4.2). Overall, salt addition in decreased inundation plots increased plant chlorophyll fluorescence ($F_{1,24} = 8.537$, $p = 0.008$; Fig. 4.3). Our study revealed a significant effect of added salt on plant survival, evidenced by fewer plant deaths after 1 year in decreased inundation plots when compared to decreased salt & inundation plots ($F_{1,24} = 6.750$, $p = 0.014$; Fig. 4.4). Our data showed no statistically significant differences in treatment effects among species for growth, chlorophyll fluorescence, or survival ($p > 0.05$ in all cases).

Effects of Inundation

Soil characteristics

Our findings showed no significant effects of decreased inundation on substrate salinities in plots receiving salt addition when compared to the control plots in lower marsh ($F_{1,24} = 0.130$, $p = 0.731$; Fig. 4.1). Mean soil moisture and redox potential were both significantly impacted by decreased inundation ($F_{1,24} = 7.352$, $p = 0.012$; $F_{1,24}=11.273$, $p = 0.003$, respectively; Fig. 4.1). Lower frequency and duration of inundation in terrestrial fringe plots resulted in higher redox potential and lower moisture when compared to control plots in lower marsh. Substrate pH was also higher in plots exposed to less inundation, although variation across zones was minimal, resulting in a marginally significant treatment effect ($F_{1,24} = 4.021$, $p = 0.056$). Our data revealed no significant effects of plant species on substrate salinities, soil moisture, redox potential, or pH ($p > 0.05$ in all cases). All soil characteristics showed very similar trends for the one year duration of the experiment.

Plant performance and survival

When compared to plants in control plots, those exposed to decreased inundation experienced more than a two-fold increase in height growth, % cover, and leaf production ($F_{1,16} = 9.633$, $p = 0.004$; $F_{1,24} = 13.443$, $p = 0.001$; $F_{1,16} = 6.057$, $p = 0.020$, respectively; Fig. 4.2). Additionally, plants in decreased inundation plots also experienced an increase in chlorophyll fluorescence yield ($F_{1,24} = 14.405$, $p < 0.001$; Fig. 4.3). Our data showed no significant treatment effects among species in growth, chlorophyll fluorescence, or survival ($p > 0.05$ in all cases). Reductions in inundation had no effect on survival after 1 year as most plants in both control and reduced inundation plots survived ($F_{1,24} = 0.119$, $p = 0.830$; Fig. 4.4).

Effects of Neighbor Manipulation

Soil characteristics

Neighbor manipulation resulted in a significant increase in mean substrate salinities in comparisons between control vs. decreased inundation ($F_{1,24} = 4.793$, $p = 0.037$), and decreased salt & inundation vs. decreased inundation ($F_{1,24} = 9.112$, $p = 0.006$; Fig. 4.1a). Effects of neighbor manipulation were greatest in the decreased salt & inundation plots, resulting in an interaction of neighbor manipulation and treatment on soil salinity ($F_{1,24} = 11.347$, $p = 0.002$). Additionally, neighbor manipulation resulted in a decrease in soil redox potentials in control plots compared to decreased inundation plots ($F_{1,24} = 11.451$, $p = 0.002$; Fig. 4.1c). Neighbor manipulation did not result in any change in soil moisture or pH in all treatments ($p > 0.05$ in all cases).

