Salt Marsh Migration into Abandoned Agricultural Fields and the Role of *Kosteletzkya pentacarpos* in Ecosystem Transition

Emily Victoria Scott Long Rubin
Cape Charles, Virginia

B.S., University of Virginia, 2015

A Dissertation presented to the Graduate Faculty
of the University of Virginia in Candidacy for the Degree of
Doctor of Philosophy

Department of Environmental Sciences

University of Virginia
May 2024

Linda K. Blum, Advisor
Aaron L. Mills, Advisor
David E. Carr, Committee Member
Michael P. Timko, Committee Member

ABSTRACT

Understanding the process of marsh migration into coastal areas, particularly low-lying old fields, will help to inform adaptive strategies that facilitate ecosystem change from upland to salt marsh. This study sought to understand better the drivers of old-field plant community response to sea-level rise and to evaluate how two types of disturbance, tilling the soil and introducing a new species, alter community response.

From 2017-2019, water levels and salinity were measured in seven shallow wells in an abandoned agricultural field adjacent to a salt marsh. Water-table fluctuations greater than 10 cm were associated with flooding events from storm surges, precipitation, or a combination of the two. Groundwater elevation and salinity showed a temporal response to freshwater flooding from precipitation and saltwater flooding from storm surge and extreme tides that suggest overland flooding with saline water from nearby tidal creeks is the source of salinity in the groundwater. However, salinization of the groundwater may not persist if seawater flooding events are followed or accompanied by freshwater inputs from precipitation. These findings show that the magnitude and timing of precipitation events can reduce salinity stress to the plant community by retarding the salinization of old fields experiencing high rates of sea-level rise.

Greenhouse studies of *Panicum virgatum* (switchgrass) and *Kosteletzkya pentacarpos* (salt marsh mallow) seed germination and seedling growth in three levels of saline water showed that salt marsh mallow germination and survival was greater than that of switchgrass at all treatment levels, and that mallow began linear growth sooner than switchgrass. Mallow seed germination and seedling growth appeared more tolerant of saline water than switchgrass, and these findings suggest that mallow should become established more rapidly than switchgrass in abandoned agricultural fields experiencing increased frequency of flooding with saltwater.

A field experiment was conducted to determine the effect of increased frequency of flooding on the establishment and growth of monocultures and mixed cultures of salt marsh mallow and switchgrass. Mallow cover was higher in the wet treatment plots, which received supplemental fresh water every week during the summer, than in the dry plots, while switchgrass cover was unaffected by watering. Additionally, seeds of the two plants were mixed in different ratios and then planted together. Regardless of the seed mixture ratio in a plot, mallow cover was greater than that of switchgrass. Thus, salt marsh mallow may be a more suitable species than switchgrass for cultivation in abandoned agricultural fields where groundwater elevations are increasing or the fields experiencing more frequent overland flooding with saline water.

In 2015, *K. pentacarpos* seeds were planted in experimental plots at the field site to determine if the recruitment of a native high marsh species, *Distichlis spicata*, was enhanced by disturbing the existing plant community by tilling and adding marsh mallow. Species richness and percent cover at the site were measured at the end of each growing season from 2015 to 2019. After two years, coverage by high marsh species, including *D. spicata*, and transition species, including *K. pentacarpos*, increased in all treatment plots. Disturbance of the native plant community by tilling increased *D. spicata* cover in the plots one year after the initial treatment. Changes in hydrological conditions in response to seawater flooding in three distinct zones within the field resulted in different plant communities. These results suggest that cultivating *K. pentacarpos* in salinized agricultural fields may improve the natural recruitment of high marsh and transition plant species in coastal agricultural land experiencing sea-level rise.

Based on the results of these experiments, a new conceptual model was developed to explain the drivers of ecosystem transition, especially groundwater elevation and salinity, from abandoned agricultural fields to high marsh. This model decouples those drivers, which occur at different rates, and emphasizes the role of precipitation in plant community change. In fields experiencing high rates of salinization, disturbance facilitates the transition from upland to salt marsh. Thus, the rate of inland marsh migration depends on the abiotic conditions at a given site and the resiliency of the plant community to environmental change, which vary at different spatial and temporal scales. Furthermore, the addition of new species, such as salt marsh mallow, that thrive under dynamic environmental conditions may preserve important ecosystem services that otherwise may be lost, at least temporarily, during transition.

ACKNOWLEDGEMENTS

First and foremost, I would like to express my deepest gratitude to my advisor, Linda Blum, for her unwavering support and mentorship over the past fifteen years. Linda began fostering my interest in salt marsh ecology when I was a junior in high school, and her continuous encouragement has fueled my passion throughout my undergraduate and graduate career. By encouraging me to leverage my personal story, Linda has shaped my development as both a scientist and an individual. I am profoundly thankful for her mentorship and friendship.

I also extend a heartfelt thanks to my co-advisor, Aaron Mills, for sharing his expertise and knowledge. This work would not have been possible without Aaron's invaluable contributions, including fieldwork assistance, data analysis, and alternative perspective, all of which have played a crucial role in my academic journey.

My family has been a constant source of support, and I am incredibly fortunate to have them by my side. To my husband, Jordan, your unwavering support and encouragement have been my anchor. To my mother, thank you for showing me that personal and professional success are not mutually exclusive. To my father, thank you for teaching me the importance of responsible environmental stewardship and for sharing your farming wisdom with me. To my siblings, Theresa, Bridget, and Suzanna, thank you for your expertise, time, and energy.

During my graduate studies, the Lab of Microbial Ecology (LMECOL) group provided invaluable assistance. I extend my gratitude to all past and present students and faculty members for their feedback and support. A special thanks to my officemates, Jessica and Emma, for their field assistance, laughter, and encouragement, making our journey memorable.

My research would not have been possible without the assistance of the dedicated staff at the Anheuser Busch Coastal Research Center (ABCRC). I extend special thanks to Donna Fauber for the many hats she wears to support all students affiliated with the ABCRC. I am grateful to the many individuals who have helped me with data collection in the field: Katie Spady Sanders, Jessica Flester, Emma Cronin, Kinsey Tedford, Suzanna Long, Catherine Long, and many others.

I extend my appreciation to The Nature Conservancy's Virginia Coast Reserve for providing access to the Brownsville Preserve and Upper Phillips Creek, and to the Eastern Shore Agricultural Research and Extension Center for the use of their greenhouse facilities and equipment.

Funding for this project was provided by the National Science Foundation (Grant No. DEB-1832221), the National Oceanic and Atmospheric Administration (NOAA) (Award No. NA21OAR4170012), the Virginia Sea Grant College Program Project V723420, and the NOAA National Sea Grant College Program, U.S. Department of Commerce.

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Chapter 1.

Introduction

1.1. Background and Motivation

Sea-level is rising rapidly on the Mid-Atlantic coast (Sallenger *et al.*, 2012). Recent estimates of local sea-level rise for the Virginia Coastal Bays are 5.63 mm year^{-1} between 1978-2023 (NOAA, 2023). The rapidly rising sea level combined with the gently sloping topography along the Mid-Atlantic Coast allows for landward migration of salt marshes that results in the conversion of uplands, including forests and agricultural land, to high-marsh ecosystems (Anisfeld *et al.*, 2017; Brinson *et al.*, 1995; Fagherazzi *et al.*, 2019a; Gedan *et al.*, 2020; Gedan & Fernández-Pascual, 2019; Jobe IV & Gedan, 2021; Kirwan & Gedan, 2019; Molino *et al.*, 2022; Schieder *et al.*, 2018; Tully *et al.*, 2019; Voutsina *et al.*, 2015a). Titus *et al.*, (2010) estimated that 192 ha of farmland on the Eastern Shore of Virginia (Eastern Shore) are converted to salt marsh annually. That is an area more than 1.5 times the size of an average Eastern Shore farm field (116 ha, Accomack County, 2014). While this conversion preserves and increases the ecosystem services provided by marshes (Craft *et al.*, 2009), there is a cost to the local economy, *viz.* the loss of productive land for farming operations.

The loss of farmland can be especially devastating in places like the Eastern Shore where agriculture is the largest contributor to the economy, valued at $243 million annually (Accomack-Northampton Planning District Commission, 2012). The production value of a single ha of farmland is between $4000 and $5000 annually (Accomack-Northampton Planning District Commission, 2012), such that the conversion of 192 ha per year of farmland to marsh represents a loss of $768,000 to $960,000 annually to the local economy. As the sea level continues to rise, fields that are beginning the transition from upland to high marsh start to experience occasional flooding with salt water from the coastal lagoons and marsh creeks. Thus, the fields gradually become wetter over time, but the effect of the salt on crop plants is felt almost immediately. In a survey of farmers on the Eastern Shore of Virginia, 70% of respondents indicated that they had abandoned portions of their fields due to prolonged periods of flooding and increasing poor drainage (unpublished data).

In these cases, farmers are left with few choices for land management. One option is to undertake the costly task of constructing barriers to prevent flooding or extensive drainage systems to move water off the land. A less costly strategy would be to plant salt-tolerant crops to extend the agricultural life of salinized fields and mitigate the economic loss. Two native perennial plants, salt marsh mallow (*Kosteletzkya pentacarpos*) and switchgrass (*Panicum virgatum*) have been identified as potential alternative crops for wet and salinized soils in coastal areas like the Eastern Shore of Virginia (Gallagher, 1985; Liu *et al.*, 2014).

Currently, switchgrass is cultivated for biofuel production in the United States (Andrea *et al.*, 2018; Parrish & Fike, 2005; Sanderson *et al.*, 1996) and salt marsh mallow (mallow) has been identified as another plant source for biodiesel (Moser *et al.*, 2013; Ruan *et al.*, 2008). Additionally, mallow has a large number of other, economically beneficial uses for all parts of the plant, and it can contribute substantially to ecosystem services in the places where it grows (Figure 1). The transition from annual crops to perennial biofuel crops like salt marsh mallow and switchgrass has the ability to boost carbon sequestration and nitrogen retention by 50% due to greater root depths and longer growing seasons (Glover *et al.*, 2007; Tolbert *et al.*, 2000) compared with shallow-rooted, short-lived annuals such as corn, soybeans, and wheat that are predominantly grown on the Eastern Shore.

A third option for farmers is to abandon fields to natural successional processes allowing abandoned agricultural fields to develop old field communities, and, finally, salt marsh communities. However, as Voutsina *et al.* (2015a) pointed out, unmanaged land is not only an economic loss to a region, but abandoned farmland may not contain suitable nutrients or organic matter to support wetland transgression due to weakened or sparse plant colonization. For example, the occurrence of halotolerant, invasive *Phragmites australis*, as opposed to typical wetland plants such as *Distichlis spicata*, was strongly and positively correlated with cleared, but unmanaged open land along the Chesapeake Bay shoreline in Virginia (Chambers *et al.*, 2008) resulting in a loss of crucial habitat provided by native salt marsh plant communities. In contrast to upland colonization by *P. australis*, cultivation of mallow and switchgrass may promote coastal wetland transgression thus “creating an opportunity to turn the ultimate loss of agricultural services into a positive gain in salt marsh services” (Voutsina *et al.*, 2015a).

Four plant communities are characteristic of U.S. east coast salt marshes. These communities are associated with differences in the frequency and duration of tidal flooding and are generally referred to as the creek bank, low marsh, high marsh, and upland transition. Each section of the marsh has a distinct plant community that identifies each zone (Figure 2). Plant community dynamics play an important role in the transition from one zone to another, particularly as the high marsh becomes low marsh (Bertness &

Hacker, 1994; Bertness & Leonard, 1997; Pennings *et al.*, 2005), and might be important in inland marsh migration. One would expect this pattern of zonation to be present in any location undergoing a transition from upland to marsh.

Brinson *et al.* (1995) hypothesized that the transition from upland to high salt marsh occurs when infrequent, extreme storm tides flow overland into fields or forests where the saline water infiltrates into the soil such that plants experience water stress and, ultimately, death (Figure 3). Fagherazzi *et al.* (2019a), proposed that, as sea level rises and the frequency of tidal inundation increases, waterlogging and continued inputs of salt lead to soil changes that are more favorable for the growth of wetland species than upland species resulting in shifts from upland fields to salt marshes (Figure 4). While there is some understanding of how abiotic factors affect marsh transgression, what is not clear is the role that biotic factors, such as plant community dynamics, play in transgression. Examples of biotic disturbances include fire (Bowman *et al.*, 2009; Lynch, 1941; Taillie *et al.*, 2019), flooding (R. R. Christian *et al.*, 2000; Kang *et al.*, 2016; Knowles *et al.*, 1991), increased salinity (Brinson *et al.*, 1995; Fagherazzi *et al.*, 2019a; Janousek & Folger, 2014; Kearney *et al.*, 2019; Nordio & Fagherazzi, 2022; Raposa *et al.*, 2017; Taillie *et al.*, 2019; Tully *et al.*, 2019; Wasson *et al.*, 2013), and intense grazing or predation (Connell & Slatyer, 1977; Hallett *et al.*, 2017).

Previous studies have focused on marsh migration into fallow fields (Wasson *et al.*, 2013), forests (Brinson *et al.*, 1995; Fagherazzi *et al.*, 2019a; Jobe IV & Gedan, 2021; Kearney *et al.*, 2019; Kirwan & Gedan, 2019; Nordio & Fagherazzi, 2022; Taillie *et al.*, 2019), or suburban lawns (Anisfeld *et al.*, 2017). Others have looked at marsh migration into agricultural fields (Fagherazzi *et al.*, 2019a; Gedan *et al.*, 2020; Gedan & Fernández-Pascual, 2019; Gewin, 2018; Voutsina *et al.*, 2015a) that are actively maintained as a monoculture. The work presented here examines the process of marsh migration into an established old field that is experiencing environmental disruptions from sea-level rise, a topic previously unexplored. The present work focused primarily on the process of transition between old-field and high-marsh plant communities. Earlier work by Fagherazzi *et al.* (2019a) (Figure 4) presented a descriptive model that comprised a monotonic change in groundwater elevation, soil salinity, and plant community composition. However, they recognized that predicting how plant communities will respond to the interaction between increasing water table elevation and salinity is problematic due to the non-linear interactions between these drivers (Fagherazzi *et al.*, 2019a). The present study documents two drivers of marsh migration (flooding and groundwater salinity) and the resulting changes in species richness and abundance to inform a revised conceptual model.

1.2. Research Objectives

The overarching goal of this dissertation work was two-fold: 1) to identify the drivers of marsh migration into abandoned agricultural fields, and 2) to understand how the plant community in an abandoned agricultural field undergoing transition from upland to a high marsh responds to anthropogenic disturbance during marsh migration.

These topics were addressed with several questions:

Objective 1) Identify the drivers of marsh migration into abandoned agricultural fields.

a. How frequently does flooding impact the abandoned agricultural study site?
b. What are the sources of the flooding water?
c. Is the source of salinity overland flooding or underground intrusion of saline water?
d. How does the elevation of the groundwater table change during and after a flooding event?
e. How does the salinity of the groundwater change during and after a flooding event?

Objective 2) How does the plant community in an abandoned agricultural field undergoing transition from an upland to a high marsh community respond to anthropogenic disturbance by tilling and planting a desired transition species into the community?

a. Does saline water affect seed germination and seedling growth of two common native species, *K. pentacarpos* and *P. virgatum* in a similar way?
b. Does increasing flooding frequency impact the establishment of two common native species, *K. pentacarpos* and *P. virgatum* in the field?
c. Does disturbing the established plant community in an old field by tilling facilitate the transition from old field to high marsh by increasing the recruitment of high marsh species into the community?
d. Does intensive planting of *K. pentacarpos*, in the old-field plant community facilitate the recruitment of species typical of the transition zones between upland plant communities and high marsh?

1.3. Dissertation organization

The chapters of my dissertation take the form of multiple manuscripts. One of these manuscripts, Chapter 2, is an early version of Rubin *et al.,* (Rubin *et al.*, 2024). Each chapter of the dissertation generally follows the format of a standard scientific journal article, including an independent abstract, site description, and relevant literature review. A complete reference list for all chapters is provided in a separate section at the end of the dissertation. The dissertation comprises six chapters. This chapter, Chapter 1, is an introduction to the dissertation and lays out the motivation, overarching goals, and specific research objectives. Chapter 2 focuses on an analysis of the groundwater elevation and salinity and addresses questions 1a, 1b, 1c, 1d, and 1e. Chapter 3 discusses the salinity impacts on seed germination and seedling growth of two native species, salt marsh mallow and switchgrass, thus addressing question 2a. Chapter 4 focuses on increased flooding frequencies of those same two species in the field, addressing question 2b. Chapter 5 examines post-disturbance changes in the plant community within an old field experiencing increased flooding frequency and groundwater salinity, thereby addressing questions 2c and 2d. Given that each chapter was written as an individual manuscript; thus, some of the introductory material in each chapter is repetitive. The final chapter (6) provides a short synthesis of the findings of the previous chapters and proposes revisions to a portion of the conceptual model published in Fagherazzi *et al.* (2019a). The revised model explains changes in groundwater elevation and salinity that lead to changes in plant community structure during marsh migration into old field environments.

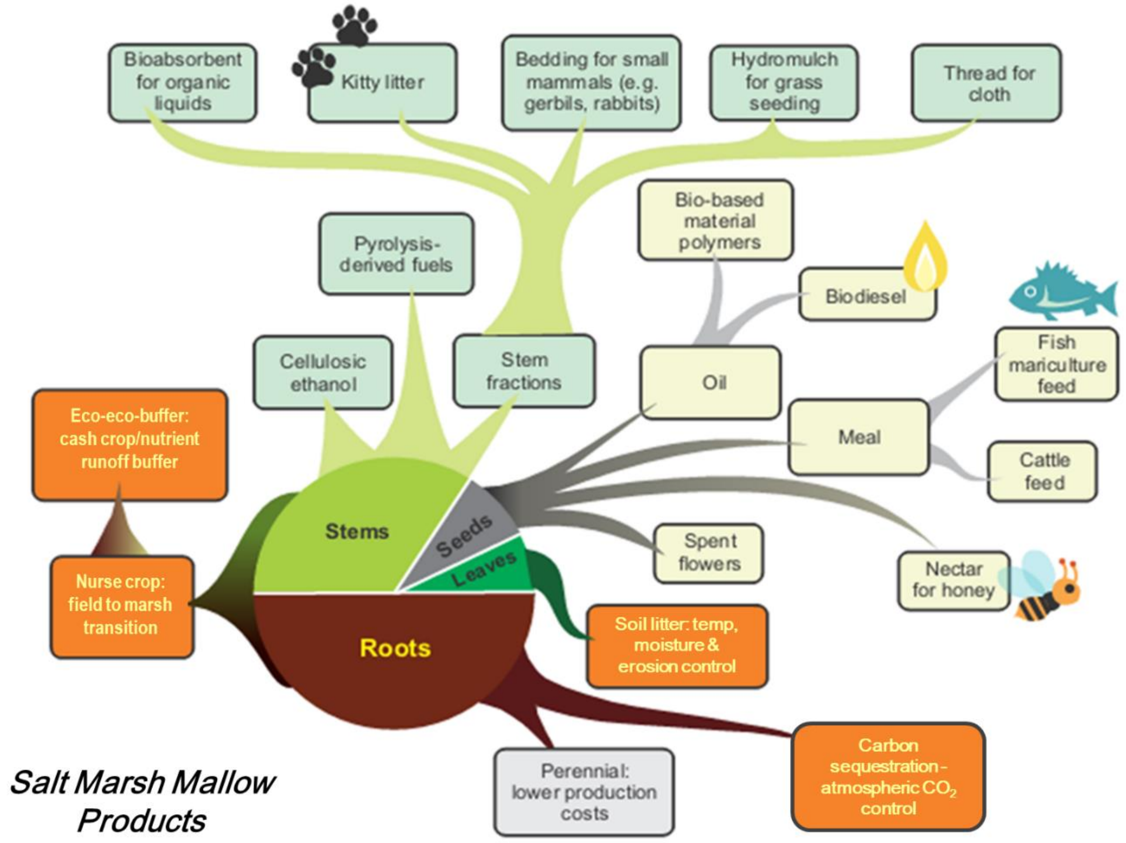

Figure 1. The uses for different parts of the salt marsh mallow plant, *Kosteletzkya pentacarpos*. Each part of a salt marsh mallow plant can be used in the production of many different goods demonstrating its potential for economic importance. The orange boxes represent the environmental benefits of salt marsh mallow establishment. (Redrawn from J. L. Gallagher, University of Delaware)

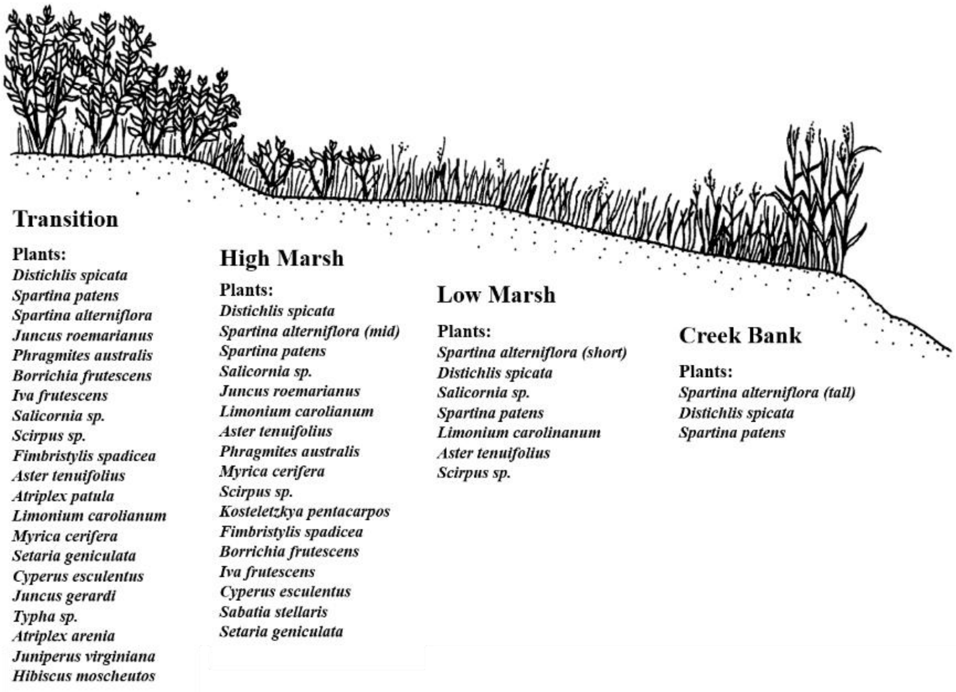

Figure 2. Zonation and common species of Virginia Coast Reserve salt marshes ranked from most to least prevalent within each zone. *Plant zonation drawing adapted from Hacker and Gaines (1997). Salt marsh species composition and relative biomass based on End-of-Year-Biomass surveys conducted by Virginia Coast Reserve Long-Term Ecological Research Program from 1999 – 2017: http://www.vcrlter.virginia.edu/cgi-bin/showDataset.cgi?docid=knb-lter-vcr.167*

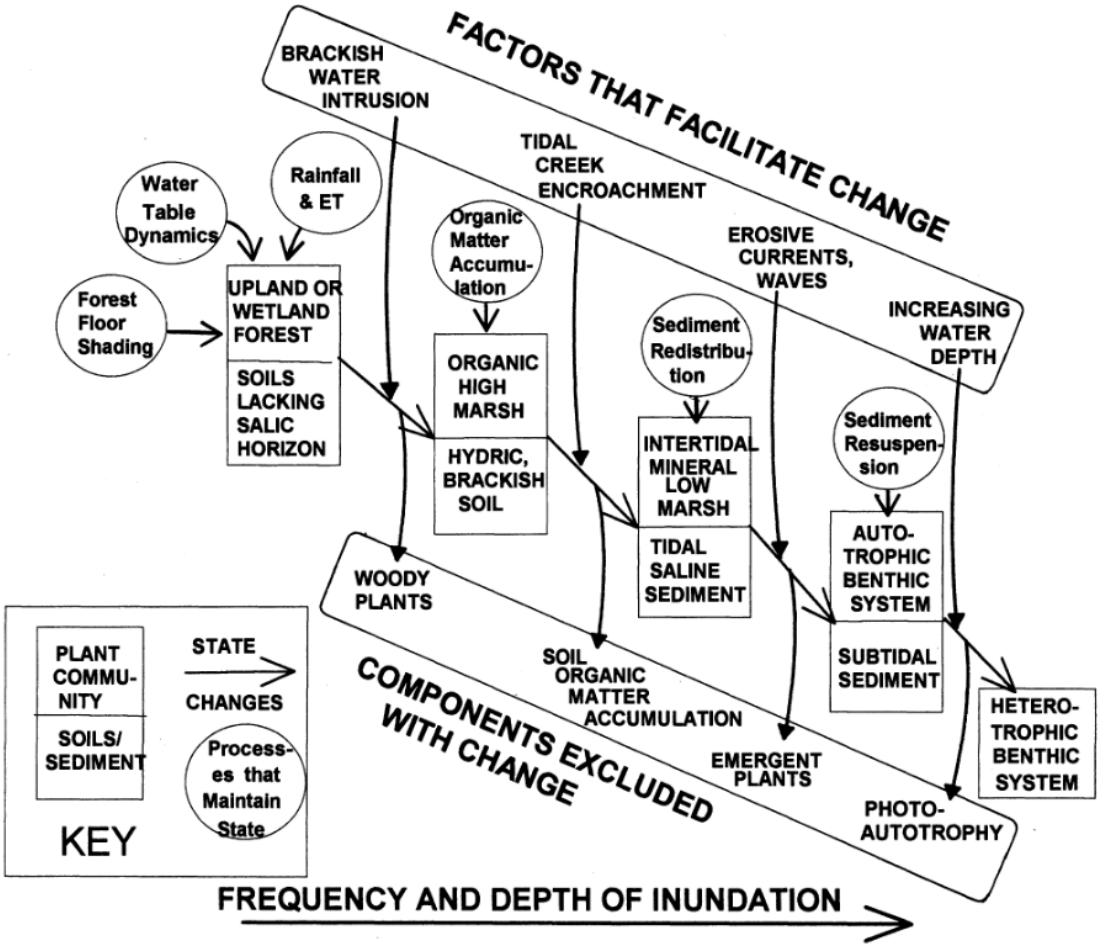

Figure 3. Conceptual model of the five states and four transitions from terrestrial forest to subtidal heterotrophic sediment. Factors that facilitate change appear at the top and components excluded with state change appear at the bottom. Source Brinson et al. (1995).
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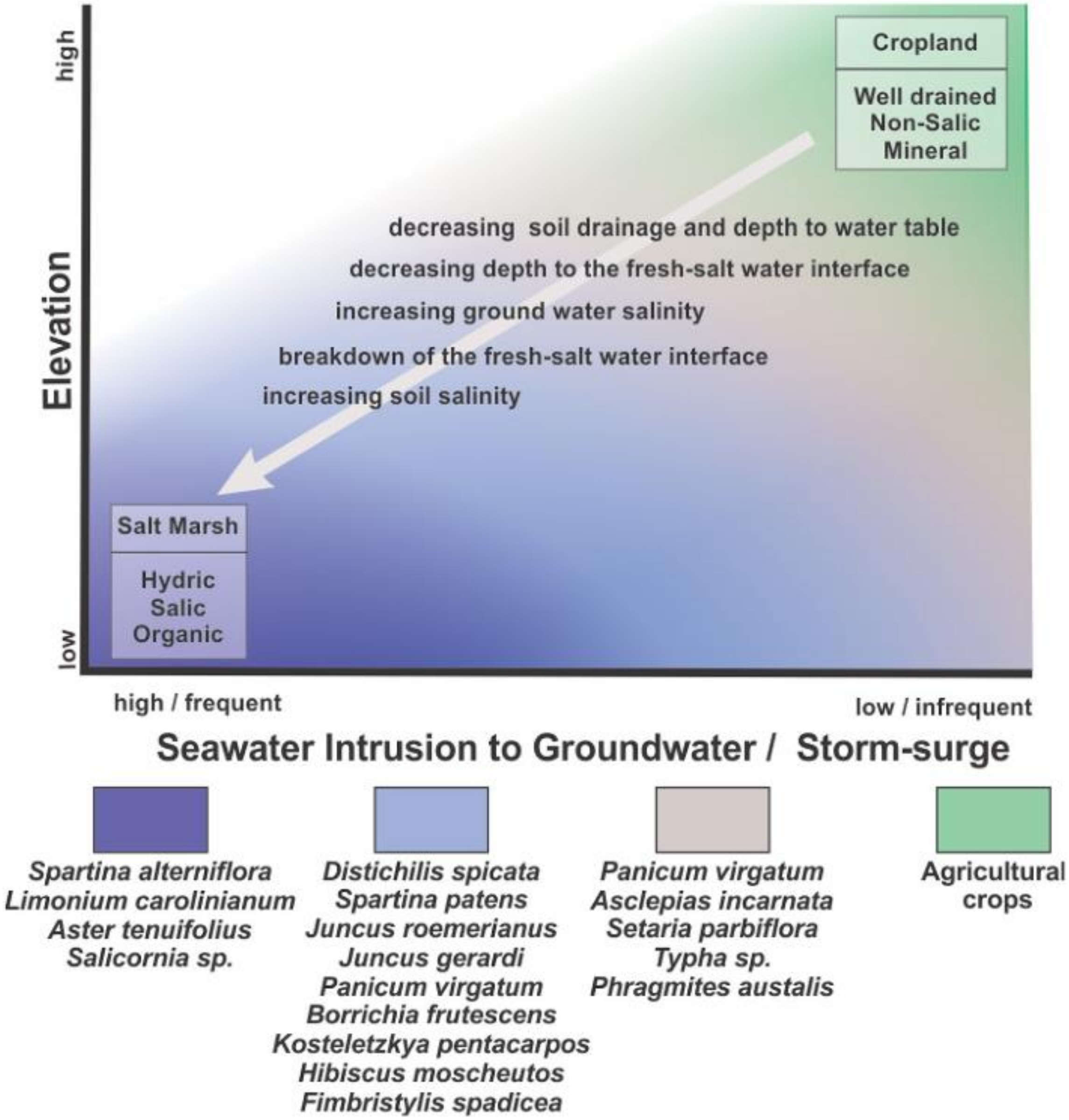


Figure 4. Conceptual model of the changes in soil drainage and salinity leading to marsh migration into cropped farmland. Plant community composition observed during the stages of transition is shown for coastal Virginia. Source: Fagherazzi et al. (2019).