Plant performance and survival

Neighbor manipulation had significant effects on plant height growth, % cover, and leaf production in both the control vs. decreased inundation comparison ($F_{1,24} = 4.578$, $p = 0.040$; $F_{1,24} = 5.541$, $p = 0.033$; $F_{1,24} = 5.531$, $p = 0.036$, respectively) and decreased inundation vs. decreased salt & inundation comparison ($F_{1,24}$ = 10.463= 0.005; $F_{1,24} = 13.957$, $p < 0.001$; $F_{1,24} = 12.893$, $p = 0.002$, respectively; Fig. 4.2), but there was a shift in the nature of this effect with landward progression from marsh to fringe. Neighbor manipulation resulted in increased height growth, % cover, and leaf production for all species in both decreased salt & inundation and decreased inundation plots in the terrestrial fringe but had the opposite effect in the control plots in the lower marsh. These findings signify a significant interaction of neighbor manipulation and treatment in the control vs. decreased inundation comparison plots for all plant growth parameters, height, % cover, and leaf production ($F_{1,24}$ = 8.093, p = 0.008; $F_{1,24}$ = 13.450, p = 0.001; $F_{1,24}$ = 11.773, p = 0.002, respectively; Fig. 4.2). Although neighbor manipulation had a positive effect on plant growth in both treatment plots in the terrestrial fringe, this benefit was less for plants experiencing added salt stress in decreased inundation plots, yielding a neighbor manipulation x treatment interaction in the decreased salt & inundation and decreased inundation plot comparison for all growth parameters, height, % cover, and leaf production ($F_{1,24}$ = 6.629, p = 0.020; $F_{1,24}$ = 8.571, p = 0.008; $F_{1,24}$ = 5.947 p = 0.022, respectively; Fig. 4.2).

Neighbor manipulation had significant effects on potential quantum yield after 1 year in both the control vs. decreased inundation comparison and decreased salt & inundation vs. decreased inundation comparison ($F_{1,24}$ = 6.686, p = 0.018; $F_{1,24}$ = 6.713, p = 0.017, respectively; Fig. 4.3). After 1 year, plants transplanted into fringe areas experienced less photosynthetic inhibition without neighboring above ground vegetation, while controls in marsh areas were less inhibited with neighbors, resulting in an interaction of vegetation manipulation with landward distance on potential quantum yield ($F_{1,24}$ = 13.457, p = 0.001 in control vs. decreased inundation comparison).

Neighbor manipulation impacted plant survival in decreased salt & inundation plots ($F_{1,24}$ = 6.835, p = 0.013; Fig. 4.4), as evidenced by increased mortality in plots with neighbors. Our study showed no significant treatment effects among species in growth, chlorophyll fluorescence, or survival ($p > 0.05$ in all cases).

Discussion

Effects of Abiotic Interactions

Ecologists debated for decades whether salt marsh plants require the saline conditions and frequent inundation prevalent in their low marsh habitat or merely tolerate it better than other species (Adams 1963). Our findings concur with Bertness et al. (1992) who established that these species don't require, but merely tolerate harsher conditions. Overall, plants transplanted to higher elevations performed better than their counterparts in the more physically stressful low marsh zone. These results concur with other work which suggests that salt marsh species are competitively displaced and restricted to more physically stressful low marsh areas by less stress tolerant, but competitively superior species at landward boundaries (Bertness and Ellison 1987; Emery et al. 2001; Pennings and Bertness 2001). Additional supportive evidence comes from our concurrent study which transplanted *Baccharis angustifolia*, *Baccharis halimifolia,* and *Iva frutescens,* from the terrestrial fringe to the forest margin. Our results also showed these fringe species merely tolerate harsher conditions and are competitively displaced seaward to fringe areas by terrestrial species at the forest margin (Hyder and Stiling unpublished). Together, these findings lend strong support to the hypothesis that a trade-off may exist between physical stress tolerance and competitive ability in salt marsh and salt marsh fringing systems (Grime 1977, 1979; Bertness 1991; Levine et al. 1998; Costa et al. 2003).

Overall, although salt addition negatively impacted all three salt marsh species, our findings suggest that inundation may play a larger role than changes in salinity in influencing salt marsh plant performance and survival. This is especially interesting because the frequency of climate change induced precipitation and storm events is predicted to increase, which would exacerbate the inundation conditions in coastal areas, allowing salt marsh plants no respite from inundation stress (Cooper 1982; Day et al. 2008; Yates et al. 2011).