Chapter 2.

Effect of Flooding on Water-Table Elevation and Salinity in an Abandoned Coastal Agricultural Field

2.1. Abstract

Water levels and salinity were measured in seven shallow (ca. 2 m deep) wells installed at distances proximal, medial, and distal to the source of tidal flooding between 2017 and 2019 in a warm-season grass meadow adjacent to a salt marsh. Water-table fluctuations greater than 10 cm were associated with seawater, precipitation, or a combination of the two. When the field was flooded by tides (> 0.5 m above predicted), groundwater salinity increased; when the field was flooded by precipitation (> 2.5 cm), the salinity of the groundwater decreased. The increased head gradient that accompanied the rise in the water table appeared to be sufficient to allow the freshwater from precipitation to push the salt water down and towards the marsh creek, resulting in a freshening of the groundwater that persisted until the next saltwater flooding event. Thus, the relative frequency between saltwater flooding, salinization, freshwater flooding, and flushing controlled the groundwater salinity. These findings indicate the importance of high tide events in the process of salinization of the groundwater and the ameliorating effects of rainfall events whose magnitude is sufficient to increase groundwater elevation at least ten centimeters. Further, they contribute to a growing body of evidence in support of the interaction between fresh- and saltwater flooding events to enhance the salinity of groundwater and drive ecosystem transition from uplands to salt marshes.

2.2. Introduction

Coastal flooding increasingly threatens human infrastructure (Kulp & Strauss, 2017), forests (Kirwan & Gedan, 2019), salt marshes (Campbell *et al.*, 2022), and agricultural lands (Nicholls & Leatherman, 1995). Globally, low-elevation coastal areas experience frequent flooding due to extreme tides and storm surge associated with accelerating rates of sea-level rise (Neumann *et al.*, 2015; Sweet *et al.*, 2014) and increasing intensity of precipitation events (Myhre *et al.*, 2019 and citations therein). Efforts to quantify the causes and impacts of coastal flooding on human infrastructure are extensive (Neumann *et al.*, 2015 and citations therein). Others have characterized the individual and combined impacts of sea-level rise, precipitation, extreme tides, storm surge, and river discharge on flooding in salt marshes and forests (Gori *et al.*, 2020; Kirwan & Gedan, 2019; Lyddon *et al.*, 2023; Wahl *et al.*, 2015). Despite agricultural fields being at greater risk for flooding than either grasslands or forests (Feng *et al.*, 2018), just a few studies consider the relative importance of coastal flooding mechanisms to agricultural lands (Fagherazzi *et al.*, 2019b and citations therein; Gedan & Fernández-Pascual, 2019; Gewin, 2018; Schieder *et al.*, 2018). Even fewer studies (e.g. (Guimond & Michael, 2021; Hingst *et al.*, 2023; Huizer *et al.*, 2017) examine changes in groundwater salinity in agricultural settings during flooding events despite coastal communities having experienced salinization of groundwater for over a century (Barlow & Reichard, 2010).

In agricultural lands, salinization of groundwater by coastal flooding can occur on both long- and short-time scales. On long-time scales, interannual and interdecadal increases in sea level influence coastal flooding(Baart *et al.*, 2012; Chen *et al.*, 2000; Hamlington *et al.*, 2020). At shorter time scales, a variety of mechanisms influence salinization. For example, Hingst *et al.* (2023) found that local hydrology, geomorphology, and geology controlled the timing and mechanism of salinization of upland agricultural lands, and that tides, storms, and event seasonality influenced by sea-level rise, affected salinity levels of the deep (> 4 m) surface- groundwater. Additionally, White and Kaplan (2017) found that the magnitude and duration of storm-induced saltwater inundation are strongly driven by storm intensity, wind direction, tide, and local hydrological conditions. Consideration of precipitation-caused flooding on groundwater salinity is rare, but see Cantelon *et al.* (2022), Nordio and Fagherazzi (2022), and Tully *et al.* (2019) who concluded that precipitation decreases groundwater salinity for a day or two before increasing to antecedent levels. The combined effect of short-term hydrological and meteorological mechanisms, and their importance to the salinization of groundwater systems, is relatively unstudied. This gap presents an opportunity for additional research to examine the impacts of episodic saltwater and freshwater flooding on groundwater dynamics that, in turn, affect plant community change in coastal agricultural lands.

Episodic flooding caused by tides, precipitation, or both, has the potential to affect groundwater salinity and therefore the suitability of coastal upland soils for agriculture. In low-elevation, shallow-sloped fields adjoining coastal wetlands, the water table is close to the land surface; the vadose (unsaturated) zone is thin; and the capacity of the soil to absorb floodwater is low. Even seemingly small precipitation and tidal events have the potential to saturate soil, and for the water table to rise above the soil surface, and stress plants. If the flood water is salty, plant roots are bathed in salt water, adding additional stress to upland plants. As upland areas experience more frequent and longer duration flooding along the upland-wetland edge, upland plants will be replaced by freshwater wetland plants or salt marsh plants if the flood water is salty (Brinson *et* *al.*, 1995; Fagherazzi *et al.*, 2019a; Wasson *et al.*, 2013). Indeed, in upland fields the presence of wetland species is a leading indicator of salt marsh migration into areas with high groundwater tables and soil salinization (Anisfeld *et al.*, 2017).

As salt marsh plants migrate inland, agricultural land is lost. If the economic value of the agricultural land exceeds that of the ecosystem services provided by the wetlands (nutrient and storm surge buffering, fisheries habitat) (Craft *et al.*, 2009), then there may be attempts to control flooding with man-made structures (levees, dikes, shoreline hardening) (Gittman *et al.*, 2016) to prolong the agricultural productivity of the land (zu Ermgassen *et al.*, 2021). Alternatively, if the value of the ecosystem services provided by the wetlands is greater than the economic value of the agricultural commodities produced in the upland, then wetland migration upland will not be impeded (zu Ermgassen *et al.*, 2021). Ultimately, as sea levels continue to rise, measures to preserve agricultural productivity will be overwhelmed and the upland will become intertidal marshes or subtidal sediments.

In areas like the Mid-Atlantic coast of the United States, where accelerated rates of sea-level rise are higher than the global average (Sallenger *et al.*, 2012), the loss of upland ecosystems, especially farmland, is happening rapidly (Campbell *et al.*, 2022; Reed *et al.*, 2008; Sallenger *et al.*, 2012). For example, an estimated 192 ha of farmland are converted to salt marsh annually in Accomack and Northampton Counties, Virginia (Titus *et al.*, 2010) at a cost of $1.8 to $2.3 million each year (2012 dollars) (Accomack-Northampton Planning District Commission, 2012). With rates of sea-level rise reported to be 5.63 mm yr^{-1} for the Mid-Atlantic region between 1978 and 2023 (NOAA, 2023), the amount of land converted annually, and the economic impact, is expected to increase (Sallenger *et al.*, 2012). This region offers an opportunity to examine short-term environmental changes resulting from inland marsh migration into agricultural land to understand how event-driven coastal flooding can impact water-table elevation and patterns of salinization. This region has gently sloping topography, rapid rates of sea-level rise, and increasing occurrences of coastal storms and high tides that will accelerate marsh migration into uplands (Fagherazzi *et al.*, 2019b).

Here is discussed coastal flooding, which introduces salt water from above the water table when land is inundated with salt water that infiltrates into soils and percolates to the underlying fresh, groundwater and is differentiated from groundwater salinization by coastal flooding from saltwater intrusion in confined aquifers. Saltwater intrusion is the lateral encroachment and vertical movement of coastal seawater inland (USGS Water Resources Mission Area, 2019), and it typically impacts the groundwater system below the water table as a result of rising sea levels, increased pumping and withdrawal, and decreased aquifer recharge. Natural saltwater intrusion occurs on timescales of months to millennia, while salinization due to surficial flooding occurs on timescales of hours to days.

The study site is an abandoned agricultural field adjacent to a salt marsh in Nassawadox, Virginia, USA. Other agricultural fields nearby have begun to transition to salt marsh (Flester & Blum, 2020; Kastler & Wiberg, 1996) where long-term (> 20 years) groundwater salinity measurements (Brinson & Stasavich, 2015a, 2015b) and plant species biomass (R. Christian, 2014) indicate that salinization of upland groundwater precedes the shift in plant community from old-field vegetation to high salt-marsh plants. This paper focuses on high precipitation and extreme tide events that increase water-table elevation and salinity of groundwater at the study site where the agriculture field's plant community appears to be transitioning from old-field plants to salt-marsh vegetation.

2.3. Methods

This section provides a description of the field site used and the techniques whereby water-table elevations and salinities were obtained. These data were then combined with existing data from additional sources to describe changes in water-table elevations and salinities associated with extreme flooding events such as storms.

2.3.1. Study Area

The study was carried out on the Delmarva Peninsula at the Nature Conservancy's Brownsville Preserve (located at 37.472318°N, 75.827455°W, https://goo.gl/maps/fTirW6yNvTPyVpBX7) which is near Nassawadox, Virginia. The Delmarva Peninsula extends from Delaware Bay southward along the seaside coast of Maryland to the mouth of the Chesapeake Bay in Virginia; it is bordered on the west by the Chesapeake Bay and on the east by the Atlantic Ocean. This area of the Mid-Atlantic coast has experienced high rates of sea-level rise of 5.63 mm yr-1 between 1978-2023 (NOAA, 2023) based on the tide gauge at Wachapreague, VA (Station ID: 8631044, 37.60833333°N/-75.68500000°W; accessed March 2024). The Delmarva Peninsula experiences a semidiurnal tidal cycle and is often affected by hurricanes and nor'easters (NOAA US Department of Commerce, 2015) that can cause coastal flooding.

The Brownsville Preserve on Upshur Creek was settled in the mid-1600s and purchased by The Nature Conservancy in 1978. The land was farmed until the early 2000s when it was planted with warm seasonal grasses because of declining agricultural yields and increasing frequency of flooding. The study site is situated in an upland field that is separated from a tidal creek and surrounding salt marsh by a failed dike system. The study site is flat with little topographic relief except for an irrigation pond built in the middle of the field (Figure 5). Excluding that pond and its mounded sides, and some depressions near Well 1 associated with the dike construction, elevations range from 0.65 m above msl at the edge of the field near the marsh to 1.37 m above msl near the road that provides a southern boundary of the field. The gentle slope across the field from Well 1 to the road is approximately 0.9%. Survey points for experimental plots (*viz.*, near Wells 3 and 7) where plant community composition was monitored as part of a separate study are included on this map and were used to draw contour lines shown in Figure 5. The current plant community composition of the study site comprises a variety of dune grasses, high-marsh native species, and old-field plant species. The predominant high-marsh species in the field included *Distichlis spicata*, *Spartina patens*, and *Iva frutescens* (Table 1).

2.3.2. Well Installation

Well locations were selected based on plant community composition at the time of installation. In 2012, examination of plant species composition found three general community types: 1) mostly *D. spicata* and other high marsh plant species, 2) a mix of *D. spicata* and upland grasses, such as switchgrass (*Panicum virgatum*), and 3) mostly switchgrass and other upland grasses (Table 1). Two wells (1 and 2) were installed in 2013, one (3) in 2014, and four (4 through 7) in 2017 (Figure 5, Table 2). Wells were augered by hand and cased with 2” (5-cm) diameter, 0.01” (0.25 mm) slotted, PVC well screen to a depth of at least two meters. The length of the well screen extended approximately 1 m above the ground surface. The exact elevation of the top of the well casing (in meters above mean sea level) was determined with high-resolution GPS as part of the topographic survey described below. Pressure transducers with data loggers (Schlumberger Cera-diver®, Van Essen Instruments) were installed in each of the wells to monitor groundwater elevation and temperature every 12 minutes. Data from the transducers were downloaded periodically.

2.3.3. Groundwater Measurements

Water level, temperature, salinity, and conductivity were measured occasionally in all wells. Water level was determined with a Solinst Model 101® Water Level Meter and recorded as the distance from the top of the casing for later conversion to elevation above mean sea level. Salinity, temperature, and conductivity (SCT) were measured using a YSI Model 30® handheld SCT meter. Measurements were made three times from June to September of 2017, four times from April to September of 2018, and ten times from May 2019 to January 2020. SCT measurements were taken starting as close to the surface of the water table as possible (*i.e.*, 3 to 5 cm) and every 10 cm thereafter from the top to bottom of the well to obtain an SCT profile of the water column in each well.

Water-table elevations were also measured continuously with the recording pressure transducer suspended near the bottom of each well. Because the transducers sense total pressure, the water surface elevation was determined by subtracting the local air pressure from the (total) pressure measured by the submerged transducer (a process termed compensation). For data collected prior to July 2017, local barometric pressure provided by the National Oceanic and Atmospheric Administration (https://tidesandcurrents.noaa.gov/stationhome.html?id=8631044) was used for compensation. Starting in July 2017, compensation of the groundwater pressure was performed using atmospheric pressure measured with a pressure transducer suspended above the water in Well 7. The compensated data represented the pressure of the water above the sensor. The elevation of the sensor was determined by measuring the distance from the sensor to the top of the well casing, the elevation of which was determined as part of a detailed topographic survey of the field using GPS Real Time Kinematic (RTK) measurements from high-resolution benchmarks established previously at Upper Phillip's Creek in 1997. Once the elevation of the top of the well was known, the elevation of the sensor was determined as the distance of the sensor from the top of the well subtracted from the elevation of the top of the well. The elevation of the water surface, then, was calculated as the depth of water above the sensor added to the elevation of the sensor. All elevations, including water-table elevations, used mean sea level (msl) as the datum. Water-table elevations calculated from the pressure transducers were verified with hand measurements of the distance from the top of the well to the water depth each time the pressure-transducer data were downloaded. Calculated water-table elevations were used to create well hydrographs for each of the wells.