Effects of Biotic Interactions

These findings supported our prediction that species interactions are pervasive and important drivers of salt marsh plant performance and survival. All three species transplanted to higher elevations with neighbors exhibited less growth than transplants with neighbors removed. As predicted, *A. germinans* outperformed both *B. maritima* and *B. frutescens* in the presence of fringe neighbors. *A. germinans* was likely not as shaded by the fringe canopy and may be more capable than the other species of intercepting more water and nutrients with its more extensive root system. Furthermore, decades of studies have shown *A. germinans* is capable of landward migration, as evidenced by the presence of cypress trees and palm tree stumps in mangrove forests (Alexander and Crook 1974). *B. maritima* exhibited the least amount of growth in the presence of neighbors. *B. maritima* is smaller in stature and may be more impacted by the reduced light infiltration imposed by its taller fringe neighbors. Overall, all plants at higher elevations were more depressed by strong competitive pressure from neighboring fringe species when compared to plants with neighbors trimmed. Taller species are prevalent in the terrestrial area fringing the marsh and can competitively exclude halophytic salt marsh species by limiting light, space, and nutrient supply. In the neighbor manipulation treatments, canopy cover was removed, which allowed light infiltration. After 1 year, plants without neighbors in both the decreased salt & inundation and decreased inundation treatments, experienced significantly increased growth which suggests that light limitation may be a major force governing strong competition at higher elevations in salt marsh systems. Once again, the current results are supported by our previous study where four terrestrial fringe plant species transplanted landward experienced more growth in the absence of neighboring above ground vegetation (Hyder and Stiling, unpublished manuscript). Landward migration of salt marsh species may only be possible if the existing fringe species at the fringe-marsh boundary are not able to tolerate changing conditions associated with sea level rise, thereby releasing their strong competitive pressure.

While plants at higher elevations were depressed by strong competitive pressure from neighboring fringe species, plants in the more physically stressful marsh areas benefited from the presence of neighbors. Marsh species endure frequent inundation and saline conditions and, and therefore, allocate much of their resources to maintaining the necessary adaptations to help alleviate inundation and salt stress. As a result, these plants are capable of mitigating some of the abiotic stress for neighboring plants at lower elevations. In one of our previous studies, fringe plants were transplanted seaward to marsh areas which endure more frequent salt and inundation and compared their performance to plants “transplanted” to their native fringe habitat. The fringe plants exhibited diminished growth and performance in their native fringe zone in the presence of neighbors but experienced enhanced growth in the presence of marsh neighbors when transplanted to lower marsh elevations (Hyder and Stiling, *personal observation*). In our current study, a shift in the direction of interspecific interactions from competitive to facilitative was noted with increasing abiotic stress. Although some studies have reported competitive interactions to be ubiquitous in marsh areas (Pennings et al. 2003, Maestre et al. 2009; Guo and Pennings 2012; Keammerer and Hacker 2013), our results support the SGH which contends that competition is pervasive in areas which experience less physical stress, but facilitation is more common as stress levels increase.

Interestingly, adding salt stress to all three species in decreased inundation plots in the fringe did not precipitate a shift in the nature of interspecific interactions from competitive to facilitative. The impact of the salt stress on the neighboring fringe plants was likely too high for these plants to moderate the conditions for the salt marsh plants. These findings indicate that increased levels of stress may not always result in a shift in the nature of interspecific interactions in all cases. Our findings suggest that information on both the magnitude and type of abiotic stress, as well as the matrix of neighbors, may be needed to predict whether shifts from competition to facilitation will occur.

Overall, our results show that the magnitude of competitive interactions increased as inundation stress decreased, lending strong support for the stress-gradient hypothesis. These findings agree with previous work demonstrating that highly competitive plants have less of a competitive effect as abiotic stress increases and the competitively subordinate, but more stress tolerant plants have stronger facilitative effects under similar conditions (Bertness and Shumway 1993; Bertness and Callaway 1994; Bertness and Hacker 1994; Bertness and Ewanchuk 2002). In this system, both the magnitude and direction of plant interactions was dependent upon (a) the severity of salt and inundation exposure, and (b) the matrix of neighboring plants. In fringe areas, governed by strong competitive interactions, salt addition likely impacted competitor performance which weakened the competitive pressure on the salt marsh transplants. As stress was applied in these more benign areas, a shift in the nature of interactions was not noted but rather, competitive release.