2.3.4. Meteorological Data

Daily precipitation data were obtained from the Historical Weather feature of weatherunderground.com, (http://www.wunderground.com/history/, September 2022), for Melfa, VA, 24 km from the study site, and tidal data from NOAA's Wachapreague tide gauge, because there was no tide gauge in Upshur Creek near the study site. The distance from Wachapreague to the Brownsville site is about 20 km, but the use of the Wachapreague tide data is justified by the strong linear relationship between the tides at Wachapreague and those in Phillips Creek, which is about 1.8 km from Brownsville (Christiansen, 1998).

2.3.5. High-Water Events

Tide and precipitation data were used to identify high-water events that coincided with a rapid increase in the water table elevation of at least 10 cm. If no record of tide or precipitation coincided with instances of a water-table elevation that met the selection criteria, the event was excluded from the analysis. In addition, known weather events were recorded even if the water-table elevation change was less than 10 cm at Well 1. Each high-water event was categorized by the dominant cause of flooding. Events with total precipitation equal to or greater than 2.5 cm were classified as precipitation events. Events with an average difference in measured and predicted tides greater than 0.5 m were classified as tide events. Events with no precipitation were also classified as tide events when the 10-cm water-table event criterion was met, even if the tide was not half a meter above predicted. Events with differences in measured and predicted tides greater than 0.5 m and more than 2.5 cm of precipitation were classified as "combined." Events classified as "combined" included cases of low tide with low precipitation, and high tide with high precipitation when the high-water criterion was met.

2.4. Results

2.4.1. Groundwater Wells

The water-table elevation generally followed the ground-surface elevation of the field although the water table exhibited fluctuations that were correlated with tidal and meteorological conditions over the duration of the study (2016-2020). During the study, the minimum and maximum measured water-table elevations were -0.005 m msl and 1.78 m msl, respectively. Groundwater measurements (including all wells and all sampling times) exhibited a range of salinities from 0 ppt to 33.2 ppt over the observation period. The seven wells fell into three distinct groups (Table 2) that reflected the distance from the nearby salt marsh and, also, the plant community composition. The groups were termed proximal, medial, and distal (to the salt marsh) and comprised Wells 1, 4, and 5; Wells 2 and 3; and Wells 6 and 7, respectively. For this study, data from Wells 1, 3, and 7 were used to illustrate the differences in groundwater observation among the groups. Ground-surface elevation at the wells within each group varied from 0.81 to 0.87 m, 0.92 to 0.96 m, and 0.97 to 1.01 m above msl for the proximal, medial, and distal groups, respectively (Table 2). In 2017, the plant community composition (Table 1) around the proximal well group was predominantly high-marsh species including *Spartina patens, Distichlis spicata, Borrichia frutescens,* and *Limonium carolinianum*. The distal well group's surrounding plant community consisted of upland species commonly found in nearby abandoned agricultural fields (Shiflett, 2013) including *Panicum virgatum*, *Asclepias incarnata*, and *Setaria parviflora*. The medial group of wells was located in areas where the plant community was comprised of a mixture of the species found in the proximal and distal groups. The dominant species in the medial group were *Distichlis spicata* and *Panicum virgatum*.

2.4.2. Groundwater Salinity

Salinity was measured in all 7 wells three times a year during the growing season beginning in 2017. Beginning in September 2019, salinity was measured in each well weekly (Figure 6, Figure 7, Figure 8). Because the water-table elevation in the wells was not constant with time, the location of salinity measurements for the water-table surface (top) and the mid-point between the top and bottom measurements varied with time, *i.e.*, the distance between measurement points at the bottom, middle, and top of the groundwater depth profile is not the same for each date that salinity was measured.

With the exception of a single measurement for Well 3 in May of 2019, water at the bottom of the wells was always more saline than at the water-table surface for all seven wells (data shown for representative wells 1, 3, and 7) and the salinity increased substantially after the summer of 2019 (compare Figure 6, Figure 7, Figure 8). With increasing distance from the marsh, bottom water salinity decreased, which accounts for the smaller difference between top and bottom water salinity from proximal to medial to distal groups. The largest variation in salinity measurements between the top and the bottom of the well was observed in the proximal group (Figure 6) and the least variation was observed in the distal group (Figure 8). Over time, the mid-point salinity became more like the salinity at the bottom of the well in all three groups. Another way to say this is that the groundwater became saltier nearer to the surface so that plants at this site were more likely to experience salt stress.

From June 2017 to July 2019, tide-dominant events coincided with an increase in groundwater salinity while precipitation-dominant events coincided with a decrease in groundwater salinity (examples described below). As water levels fell following both types of events, salinity returned to antecedent conditions. However, in the fall of 2019, high tide events following a period of relatively low precipitation coincided with higher groundwater salinities that never returned to the levels observed prior to August 2019 in any part of the well (Figure 6, Figure 7, Figure 8) during the remainder of the study.

2.4.3. High-Water Events

The largest high tide measured during the study period was 1.99 meters above msl and was associated with a 59 cm increase in the groundwater elevation in Well 1 (Table 3). Similar to extreme tide events, water-table elevations often increased after precipitation events. The most rainfall received during a high-water event was 14.7 cm over 3 days during which the water-table elevation increased by 21 cm. From 2016 to 2019 there were 38 high-water events (Table A 1) generated by extreme tides, nor'easters, hurricanes, tropical storms, and severe thunderstorms. Wind speeds varied, ranging from 3.1 m s^{-1} to 19.5 m s^{-1}, and wind direction was primarily from the northeast during the events.

The number of high-water events increased during the years of the study, and the proportion of the events associated with high tides (either as tide events or combined events) also increased. In 2016, there were six high-water events; three tide, two precipitation, and two “combination” events (Figure 9). In 2017, there were nine high-water events; four tide, three precipitation, and two “combination.” 2018 had 12 high-water events, of which six were tide-dominated, three were precipitation-dominated, and three resulted from a combination of both precipitation and tide. In 2019, there were 11 high-water events - seven tide, three precipitation, and one with both tides and precipitation. As seen in Figure 6, Figure 7, and Figure 8, peaks in the water-table elevation coincided with or lagged slightly behind the observed high tides and precipitation during identified high-water events. As expected, the magnitude of the change in water-table elevation decreased with increasing distance from the tidal creek in each of the cases examined.

2.4.4. High-Water Events: Detailed Examples

Examination of high-water events coinciding with precipitation, high tides, and a combination (both tide and precipitation) at a well representing the proximal (Well 1), medial (Well 3), and distal (Well 7) groups provides insight into the effect of the three types of high-water events.

2.4.4.1. *Precipitation Event: #30, July 7-9, 2019*

Beginning on July 7 through July 9, 2019, 14 cm of rain fell at the study site (Table 3). The effect of this rainstorm was to increase groundwater elevation in Well 1 (Figure 10). Rain was intermittent with 1.8 cm falling on July 7. A small increase in the water-table elevation (~9 cm) coincided with the July 7 rainfall. Beginning on July 7 and into the morning of July 8, 7.6 cm of rainfall fell, and the water-table elevation increased an additional 23 cm. Finally, a third water-table elevation peak was observed on July 8 when another 4.1 cm of rain fell and water-table elevation increased by an additional 39 cm. The maximum tide level during this three-day period was 1.04 m msl which was 0.42 m msl above the predicted tide. In Wells 3 and 7, groundwater elevation increases only with the third occurrence of precipitation, likely due to the higher elevation of these wells.

2.4.4.2. *Combined Event: #32, September 5-7, 2019*

On September 5-8, 2019, the remnants of Hurricane Dorian passed through the mid-Atlantic region resulting in an increase in groundwater elevation. Precipitation on September 6 totaled 6.35 cm between 7:00 AM and 2:00 PM EST which coincided with a high tide of 1.5 m above msl*, i.e.,* 0.8 m above the predicted tide. (Table 3). During this time, the water table elevation in Well 1 increased by 59.5 cm (Figure 11). A similar increase in water-table elevation was observed in Well 7. In Well 3, an initial water-table-elevation increase of 46.9 cm occurred with the start of precipitation on September 6, and a second increase of 11.9 cm coincided with the following high tide event (Figure 11).

2.4.4.3. *Tide Event: #38, November 16-19, 2019*

Beginning on November 16 to November 19, 2019, an extreme tide event was observed with an average difference in measured and observed high tides of 0.68 m above msl. Over the four-day event, six increases in water-table elevation in Well 1 slightly lagged the six high tides (Figure 12). The six high tides measured were 0.59 m, 0.78 m, 0.70 m, 0.74 m, 0.78 m, and 0.50 m above the predicted tide. The six observed increases in water-table elevation in Well 1 measured 26 cm, 17 cm, 27 cm, 6.4 cm, 25 cm, and 5.7 cm. Only three water-table elevation increases of 6 cm, 9.4 cm, and 10.6 cm were observed in Well 3. These water-table elevation increases occurred following the first recorded high tides on November 16, 17, and 18, 2019. In Well 7, only two water-table elevation increases of 17 cm and 6.7 cm were observed in Well 7. The Well 7 peaks lagged behind the first recorded high tides by approximately 3 hours on November 17 and 18, 2019.

2.5. Discussion

Our analysis of groundwater salinity showed a temporal response to freshwater flooding from precipitation and saltwater flooding from extreme tides (Figure 6, Figure 7, and Figure 8) that suggests overland flooding with saline water from nearby tidal creeks is the source of salinity in the groundwater. These results are consistent with the findings of Huizer *et al.* (2017) and others (Cantelon *et al.*, 2022; Hingst *et al.*, 2023; Kearney *et al.*, 2019; Nordio & Fagherazzi, 2022; Tully *et al.*, 2019) who observed that increases in groundwater salinity coincided with tides and storm surges. As sea-level rises, smaller tides will be required to cause floods, resulting in more frequent flooding of uplands with salt water, leading to salinization of the groundwater (Hingst *et al.*, 2023; Kirwan & Gedan, 2019; Tully *et al.*, 2019). However, salinization of the groundwater may not persist if seawater flooding events are followed or accompanied by freshwater inputs from precipitation. As discussed below, our results showed a decrease in groundwater salinity in response to freshwater inputs from precipitation. Previous studies suggest that the response may be a result of dilution during high precipitation events (Cantelon *et al.*, 2022; Tully *et al.*, 2019). We suggest that the increased hydraulic gradient that accompanies a rise in the (fresh) water table enhances groundwater throughflow and that the freshwater, in response to the greater head gradient (between the water table and the saltwater level in the adjacent marsh creek) pushes the salt water down and toward the marsh creek (Cantelon *et al.*, 2022). Taken together, our findings indicate the importance of high tide events in the process of salinization of the groundwater and the ameliorating effects of rainfall events whose magnitude is sufficient to increase groundwater elevation at least ten centimeters. These findings contribute to a growing body of evidence in support of the interaction between fresh- and saltwater flooding events to enhance the salinity of groundwater and drive ecosystem transition from uplands to salt marshes.

Changes in groundwater salinity were directly related to the type of high-water event. Similar to the reports by others (Fagherazzi *et al.*, 2019b; Kearney *et al.*, 2019), we observed that tidal events in the absence of precipitation resulted in an increase in groundwater salinity (Figure 6, Figure 7, Figure 8, Figure 9). For example, two tide events in August 2019, coincided with large increases in groundwater salinity that persisted until measurements were ended later that year. Alternatively, we also observed that precipitation events in the absence of saltwater flooding resulted in a decrease in groundwater salinity (Figure 6, Figure 7, Figure 8, Figure 9). For example, between October 15 – 23, 2019, two precipitation events coincided with a decrease in salinity to pre-event levels that persisted until the next tide flood event. In a nearby forested upland adjacent to a salt marsh, Nordio and Fagherazzi (2022) found no correlation between the change in groundwater salinity and the amount of precipitation that occurred during their study. In that study, rainfall resulted in an instantaneous decrease in groundwater salinity that was attributed to dilution; once the rain stopped, the salinity of the groundwater increased to pre-rainfall levels within a day or two. In our study, groundwater salinity decreased during precipitation events (10 cm increase in water-table elevation) and persisted until the next saltwater flooding event. Perhaps the difference between the studies is due to the difference in the magnitude of the precipitation events examined. Nardio and Fagherazzi (2022) examined all occurrences of rainfall regardless of the amount of rainfall or the groundwater elevation response, whereas we included only precipitation events that caused a substantial increase in the water-table elevation. The increased groundwater elevation increases the hydraulic gradient pushing the saline water downward and towards the salt-marsh creek until the next tidal-flooding event brings in additional saline water and reduces or even reverses the head gradient. Another important difference between the two studies is that Nordio and Fagherazzi (2022) never observed surface flooding by tides or storm surge at their study site, whereas many of the flooding events we examined were caused by extreme high tides or storm surge.

Groundwater salinity changes resulting from the combined impacts of precipitation and tidal events, including storm-surge flooding (*i.e.* tropical storms, hurricanes, and nor'easters), will vary based on the magnitude of the source of flood waters: freshwater from precipitation or saltwater from high tides and storm surge. When precipitation inputs were greater than saltwater inputs, the salinity in the groundwater decreased; during the five combination events accompanied by both high tides and precipitation (Figure 9), the high precipitation mitigated the impact of the saltwater input from the high tides (Figure 11). A similar response was observed during the remaining three combination events that were sufficient to raise the level of the water table but in which the saline flooding was less extreme (measured tide < 0.5 m above predicted) and precipitation was less (Figure 9), but in which a 10-cm increase in the water table was observed. That the frequency of precipitation plus combination events increased (from 2016 to 2020) may be evidence of increased regional storminess which is in agreement with the predictions of Najjar *et al.* (2000). Understanding the impact of increased storminess on flooding event type will be important to informing predictions of short-term effects of coastal flooding on groundwater salinity, especially when considering the source and salinity of the flood waters.

The cycle of flooding, inundation, salinization, and flushing can happen over varying timescales (Cantelon *et al.*, 2022). We provide evidence to support the claim that a persistent shift in groundwater salinity depends on the frequency and duration of flooding from extreme tides relative to the frequency and amount of precipitation. In the short term, precipitation events in our system can slow the conversion of upland to salt-marsh plant communities. Eventually, as sea level rises and the hydraulic gradient between upland and mean sea level decreases, the ability of precipitation events to freshen the groundwater will gradually diminish, and the freshwater and saltwater interface will gradually move inland so that what is currently a fresh groundwater system will become fully salinized.

Because the cycle of flooding, inundation, salinization, and flushing can happen over varying timescales (Cantelon *et al.*, 2022), the timing and magnitude of the fresh- and saltwater events relative to one another will determine how rapidly the groundwater becomes salinized. During the study period, the number of precipitation events remained constant (~3 events per year) while the frequency and magnitude of tide- and storm-surge-caused events increased each year of the study (from five to eight over the period examined). The increase in groundwater salinity at all wells occurring in 2019 (Figure 6, Figure 7, Figure 8), likely reflects the more closely spaced tidal flooding events with few interspersed precipitation events (Figure 9).

Earlier we proposed that the transition from agricultural land to salt marsh would be accompanied by decreasing soil drainage, higher water table elevations, decreasing depth to the fresh-salt water interface, and increasing salinities in both the soils and groundwater (Fagherazzi *et al.*, 2019a). Our current observations of the water table elevation, groundwater salinity, and plant communities agree with our conceptual model, and the three groups of wells – proximal, medial, and distal – used in this study fall along the gradient hypothesized in our model. A decrease in groundwater salinity and an increase in depth to the fresh-salt water interface was observed along this gradient with increasing distance from the tidal creek. Additionally, we observed that the increase of the water table due to the flooding decreased with increased distance from the tidal creeks (compare Figure 10, Figure 11, and Figure 12). The measured groundwater response to tidal events was highest in the proximal wells and decreased with increasing distance from the tidal creek (Figure 12). This is similar to the findings of Anisfeld *et al.* (2017) where tidal flooding variability at higher elevations was driven by individual storm events.

The hydrologic systems of farm fields are heavily influenced by the vertical exchanges of water between the atmosphere, soil, and groundwater (Brinson *et al.*, 1995), and also by tidal and storm-surge flooding. Infiltration into the soil is controlled by the amount of water reaching the soil surface (precipitation or tidal flooding or storm surge) and by the antecedent moisture content such that wet soils admit less water than drier soils. Differing antecedent moisture conditions can result in different similar groundwater levels and salinity responses to flooding events of the same type and magnitude, as observed in our studies. Similar flooding depths were achieved whether they were the result of a precipitation or tide event but the timing of water table responses to individual events of similar magnitude varied. The short-term variation in water table elevation response time could be dependent on the antecedent soil moisture conditions. Wetter soils have less storage capacity available for flood waters to infiltrate leading to deeper flood waters above the ground surface than for dry soils experiencing the same level of tidal inundation or precipitation. When the soils were previously dry (*i.e.* low water table elevation, Figure 10), peaks in water table elevation lagged the event by a greater time than for wetter soils. This lag could be due in part to a poor hydraulic connection between the surficial soil water and the groundwater. When soils were previously saturated, a smaller event resulted in a much larger peak in water table elevation (Figure 10) that evolved more rapidly than in the drier soils. Antecedent soil moisture conditions likely also influenced groundwater salinity. Studies have shown that wetter periods and high antecedent soil moisture conditions can reduce saltwater impacts, whereas, drier periods can enhance saltwater impacts (Bailey & Jenson, 2014; Cantelon *et al.*, 2022). Future studies should consider antecedent moisture conditions when examining the mechanisms of coastal flooding, saltwater introduction, and marsh migration.

At longer temporal scales, evapotranspiration has a significant impact on groundwater levels, increasing in the summer when air temperatures are higher and photosynthesis is occurring (Nordio & Fagherazzi, 2022). Although not presented in this study, we observed daily and seasonal trends related to evapotranspiration in the water-table elevation like those reported by Kearney *et al.* (2019) and Flewelling *et al.* (2014) in coastal systems. The presence of short-term and long-term evapotranspiration signals has implications for the hydrologic fluxes and the extent of salinization within old fields, especially related to antecedent environmental conditions. High rates of evapotranspiration can lower the water table, especially in periods of prolonged drought, and increase groundwater salinity. We did not observe any meaningful impact of evapotranspiration on groundwater salinity; however, there is a need to explore what impact if any evapotranspiration may have over longer time scales as salinization of groundwater may drive plant community changes.

Inevitably, increases in sea level will result in increased water-table elevations near coastal marshes. When the water table is closer to the ground surface, the water storage capacity of the overlying soil is decreased, and less water is required to inundate the land during precipitation and tide events. A higher frequency of waterlogged soils will require more time for soils to drain, and place additional physical stressors on the established plant community. The higher water-table elevation observed in the proximal, medial, and distal wells may be a result of the increased frequency of flooding events over the observation period. We identified six high-water events in 2016, nine in 2017, twelve in 2018, and 11 in 2019. Given the accelerating rates of sea-level rise in the region, we would expect to see similar tide and precipitation events result in deeper floods over time. Deeper and more frequent flooding may have already increased the groundwater salinity permanently in the proximal locations at our study site. Eventually, we expect the plant community in the distal zone to begin to resemble that of the medial zone and the medial plant community will more closely resemble that of the proximal zone (Table 1) and would consist of a mix of upland and wetland species, before eventually mirroring that of the proximal group dominated by the high marsh species *Distichlis spicata* and *Spartina patens*. This is an extension of the marsh-transgression model of Brinson *et al.* (1995).

Our results provide important insights into the effect of increased saltwater flooding on the salinization of groundwater in abandoned old fields. When soils are saturated for extended periods of time, the resulting conditions can facilitate plant community change from upland to wetland species (Brinson *et al.*, 1995; Fagherazzi *et al.*, 2019b); even in the absence of further sea-level rise, changes to plant-community composition can be expected (Fagherazzi *et al.*, 2019b; Kearney *et al.*, 2019; Tully *et al.*, 2019). Wasson *et al.* (2013) found evidence that increased flooding frequency and duration with salt water was driving the landward movement of salt marsh plant communities. Raposa *et al.* (2017) suggested that soil waterlogging from increased tidal inundation was a primary factor in vegetation shifts from the salt-meadow species *S. patens* to the low-marsh species *S. alterniflora* as predicted by Brinson *et al.* (1995). Increased flooding with saline water over time is a result of increases in the magnitude and frequency of tidal inundation and storm surge. The expected increase in frequency of tide-dominated high-water events due to sea level rise will result in a shallower water table, and, in the absence of precipitation, in a permanent increase in groundwater salinity. Consequently, changes to the groundwater will promote plant community change from old-field species to those of a salt marsh. Despite the effect of precipitation in retarding permanent salinity increases in shallow groundwater, eventually, sea-level rise will result in regular flooding with saline water that will lead to permanent changes in vegetation.

Figure 5. Brownsville field topography and monitoring well locations. Contour units are m above mean sea level.

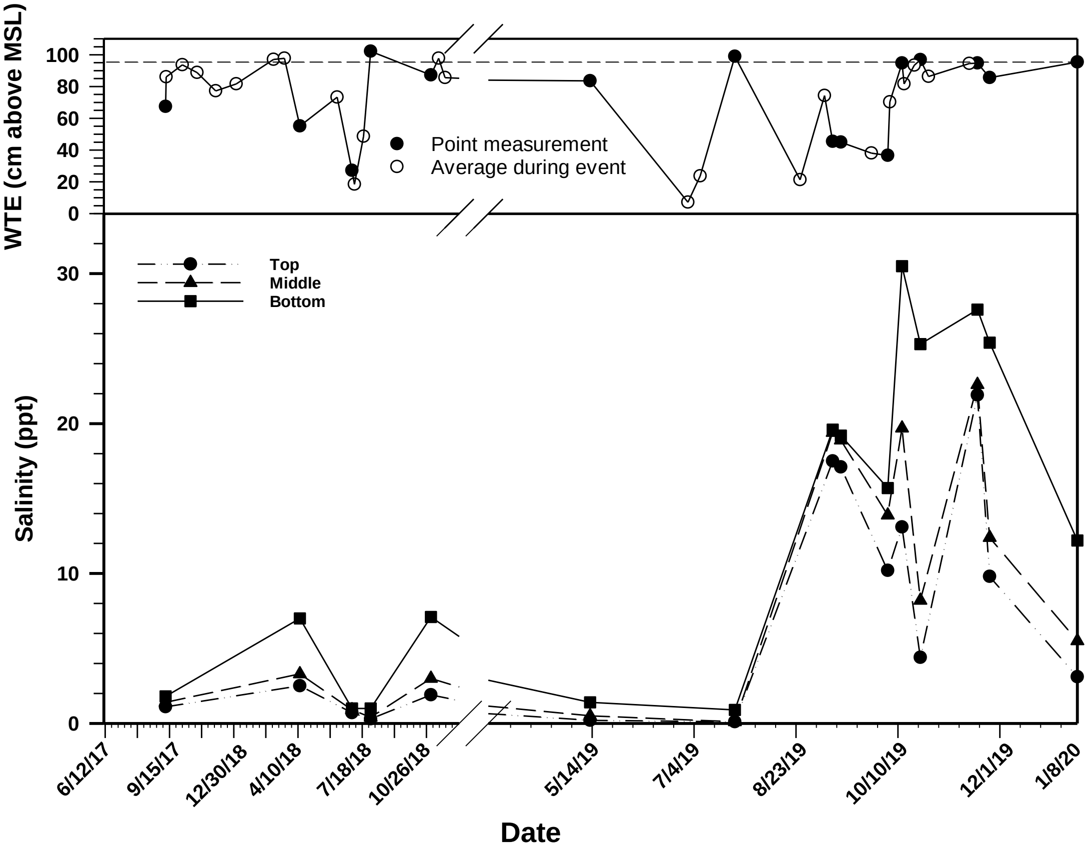


Figure 6. Water table elevation and salinity - Proximal Group Well 1.

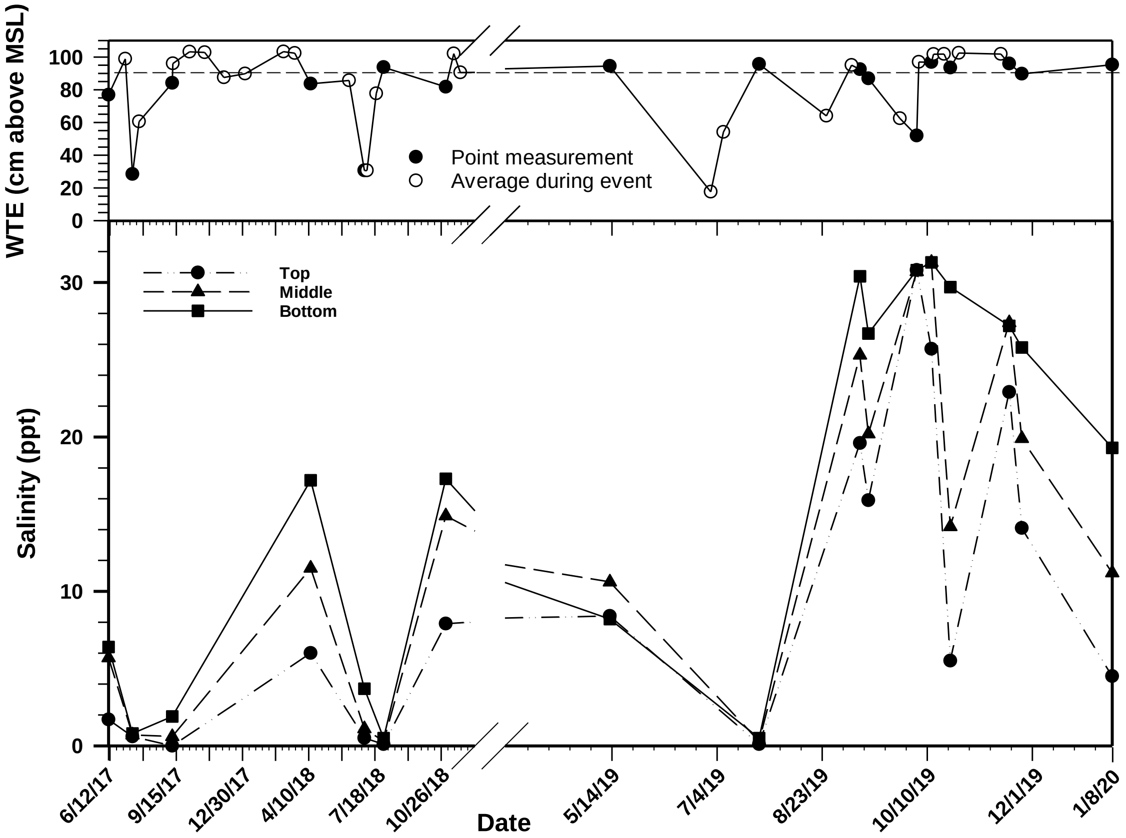


Figure 7. Water table elevation and salinity - Medial Group Well 3.

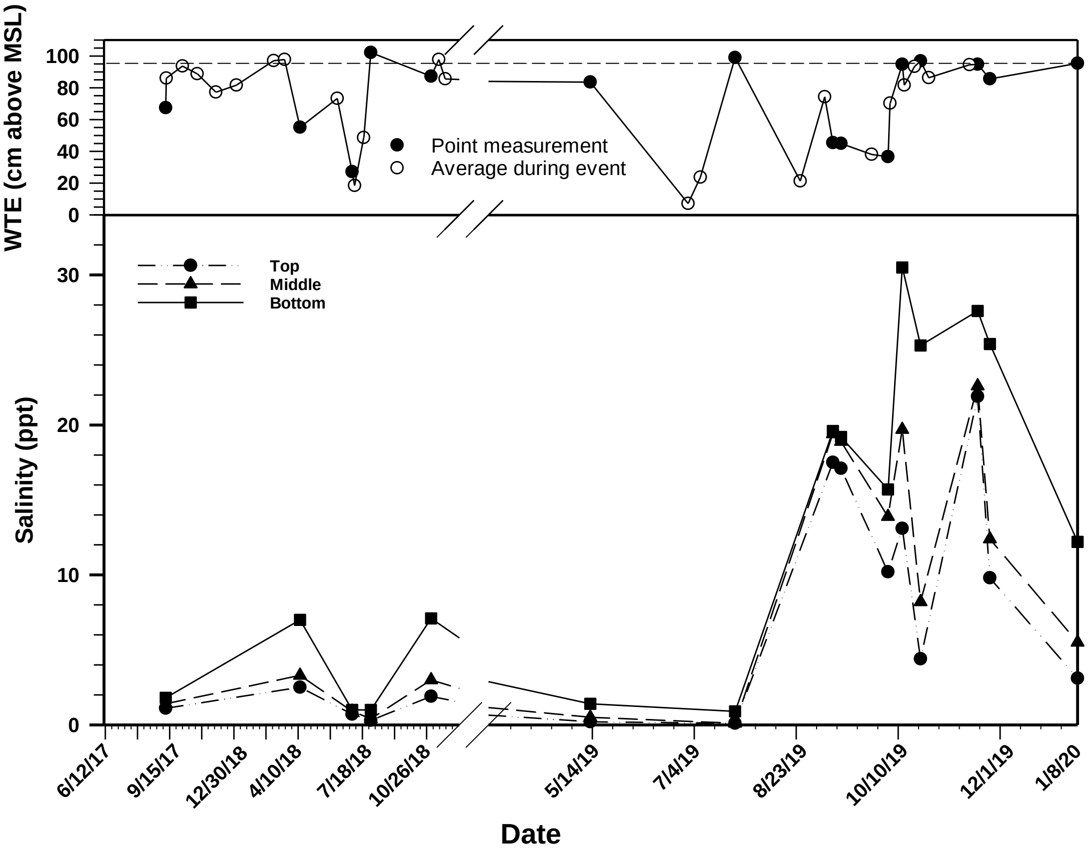


Figure 8. Water table elevation and salinity over time in the Distal Group Well 7.