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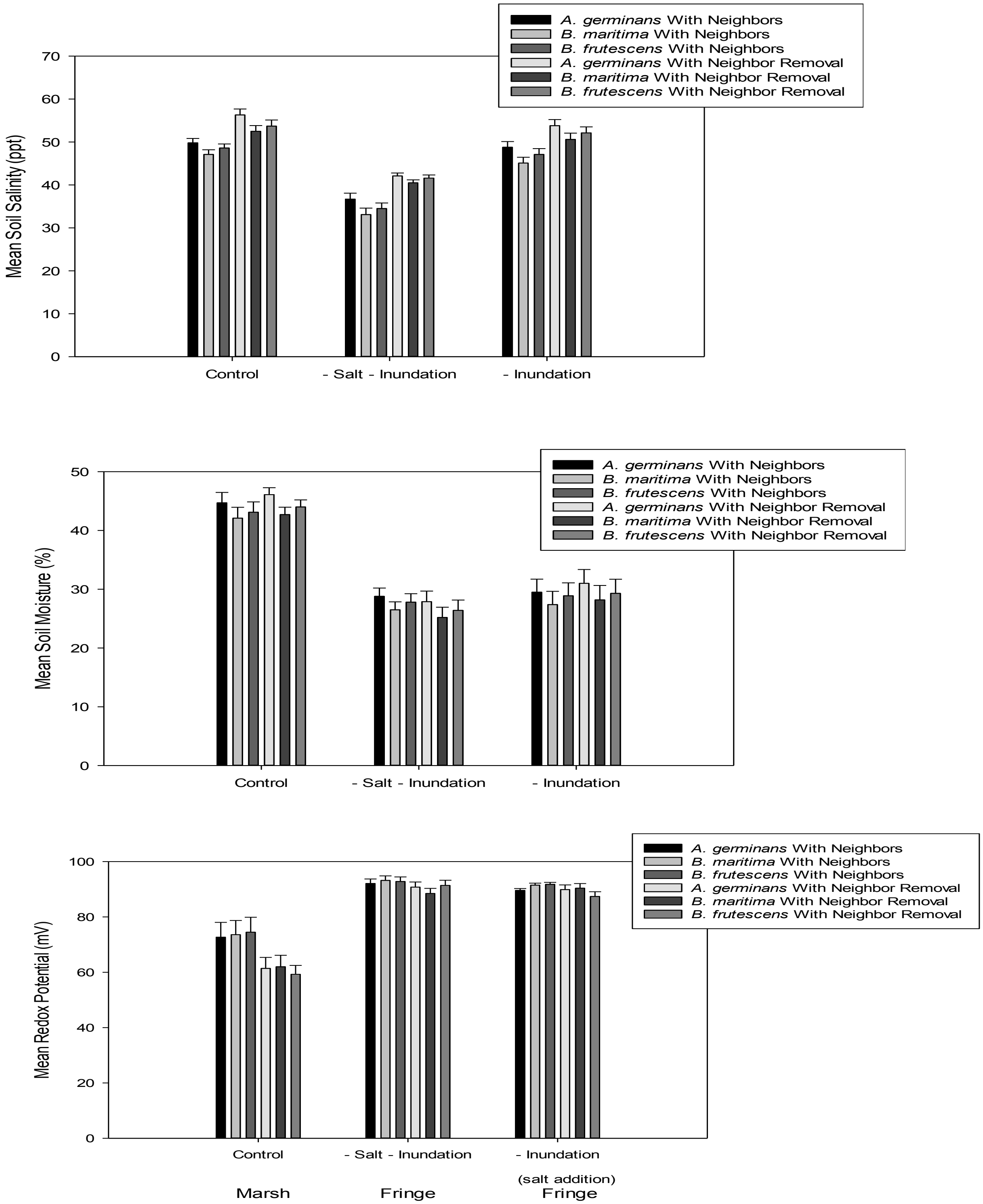


Figure 4.1: Mean (a) interstitial soil salinity (ppt), (b) soil moisture (%), and (c) redox potential (mV) for *A. germinans*, *B. maritima*, and *B. frutescens*, in control, decreased salt & inundation, and decreased inundation plots with and without neighboring above ground vegetation after 1 year. Bars represent ± 1 SE. n=9

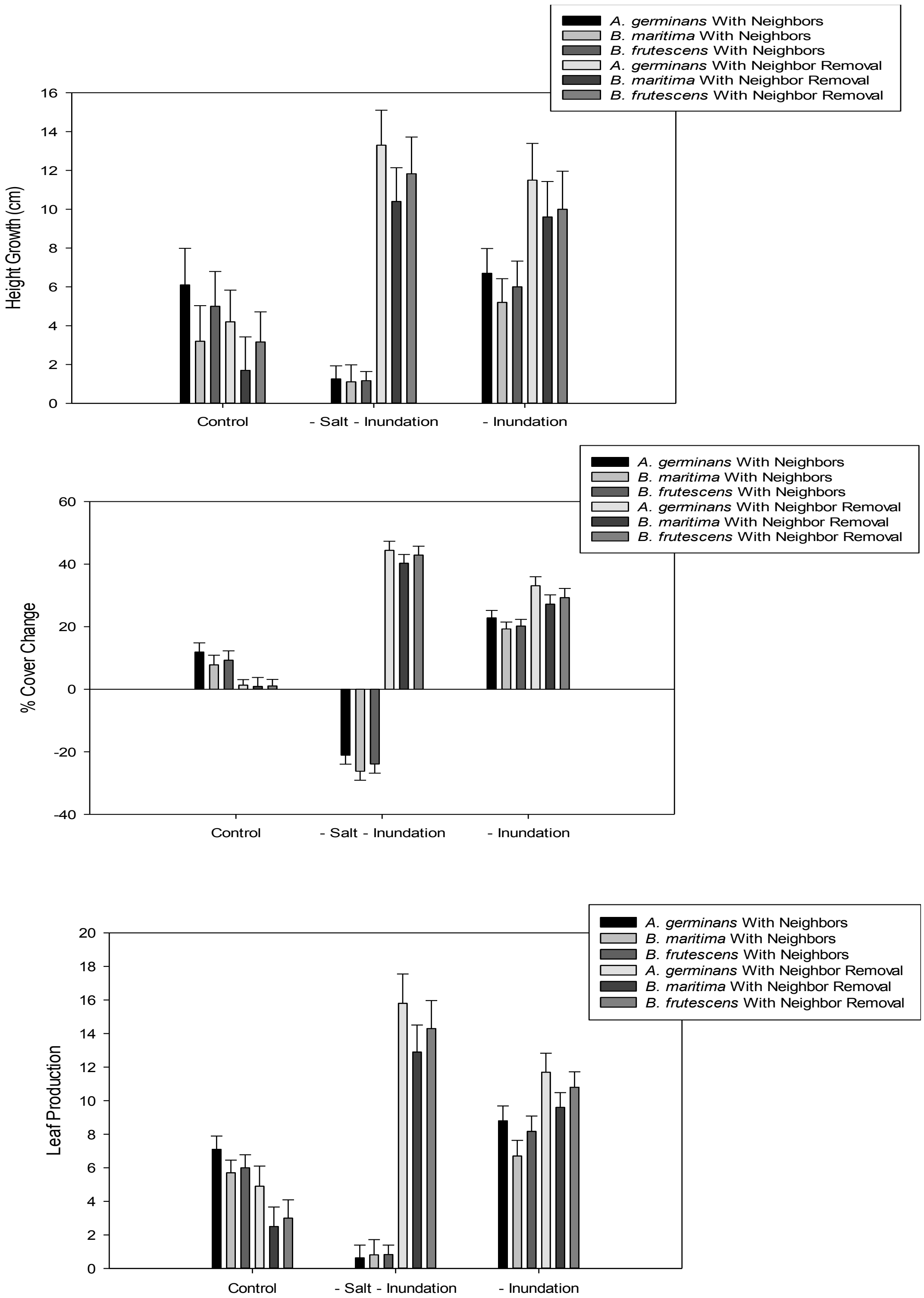
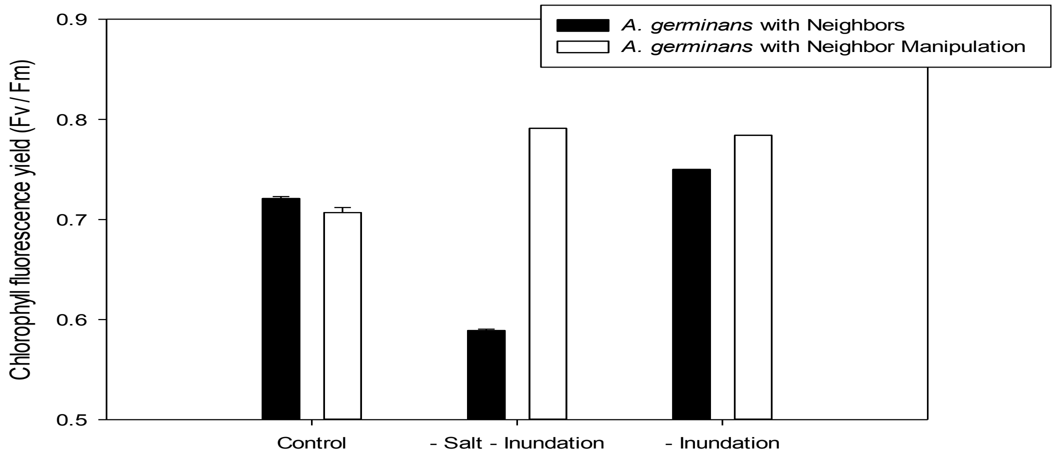
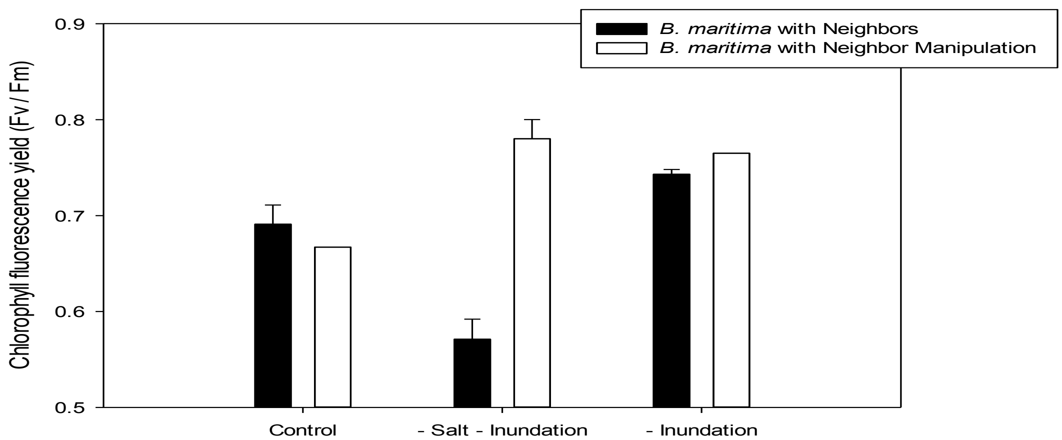