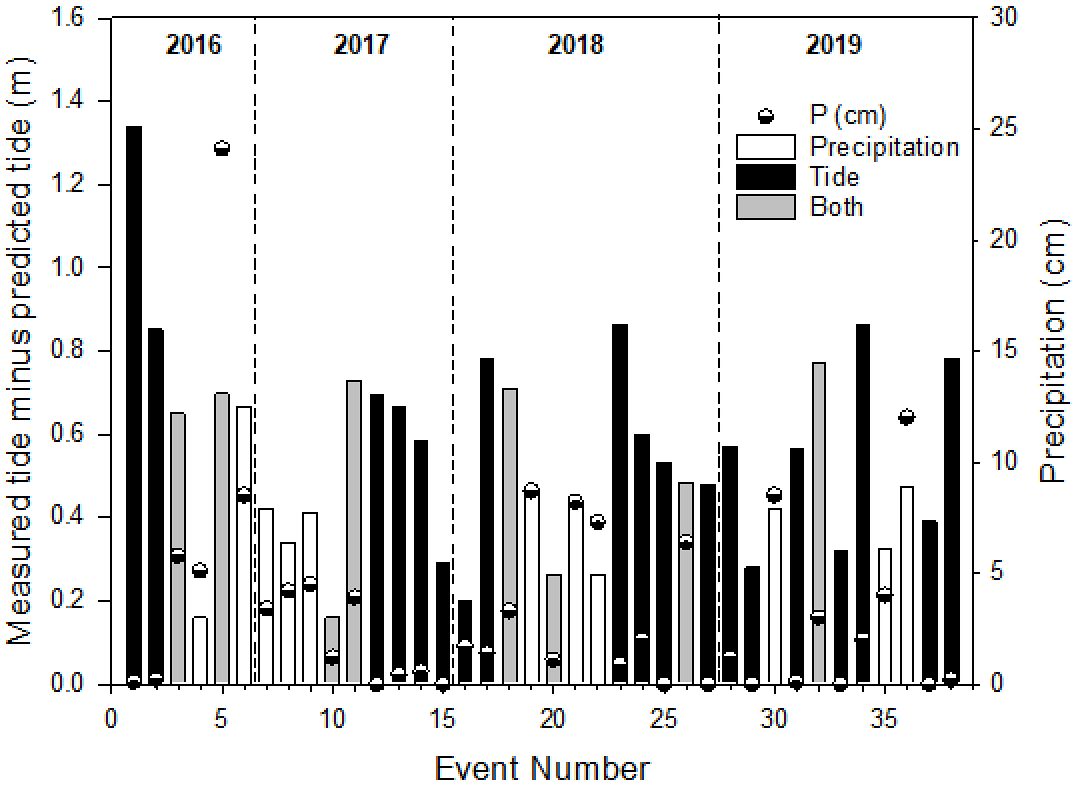


Figure 9. All flooding events in a 4-year period (2016 – 2019). An event was defined as when the pressure transducers measured a 10-cm increase in water-table elevation in a short period of time at well 1. Events are numbered sequentially from the beginning of the record. Black bars indicate tide events. White bars indicate precipitation events. Gray bars indicate events with both tides and precipitation (combined events). Black and white dots indicate the total precipitation over the duration of the event.

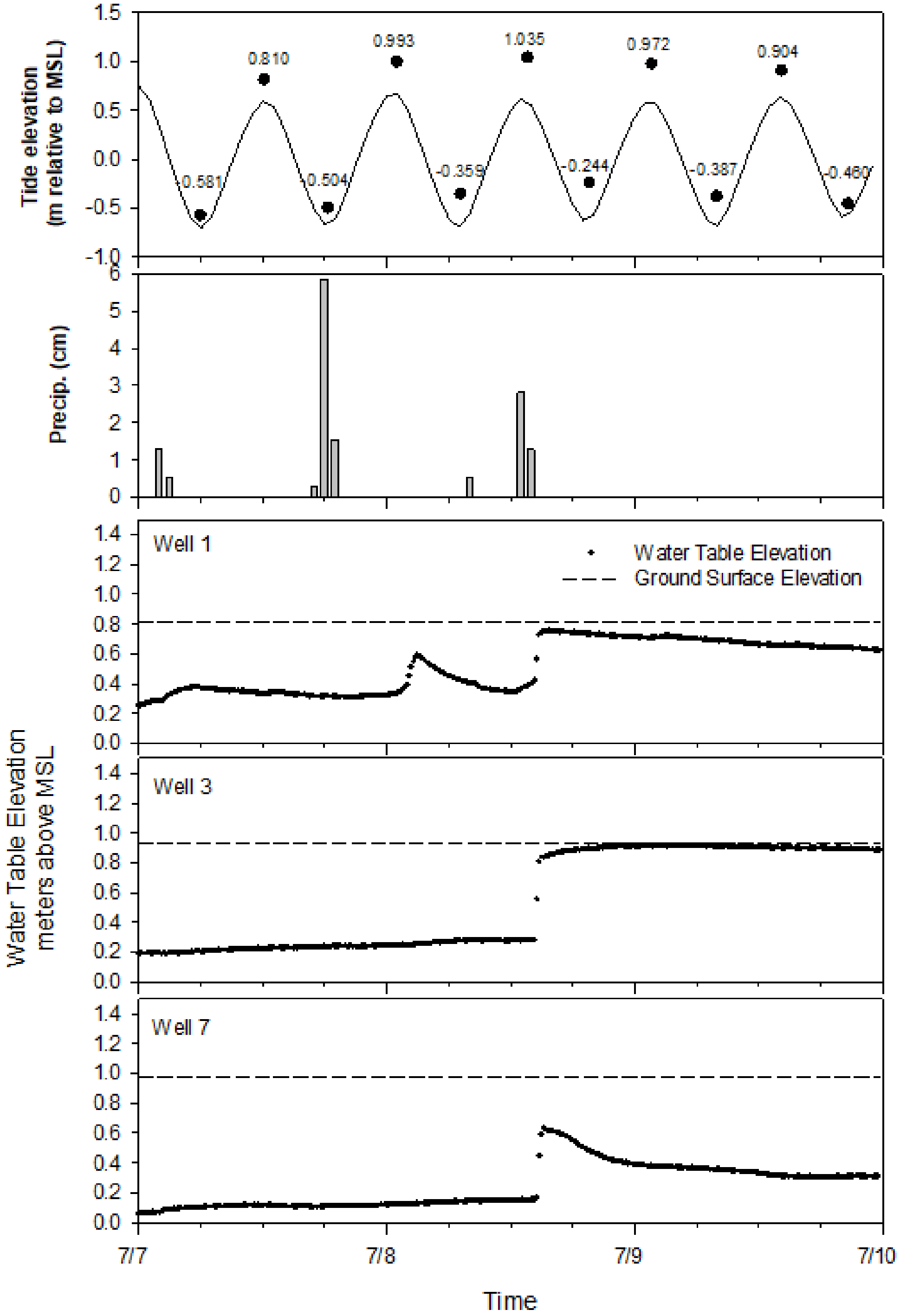


Figure 10. An example of a high-water event associated with precipitation. The top panel shows the predicted tide (solid line) and the actual high and low tide evaluated at a stream a short distance from the field under study. The second panel shows the precipitation received during the event, and the bottom three panels show the water table elevation for each of the three example wells representing the portion of the field proximal, medial, and distal from the stream.

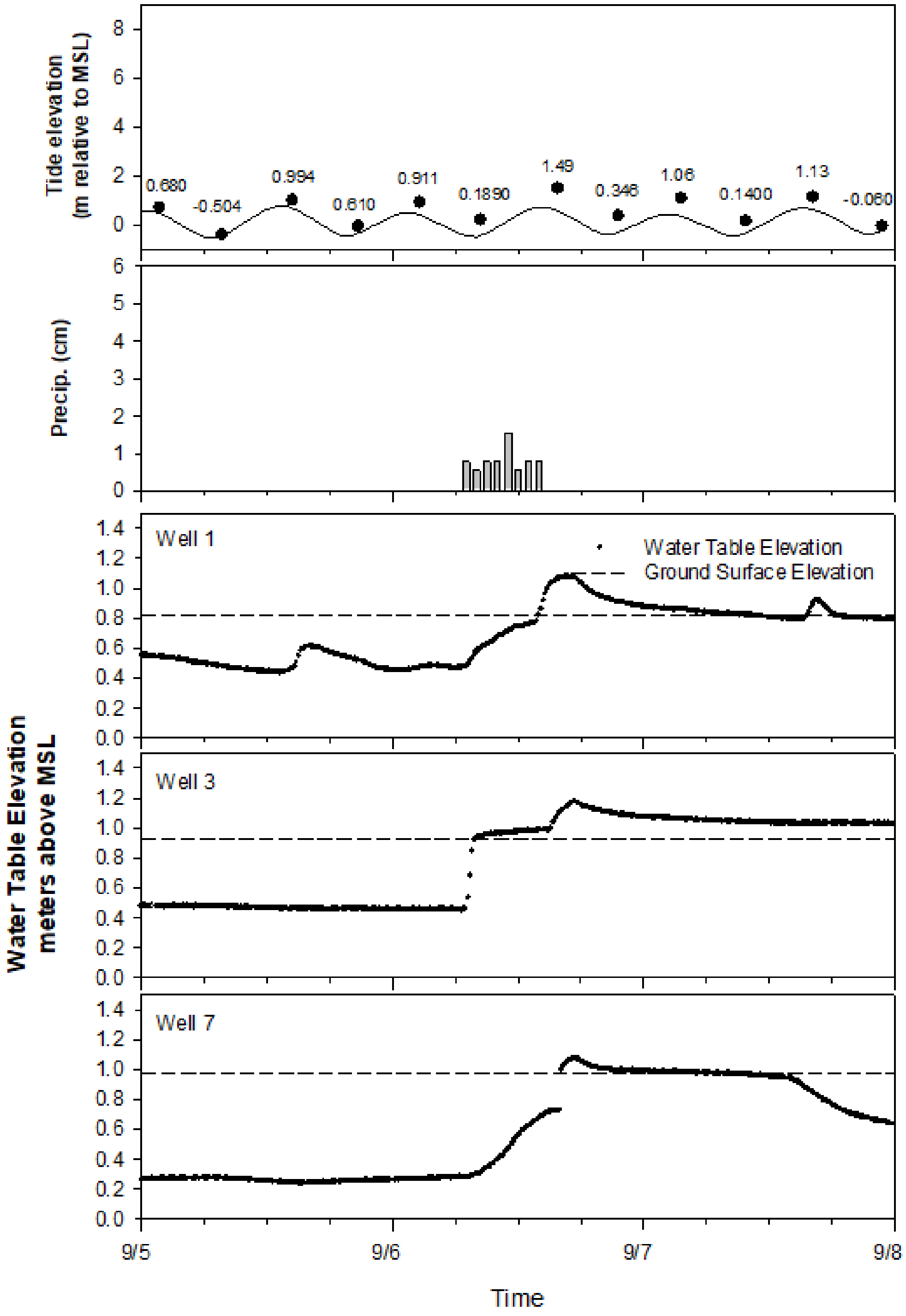


Figure 11. An example of a high-water event associated with tide. The panels show information as described in Fig 6.

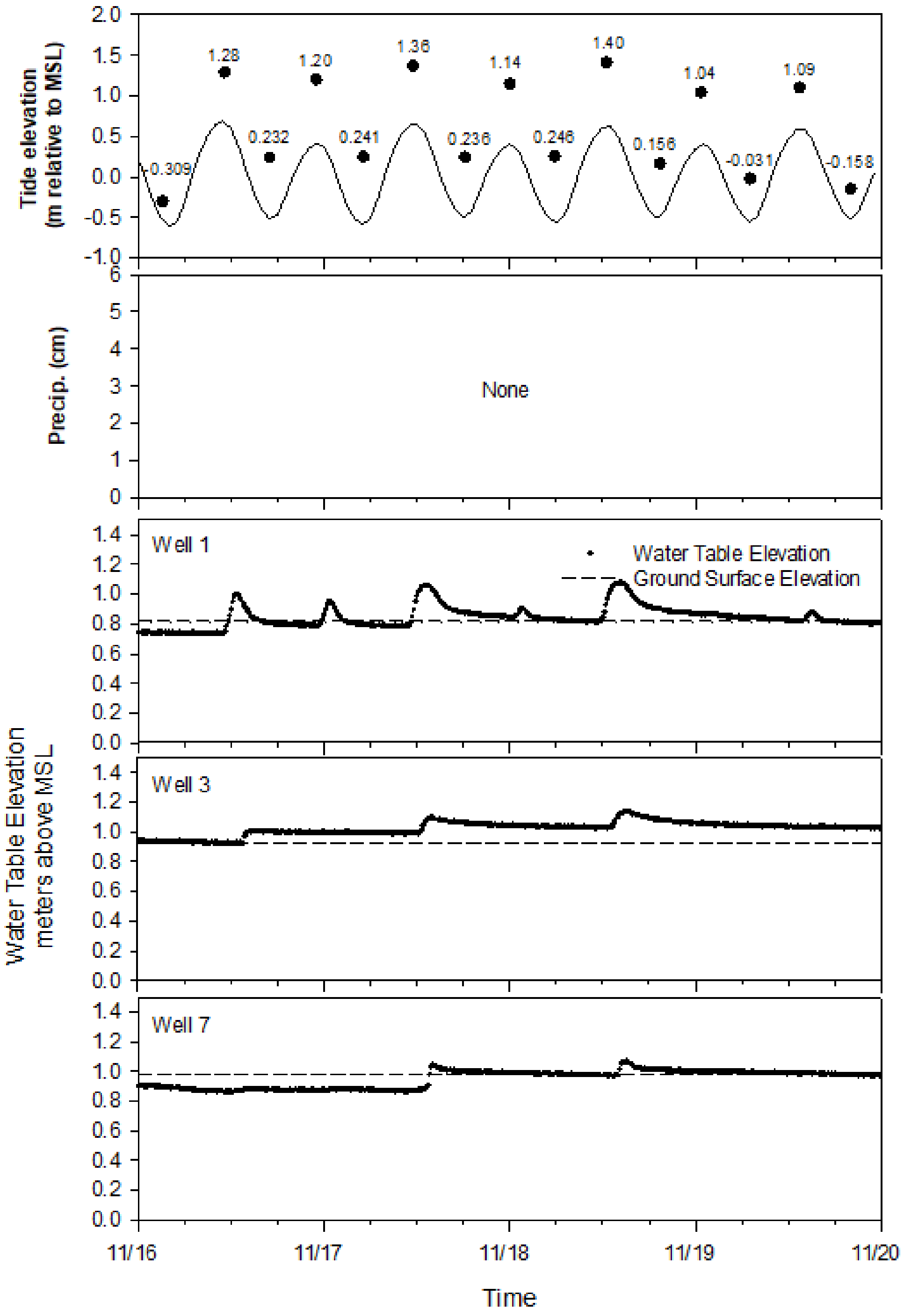


Figure 12. An example of a high-water event associated with both precipitation and tide. The panels show information as described in Fig 6.