Figure 4.2: Average (a) height growth, (b) % cover, and (c) leaf production of *A. germinans*, *B. maritima*, and *B. frutescens*, in control, decreased salt & inundation, and decreased inundation plots with and without neighboring above ground vegetation after 1 year. Bars represent ± 1 SE. n=9





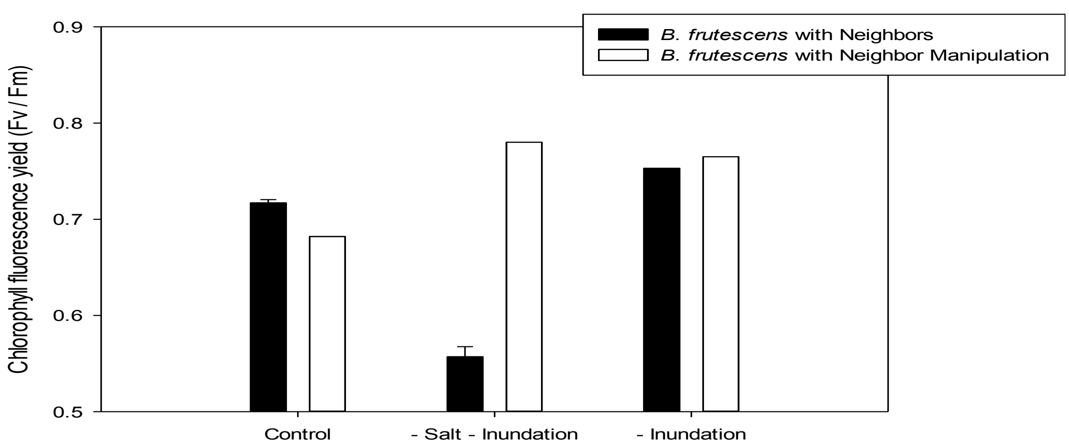


Figure 4.3: Average plant chlorophyll fluorescence yield (Fv/Fm) for *A. germinans*, *B. maritima*, and *B. frutescens*, in control, decreased salt & inundation, and decreased inundation plots with and without neighboring above ground vegetation after 1 year. Bars represent ± 1 SE. n=9

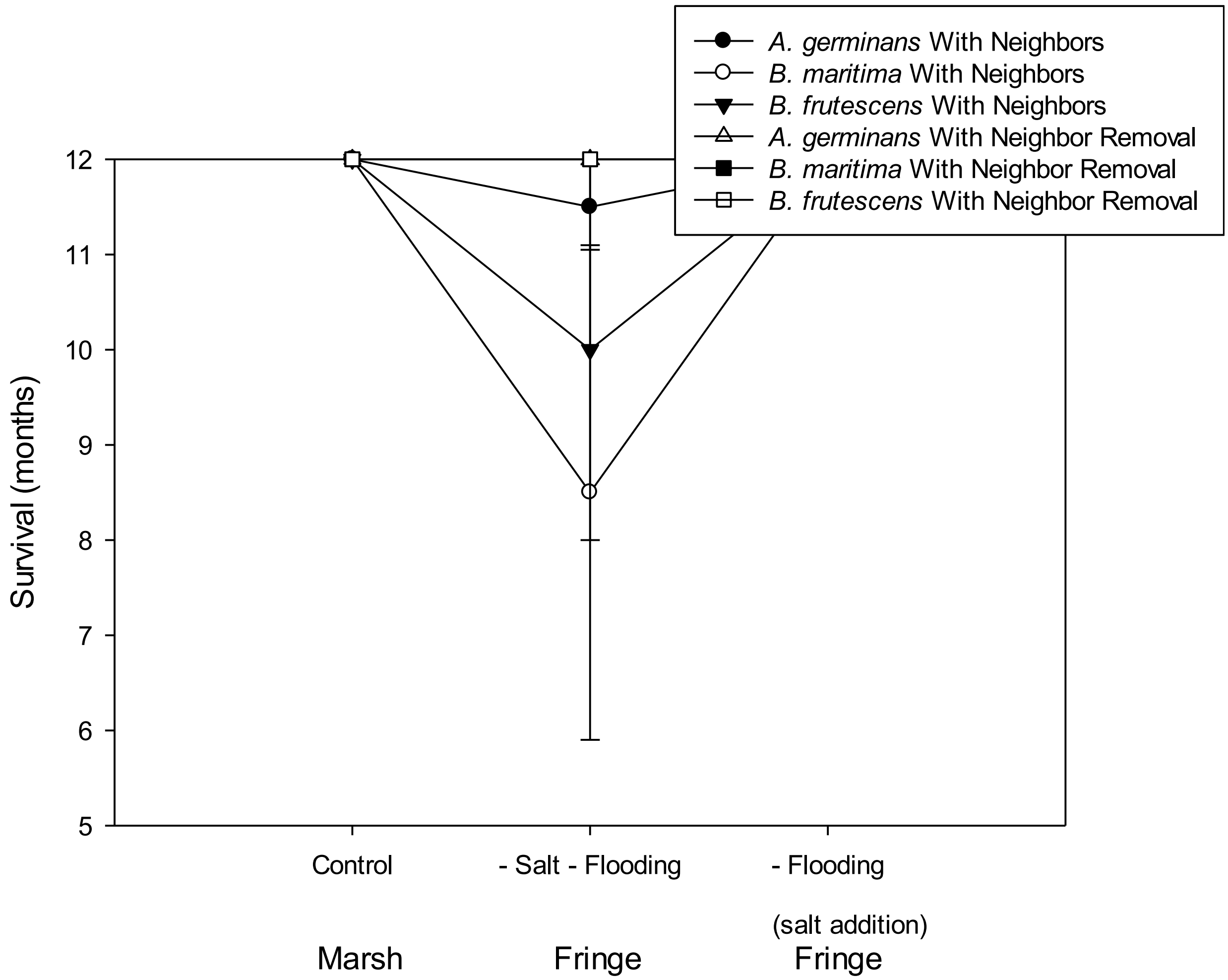


Figure 4.4: Mean survivorship of *A. germinans*, *B. maritima*, and *B. frutescens*, in control, decreased salt & inundation, and decreased inundation plots with and without neighboring above ground vegetation after 1 year. Bars represent ± 1 SE. n=9