Table 1. Plant community composition surrounding groundwater wells proximal (wells 1, 4, and 5), medial (wells 2 and 3), and distal (wells 6 and 7) to the nearby salt marsh and tidal creek. Species are listed in order of relative abundance based on personal observation. Superscripts indicate species with synonymous names. Plant scientific names were determined using the Integrated Taxonomic Information System (ITIS).

Proximal	**Medial**	**Distal**
Spartina patens (Aiton) Muhl.[1]	*Distichilis spicata* (L.) Greene	*Panicum virgatum* L.
Distichilis spicata (L.) Greene	*Panicum virgatum* L.	*Asclepias incarnata* L.
Aster tenuifolius L.[2]	*Asclepias incarnata* L.	*Setaria parviflora* (Poir.) Kerguélen
Borrichia frutescens (L.) DC	*Kosteletzkya pentacarpos* (L.) Ledeb.	*Distichilis spicata* (L.) Greene
Typha sp. (L.)	*Setaria parviflora* (Poir.) Kerguélen	*Kosteletzkya pentacarpos* (L.) Ledeb.
Limonium carolinianum (Walter) Britton	*Aster pilosus* Willd..	*Iva frutescens* L.
Kosteletzkya pentacarpos (L.) Ledeb.[3]	*Phragmites australis* (Cav.) Trin. ex Steud.	*Cyperus esculentus* L.
	Scirpus sp. (L.)	*Fimbristylis thermalis* S. Watson[4]
	Fimbristylis thermalis S. Watson[4]	
	Juncus roemerianus Scheele	

[1] *Sporobolus pumilus* (Roth) P.M. Peterson & Saarela
[2] *Symphyotrichum tenuifolium* (L.) G.L. Nesom
[3] *Kosteletzkya virginica* (L.) C. Presl ex A. Gray
[4] *Fimbristylis spadicea* (L.) Vahl

Table 2. Characteristics of wells. All pressure transducers were monitored until January 8, 2020.

Well	Well Installation Date	Transducer Installation Date	Group	Plant Community at Well Installation	Location		Ground Surface Elevation (m above msl)	Well depth (m below ground surface)	Depth to sensor from top of well casing (m)[a]	Elevation of top of well casing
					Latitude (°N)	Latitude (°W)				
1	7/8/2013	7/9/2013	Proximal	High-marsh species	37.4729	-75.82700	0.81652	2.940	2.835	1.889
2	7/8/2013	7/9/2013	Medial	Switchgrass and mixed forbs	37.4725	-75.82780	0.95461	2.920	2.915/2.816	1.983
3	8/6/2014	8/7/2014	Medial	Switchgrass and mixed forbs	37.47271	-75.82816	0.92884	2.450	2.328	1.523
4	7/31/2017	9/16/2017	Proximal	High-marsh species	37.47280	-75.82923	0.87083	2.554	1.748/0.782	1.375
5	7/31/2017	9/16/2017	Proximal	High-marsh species	37.47273	-75.82920	0.85868	2.560	2.318	1.508
6	8/1/2017	9/16/2017	Distal	Old-field species	37.47103	-75.82883	1.00280	2.662	2.222	1.823
7	9/16/2017	9/19/2017	Distal	Old-field species	37.47253	-75.82553	0.97978	2.740	2.112	1772

[a] Where two depths are indicated, a second transducer was added when the first was destroyed or malfunctioned.

Table 3. Summary of case-study weather events. NOAA Tides and Currents

Event Number	Date	Type	Measured Maximum Tide (msl)	Predicted Maximum Tide (msl)	Difference in Measured and Predicted Tide (m)	Maximum Wind Gust (m/s)	Wind Direction	Precipitation (mm)
30	July 7-9, 2019	Precipitation	1.035	0.615	0.31	9.1	SW	140
32	Sept. 6-7, 2019	Combined	1.493	0.724	0.61	19.5	NE	64
38	Nov. 16-19, 2019	Tide	1.403	0.624	0.68	15.8	NE	2

(https://tidesandcurrents.noaa.gov/waterlevels.html?id=8631044&type=Tide+Data&name=Wachapreague&state=VA;); Weather Underground Historical Data (https://www.wunderground.com/weather/KMFV).

Table 4. Summary of weather events (Source: NOAA Tides and Currents, Weather Underground Historical Data).

Event Number	Date	Type	Measured Maximum Tide (m)	Predicted Maximum Tide (M)	Difference in Measured and Predicted Tide (m)	Maximum Wind Gust (m/s)	Wind Direction	Precipitation (cm)
12	September 17-21, 2017	Precipitation	1.498	0.808	0.53	9.5	NE	0
18	March 20-22, 2018	Combined	1.368	0.66	0.52	19.1	NE	3.3
19	June 10-13, 2018	Precipitation	1.21	0.747	0.34	17	NE	8.7
23	September 8-12, 2018	Tide	1.762	0.9	0.51	16.7	NE	0.8
32	September 6-7, 2019	Precipitation	1.493	0.724	0.61	19.5	NE	6.4
36	October 20-23, 2019	Precipitation	1.125	0.656	0.32	10.3	E	12
38	November 16-19, 2019	Tide	1.403	0.624	0.68	15.8	NE	0.2

Chapter 3.

Effect of salinity on germination, survival, and growth of two salt tolerant species – salt marsh mallow (*Kosteletzkya pentacarpos*) and switchgrass (*Panicum virgatum*)

3.1. Abstract

Rising sea levels are resulting in increased frequency of flooding and salinization of low-lying coastal farmlands. In response to the loss of suitable farmland for the production of traditional crops, cultivation of salt-tolerant crops may be a suitable alternative to extend the economic viability of farming operations. Salt marsh mallow (Kosteletzkya pentacarpos) and switchgrass (Panicum virgatum) are proposed crops for cultivation on salinized farmland. To determine the effects of salinity on seed germination and seedling growth of salt marsh mallow and switchgrass, a greenhouse experiment was done. Each of the 60 pots was randomly assigned either switchgrass or mallow and a salinity treatment (7, 3, or 0 ppt) to give 10 pots of each combination of plant and salinity level. Pots were rearranged randomly within a grid design every two weeks to control for differences in light and temperature within the greenhouse. A 2x3 ANOVA was used to test differences in salinity tolerance between mallow and switchgrass. Mallow had higher percent germination and survival than switchgrass. Mallow also experienced linear growth much sooner than switchgrass. Salt marsh mallow's higher germination efficiency and seedling survival than switchgrass provide evidence that mallow will establish rapidly especially in the borders of agricultural fields and along upland-to-high-marsh transition zones experiencing salinization where mallow has the potential to provide both economic and environmental benefits.

3.2. Introduction

As sea levels rise, coastal agricultural fields experience occasional tidal flooding with salt water from the coastal lagoons and marsh creeks (Kearney *et al.*, 2019; Titus *et al.*, 2010). While the fields gradually become wetter over time, the effect of salt on crop plants is felt almost immediately. One strategy for extending the agricultural life of salinized fields and mitigating the economic loss of these farmlands is the planting of salinized fields with salt-tolerant crops (Flowers & Colmer, 2015; Glenn *et al.*, 2013; Ruan *et al.*, 2008). Two native perennial plants, salt marsh mallow (*Kosteletzkya pentacarpos*) and switchgrass (*Panicum virgatum*) have been identified as potential alternative crops for wet and salinized soils in coastal areas like the Eastern Shore of Virginia (Gallagher, 1985; Liu *et al.*, 2014). Currently, switchgrass is cultivated for biofuel production in the United States (Parrish & Fike, 2005) and salt marsh mallow has been identified as another plant source for biodiesel (Ruan *et al.*, 2012).

Salt marsh mallow is a perennial dicot native to high marshes along the Gulf and Atlantic coasts of the United States (Snell, 2018). Initially studied for its potential as a grain crop (Gallagher, 1985), mallow has also shown promise for the production of biodiesel and ethanol using the oil from pressed seeds (Moser *et al.*, 2013); as a feedstock for biodegradable absorbents, textile production (Vaughn *et al.*, 2013); and food production (Islam *et al.*, 1982). In addition to these commercial products, mallow also provides important ecosystem services including erosion mitigation, carbon sequestration, nutrient retention, and, potentially, facilitation of inland marsh migration (Voutsina *et al.*, 2015a).

Switchgrass is a perennial grass native to most of the contiguous United States, except California and the Pacific Northwest. Switchgrass is currently grown as an agricultural commodity for biofuel production and hay for livestock in the United States (USDA NRCS, 2012). While some varieties of switchgrass are not very salt tolerant, native cultivars can be found growing in the transition zone between high marsh and old agricultural fields. One cultivar in particular, Alamo, has shown promise as a more salt-tolerant variety (Hu *et al.*, 2015). Similar to mallow, switchgrass also provides important ecosystem services, including erosion mitigation, and habitat and shelter for birds and small mammals (USDA NRCS, 2012).

The mid-Atlantic region of the USA, which includes, the Eastern Shore of Virginia, is located in a region of very rapid sea-level rise (SLR) that is the highest along the United States Atlantic coast. The most recent estimate of SLR at the Virginia Coast Reserve is 5.63 mm yr^{-1} from 1978-2021 (https://tidesandcurrents.noaa.gov/sltrends/sltrends_station.shtml?id=8631044) based on the tide gauge at Wachapreague, VA (Station ID: 8631044, 37.60833333°N/-75.68500000°W); accessed March 2024). Groundwater wells monitored by Long-Term Ecological Research Virginia Coastal Reserve (LTER-VCR) that are located between salt marsh and abandoned upland agricultural fields show a stable level of water table and increasing salinity from 1992 to 2015 (Brinson & Stasavich, 1997) (Figure 13). This increase in salinity is one indicator of the transition of uplands to coastal wetlands.

Brinson *et al.* (Brinson *et al.*, 1995) hypothesized that the transition from upland to high salt marsh occurs when infrequent, extreme storm tides flow overland into fields or forests where the saline water infiltrates into the soil such that plants experience water stress and, ultimately, death. As the sea level rises and the frequency of tidal inundation increases, waterlogging and continued inputs of salt lead to soil changes that are more favorable for the growth of wetland plants than upland plants. In Chapter 2, I discussed the impact of flooding on the groundwater elevation and salinity in coastal uplands.

As a native marsh species, mallow is considered to be more salt tolerant than switchgrass, but neither species's response to salt stress, nor a comparison of the degree of salinity tolerance between the two species has been studied. To fill the knowledge gap pertaining to the suitability of cultivating mallow or switchgrass in salt-affected fields, it is critical to examine the salinity tolerance of both species. Therefore, this greenhouse study was done to determine how salinity affects seed germination, survival, and plant growth of mallow and switchgrass var. Alamo.

3.3. Methods

3.3.1. Plant Materials

Salt marsh mallow seeds (*Kosteletzkya pentacarpos*) used for this experiment were collected from local, native populations on Virginia's Eastern Shore. Seeds of the switchgrass var. Alamo was purchased from a commercial seed source (Hancock Seed & Company, Inc., Dade City, FL USA). The Alamo cultivar was selected for its salinity tolerance and high biomass production (Hu *et al.*, 2015; J. Kim *et al.*, 2016; Liu *et al.*, 2014, 2015).

3.3.2. Study Site

The study was conducted in a controlled greenhouse on the Delmarva Peninsula at the Virginia Tech Agricultural Research and Extension Center in Painter, Virginia. The duration of the experiment was 116 days post-seed planting and 115 days post-application of first salinity treatments (see details below).

3.3.3. Experimental Design

On December 15, 2016, seeds were sown into sixty 10 cm x 10 cm x 35.6 cm treepots (Peaceful Valley Farm Supply, Grass Valley, CA, USA) that were filled with moist potting soil. Seeding rates were based on reported germination efficiencies for salt marsh mallow (Poljakoff-Mayber *et al.*, 1992, 1994) and switchgrass (Grabowski *et al.*, n.d.; Schmer *et al.*, 2012). Mallow seeds were nicked with a scalpel to promote germination (personal communication with J. Gallagher). The target for germination was 4 mallow and 10 switchgrass plants per pot. Based on previous germination tests for mallow (80%; personal observations) and literature values for switchgrass (33%; (S. Kim *et al.*, 2012; Zanetti *et al.*, 2019), mallow pots were planted with 5 seeds while switchgrass pots were planted with approximately 100 seeds. Seeds were covered with 3 cm of potting mix and lightly packed.

Each pot was assigned one of the two plant species – salt marsh mallow or switchgrass – and one of the three salinity treatments – 0, 3, or 7 ppt for a total of 10 replicates of each treatment combination. The pots were arranged on a table in a 10 x 12 grid pattern within a 105 x 130 cm frame (Figure 14). To account for variations in sunlight and temperature within the greenhouse, pots were randomly assigned a location within the grid and rearranged every two weeks.

The watering solutions were prepared by dissolving NaCl, $MgSO_4$ $7H_2O$, and KCl in deionized water to obtain three salinity levels of 0, 60, and 140 ppt. Chemilizer Adjustable Ratio Pumps (QC Supply, Clinton, NC, USA) were used to dilute the solutions with groundwater to achieve the desired salinity levels of 0, 3, and 7 ppt. These salinity levels were based on the measured groundwater salinity in an old agricultural field experiencing periodic flooding with saltwater (Chapter 2). HCl was added to the concentrated solutions to adjust for the high pH of the groundwater.

Beginning on December 16, 2016, (one day after planting), salinity treatments were started. The pots were watered using a system of individual spray stakes, drippers, and micro tubing (Berry Hill Drip Irrigation, Buffalo Junction, VA USA) for three minutes every six hours (rate of 1.89 L $hour^{-1}$). Individual pots were fertilized by hand in December and March using MiracleGro water-soluble all-purpose plant food and Osmocote Plus Smart-Release Plant Food. Each pot was watered with 0.3 L of a 0.65 mL/L solution of Miracle-Gro and 22 mL of Osmocote, as recommended.