Table 4.1: Three-way ANOVA *F* statistics and significance are presented for the effects of species, salt, and neighbor manipulation on soil characteristics, performance, and survival of three salt marsh species. Growth, fluorescence, and soil characteristics were analyzed after 1 year. Plant survival was analyzed on mean plant longevity after 1 year. There were no significant three-way interactions to report.
*P<0.05; **P<0.01; ***P<0.001; NS P>0.05

	Soil Salinity	Soil Moisture	Soil Redox	Soil pH
Source of variation	F	F	F	F
Salt	6.050*	2.793 NS	1.541 NS	0.122 NS
Neighbor Manipulation	9.112**	1.055 NS	11.457**	0.341 NS
Species	0.415 NS	1.543 NS	1.019 NS	0.284 NS
Species x Salt	0.841 NS	1.067 NS	0.968 NS	0.952 NS
Species x Neighbor Manipulation	1.168 NS	0.971 NS	2.041 NS	0.715 NS
Salt x Neighbor Manipulation	11.347**	0.182 NS	0.802 NS	0.052NS

	Height	%Cover	Leaf Production	Chlorophyll Fluorescence Yield	Survival
Source of variation	F	F	F	F	F
Salt	11.250**	11.252**	6.325*	4.333*	6.750*
Neighbor Manipulation	10.463**	13.957***	12.893**	6.713*	6.835*
Species	0.512 NS	1.239 NS	1.592 NS	0.263	0.578 NS
Species x Salt	1.250 NS	1.425 NS	2.981 NS	0.831 NS	1.192 NS
Species x Neighbor Manipulation	0.460 NS	1.098 NS	3.162 NS	0.462 NS	1.793 NS
Salt x Neighbor Manipulation	6.629*	8.571***	5.947**	0.341 NS	0.103 NS

Table 4.2: Three-way ANOVA *F* statistics and significance are presented for the effects of species, inundation, and neighbor manipulation on soil characteristics, performance, and survival of three salt marsh species. Growth, fluorescence, and soil characteristics were analyzed after 1 year. Plant survival was analyzed on mean plant longevity after 1 year. There were no significant three-way interactions to report.
*P<0.05; **P<0.01; ***P<0.001; NS P>0.05

	Soil Salinity	Soil Moisture	Soil Redox	Soil pH
Source of variation	F	F	F	F
Inundation	0.130 NS	7.352*	11.273**	4.021 NS
Neighbor Manipulation	4.793 NS	2.568 NS	11.451**	0.451 NS
Species	1.471 NS	1.537 NS	2.142 NS	1.130 NS
Species x Inundation	0.898 NS	0.817 NS	1.153 NS	0.722 NS
Species x Neighbor Manipulation	1.568 NS	1.821 NS	0.476 NS	0.970 NS
Inundation x Neighbor Manipulation	1.753 NS	0.389 NS	0.946 NS	0.130 NS

	Height	% Cover	Leaf Production	Chlorophyll Fluorescence Yield	Survival
Source of variation	F	F	F	F	F
Inundation	9.633**	13.443**	6.057*	14.405***	0.119NS
Neighbor Manipulation	4.578*	5.541*	5.531*	6.686*	0.256NS
Species	1.186 NS	1.793 NS	0.590 NS	0.593 NS	1.118 NS
Species x Inundation	1.461 NS	1.618 NS	1.275 NS	0.844 NS	1.672 NS
Species x Neighbor Manipulation	1.571 NS	0.856 NS	1.167 NS	0.947	1.437 NS
Inundation x Neighbor Manipulation	8.093**	13.450**	11.773**	13.457**	0.166NS