Because the seeds were buried when they were planted, seedling emergence was used as a surrogate for seed germination. The number of seeds emerging was counted daily for 10 days and after that weekly. The percentage of seeds that germinated was calculated as a fraction of the number of seeds planted using the following relationship:

Equation 1

$$seed\ germiantion\ efficiency\ (\%) = \frac{\text{number of seedlings emerged}}{\text{number of seeds planted}}\ \text{x}\ 100$$

Once the seedlings were 2 mm or taller, their height was measured weekly for the remainder of the experiment (115 days post initiation of salinity treatment). Seedling survival was expressed as a percentage of the total number of seedlings that emerged for each treatment was calculated using the following relationship:

Equation 2

$$Seedling\ survival\ (\%) = \frac{\text{number of plants on the last day of sampling}}{\text{number of seedlings emerged}}\ \text{x}\ 100$$

Three measures of plant growth were determined: the length of time between seedling emergence and the beginning of linear increases in plant height (days), growth rate during the linear phase (cm d^{-1}), and mean plant height (cm) in each pot at the end of the experiment (116 days after planting). Because plant height was measured weekly, it was necessary to estimate days to linear growth using a modeling approach. To determine days to linear growth, a growth curve was constructed for each pot (n=60) by plotting the mean plant height versus days from seed planting. Then, the linear growth phase was identified visually from plots of the growth curve. Next, using a linear model, a best-fit approach was used to select the line with the highest R^2 value during the rapid growth phase. Finally, the date of seedling emergence was subtracted from the x-intercept to calculate the number of days to linear growth for each pot. Finally, the average number of days to linear growth was calculated for each species-salinity treatment combination (n=10).

Growth rate (cm day^{-1}) is the slope of the best-fit line during the period of rapid linear growth from plots of mallow and switchgrass growth curves and the error terms are the 95% confidence intervals of the best-fit line. The best fit for each species-salinity treatment was determined by examining the r^2-values from correlation analysis of points that began at the end of the lag phase to the beginning of the stationary phase for mallow or from the end of the lag phase to the end of the experiment for switchgrass.

3.3.4. Statistical analysis

The effects of species and salinity, and the interaction effects on seed germination, survival, plant growth, and mean plant height were analyzed by a 2x3 factorial analysis of variance (ANOVA) using Statistical Analysis Software version 9.4 (SAS Institute Inc., NC, USA). All percentage data were arcsin transformed before analysis. Main effects and interactions were considered significant if $P<0.05$. To meet the ANOVA assumption of homogeneity of variance, it was necessary to test for within-species effects of salinity separately; a least squares test was used.

3.4. Results

The results of this greenhouse experiment, described in detail below, indicate that there were clear differences in the way that mallow and switchgrass grow, and in their responses to saline water, which are likely to affect competition between the two species at the salinities observed at the Brownsville field study site.

3.4.1. Germination

The length of time for mallow and switchgrass seeds to germinate was between 10 and 13 days after planting and was similar (data not shown). The germination efficiency (Figure 15) was significantly different between the two species (*F=229.04; P<0.0001*) (Table 5). Mallow seeds germinated at a much higher rate than switchgrass, 80-88% and 16-29%, respectively. There was no effect of salinity on germination efficiency for either species at the 0, 3, or 7 ppt salinity levels (*F=1.66; P<0.2005)*. The ANOVA analysis showed a significant interaction effect of species and salinity (*F=4.87; P<0.0114*). The final germination rate at 0, 3, and 7 ppt was 85%, 88%, and 80% for mallow, and 23%, 29% and 16% for switchgrass, respectively (Figure 15).

3.4.2. Seedling Survival

Seedling survival is expressed as the percentage of plants at the end of the experiment (116 days) compared to the maximum number of seeds that germinated (recall that germination is defined as seedlings emerging from the potting mix). While there was a significant difference between mallow and switchgrass survival (Table 2; *F=83.84, P<0.0001*), there was no significant difference between salinity treatments for the same plant species (Figure 16, Table 6). Over 80% of all mallow plants survived at all three salinity levels. In contrast, less than 30% of switchgrass plants survived to the end of the experiment. Within each plant species, salinity treatments had no detectable effect on seedling survival compared to plants receiving freshwater.

3.4.3. Seedling Growth

The growth curves of both mallow and switchgrass were classical S-shaped curves (Figure 17 and Figure 18); however, the curves differed in the length of the lag phase, the rate of rapid linear growth, and the timing of the stationary phase. In fact, switchgrass had not reached the stationary phase when the growth experiments ended after 116 days. While nearly all the seedlings of both plants emerged from the soil between 10 and 13 days after planting, mallow began increasing in height linearly immediately after the seedlings emerged (Figure 17, Figure 19). Around 20 days after emergence (*i.e.*, 40 days post-planting), the height of the seedlings no longer increased (Figure 17). Conversely, switchgrass grew very slowly initially (Figure 18, Figure 19). After approximately 65 to 75 days post-emergence (*i.e.*, 80 to 90 days post-planting) these seedlings entered a rapid period of linear growth (Figure 18) that continued until the experiment ended 116 days after the seeds were planted and the switchgrass plants were much taller than the mallow plants (Figure 20, Table 7; $F=81.23$, $P<0.0001$). During the rapid, linear phase of growth, the rates of growth were 0.13, 0.12, and 0.11cm day^{-1} for mallow at 0, 3, and 7 ppt, respectively. Switchgrass growth rates (0.47, 0.47, and 0.46 cm day^{-1} at 0, 3, and 7 ppt, respectively) were more rapid than those of mallow (Figure 21, Table 8; $F=26.69$, $P<0.0001$). While the growth rates for mallow show a decreasing trend from fresh to 7 ppt, there was no significant effect of salinity on either plant species (Table 8).

3.4.4. Final Plant Height

At the end of the experiment, the mean plant height in each pot and species-by-salinity treatment were determined. There was a clear plant species difference; mallow plants were shorter than switchgrass plants (Figure 20, Table 7; $F=81.23$, $P<0.0001$). The mean height of the plants in the switchgrass pots was 25.3, 18.2, and 17.0 cm, and 5.7, 4.8, and 4.7 cm in the mallow pots (0, 3,7 ppt, respectively). Additionally, mallow treatment differences were significant and height decreased as salinity increased (Figure

20, Table 9; *F=4. 35, P=0.0230*). The trend for switchgrass seedlings was similar to mallow (decreasing height with increasing salinity) but no significant salinity effect was detected among the switchgrass treatments (Figure 20, Table 9).

3.5. Discussion

Salt marsh mallow seedlings exhibited a higher tolerance to salinity than switchgrass (Figure 16). This is expected given the native distribution of the two species. Salt marsh mallow is a transient species in upland to high-salt marsh transition communities along the USA Eastern and Gulf coasts (Snell, 2018). Switchgrass is a codominant of climax tallgrass prairie on mesic sites (Kuchler, 1964), but has been described as being codominant with eastern grama grass (*Tripsacum dactyloides*), tall dropseed (*Sporobolus asper* var. *asper*), and/or Indiangrass (*Sorghastrum nutans*) on poorly drained coastal-lowlands in Texas (Diamond & Smeins, 1985). Personal observations suggest that switchgrass is common in similar poorly-drained and mesic settings on the Virginia Eastern Shore.

The habitats where mallow and switchgrass grow likely reflect their ability to tolerate inundation and soil salinity. The effect of soil moisture on these species is discussed in the next chapter. The effect of soil salinity on mallow seed germination is not clear. Poljakoff-Mayber *et al.* (1992) observed mallow seed germination efficiency of 90% and 80% at 0 and 5.6 ppt, respectively; however, germination declined sharply over salinity levels of 11.9 ppt to approximately 16 ppt (150 mM). These authors attribute reduced seed germination to an osmotic effect on seed imbibition and speculated that embryonic development was slowed or halted by salt. The degree of inhibition differed among seeds collected in different years and from different populations, as well as between seeds stored for different lengths of time (longer storage increased germination), and between intact seeds or seed coats nicked with a scalpel (nicked seed germination decreased as salinity increased). Contrary to these findings, Somers (1982) was unable to show a salinity effect on mallow seed germination from a single population by salinities ranging from 0% NaCl to as high as 66%. Similar to the results of Somers (1982) and Pojakoff-Mayber *et al.* (1994), the results presented here (Figure 15) show no detectable effect on seed germination. Because the seeds used in my experiments were collected from multiple populations of mallow, and no effect of salinity was detected to 7 ppt, this suggests that a good bet-hedging strategy for establishing field populations in coastal old fields experiencing occasional seawater flooding would be to seeds collected from a variety of local populations.

Switchgrass salinity tolerance of many cultivars has been widely investigated (Carson *et al.*, 2016; Hu *et al.*, 2015, 2018; Jobe IV & Gedan, 2021; J. Kim *et al.*, 2016; S. Kim *et al.*, 2012; Liu *et al.*, 2014; Schmer *et al.*, 2012; Shrestha *et al.*, 2022; Sun *et al.*, 2018; Zanetti *et al.*, 2019). While it is known that salinity causes a reduction in seed germination, seedling emergence, and seedling growth of many switchgrass cultivars, the cultivar, Alamo, which was used in this study, has been identified as salinity tolerant (Hu *et al.*, 2015; Sun *et al.*, 2018). Alamo germination efficiency ranged widely from 25-50 percent germination and generally decreased as salinity treatment increased from 0 to 12 ppt (Carson *et al.*, 2016; S. Kim *et al.*, 2012; Sun *et al.*, 2018; Zanetti *et al.*, 2019). Unlike salt marsh mallow, which excludes or partitions salt to reduce the impact on the plant, when Alamo is grown in saline soil it exhibits a salt-stress response in which intracellular levels of reactive oxygen species (ROS) are produced. Increases in ROS concentrations are accompanied by increases in cellular levels of the antioxidants, catalase, and lower proline, which reduce levels of ROS (Hu *et al.*, 2018); however, it is not clear what is the mechanistic basis for salt resistance by switchgrass seeds. What is clear from my greenhouse study is that the germination efficiency of both plant species was not reduced by either the 3 or 7 ppt relative to 0 ppt treatment (Figure 15) and that there are inherent differences in seedling germination between switchgrass and mallow.

Not only does mallow have a higher seed germination rate across all salinity treatments than switchgrass, but it also had higher survival rates (Figure 16, Table 6; $F=83.4, P<0.001$) and a shorter lag time to the beginning of rapid seedling growth (Figure 17, Figure 19). Mallow's greater survival and shorter lag time could imply faster establishment under field conditions. Similar to seed germination, these differences between the two species are likely a consequence of differences in the natural history of mallow, a dicot, and switchgrass, a monocot (https://ucmp.berkeley.edu/glossary/gloss8/monocotdicot.html, (McSteen, 2010; Nelissen *et al.*, 2016). Few studies have examined the relationship between survival and population establishment in saline environments for switchgrass (Carson *et al.*, 2016) though more have examined that relationship for mallow (Blits & Gallagher, 1990a, 1990b; Poljakoff-Mayber *et al.*, 1992, 1994; Ruan *et al.*, 2008; G. Zhou *et al.*, 2010). Even though mallow seed production per plant (ca. 393) is 25% lower than that of switchgrass (c.a. 522 seeds per plant) (see Appendix B, Table B 1), if mallow's higher germination efficiency and survival in these greenhouse experiments are realized in field conditions, these results support the assertion that mallow should establish more rapidly than switchgrass in abandoned agricultural fields that are experiencing increased frequency of flooding with saltwater.

Although the mallow seedlings grew rapidly from the time they emerged from the soil, (Figure 19), the growth rate of mallow was slower than switchgrass (Figure 21, Table 8), and the height increase ceased after about 40 days (Figure 19) which resulted in significantly shorter mallow seedlings than those of switchgrass when the experiment ended (Figure 20, Table 7). Without scarifying the seedlings, other measures of growth such as foliage and roots or increased mass could not be determined as these measures would have required harvesting the pots thereby decreasing the number of replicates each time growth was measured and killing seedlings that were planned for use in the field experiment described in Chapter 4.

The difference between the growth curve shapes (Figure 19) and final heights (Figure 20) of these two species is likely a consequence of how monocots and dicots grow. A characteristic of most dicots is that they increase in height initially and then slow when secondary growth and/or tap root development begins (https://ucmp.berkeley.edu/glossary/gloss8/monocotdicot.html), while monocots have a long lag phase followed by rapid height increase (Nelissen *et al.*, 2016; Zhang *et al.*, 2019). This difference may be related to differences in the spatial (e.g., location of meristematic tissues) and temporal (e.g., growth hormone production) processes within the plants that regulate the growth of dicots and monocots (Nelissen *et al.*, 2016).

Compared to the growth patterns of crop plants, switchgrass is characterized by relatively slow growth and a lengthy time to become established (Zhang *et al.*, 2019). Environmental factors such as photoperiod and temperature also alter the rates of leaf and stem elongation (Poiré *et al.*, 2010); however, the influence of salinity switchgrass growth rates has not been examined. Here, I show that the rate of switchgrass leaf elongation was unaffected by salinities as high as 7 ppt, while mallow seedling height decreased as salinity increased from 0 ppt to 3 ppt to 7 ppt (Figure 20, Table 7, Table 9).

This study demonstrates the ability of mallow and switchgrass to germinate and grow under elevated levels of salinity. In the early stages of salinization, switchgrass may be favored for cultivation in buffers or agricultural fields because of its well-documented ecosystem services and existing biofuel market (Liu *et al.*, 2014; Parrish & Fike, 2005; Rinehart, 2006; Sanderson *et al.*, 1996). As fields experience more frequent flooding with salt water, mallow may perform better, especially as a buffer crop, in more saline areas of fields. Mallow's higher tolerance for salinity and germination efficiency provides evidence to suggest that it will establish more quickly in saltier areas than switchgrass.

The lack of a developed economic market for the production and sale of non-traditional halophytes like salt marsh mallow, prevents farmers from utilizing these plants on a commercial scale. A more attenable option would be to cultivate mallow as a buffer crop in areas that are too wet or salty for traditional cultivation. With accelerating rates of sea-level rise, farmers are finding larger areas of their fields that are ill-suited to traditional crop cultivation because of poor drainage and salinization (personal observation). These small areas will expand with increased frequency of flooding from storm surge and rising water tables (Chapter 2), shrinking the area of usable farmland. Planting salt-tolerant species in these areas would not only offer an alternative source of income to offset the economic loss of excluding areas of a field from production. Accelerating rates of sea-level rise will lead to the eventual abandonment of coastal agricultural land (Titus *et al.*, 2010). In a common garden experiment, Voutsina *et al.* (2015) found that planting mallow facilitated colonization of desirable high marsh species while the plant community transitioned from one state to another. Mallow provides ecosystem services including mitigation of erosion and accumulation of soil organic matter resulting from leaf litter. Switchgrass also offers similar ecosystem services and perhaps even more when co-cropped with mallow in abandoned agricultural fields. In the following chapters, I will discuss the impact of increased soil moisture on both mallow and switchgrass co-croppings and monocultures.

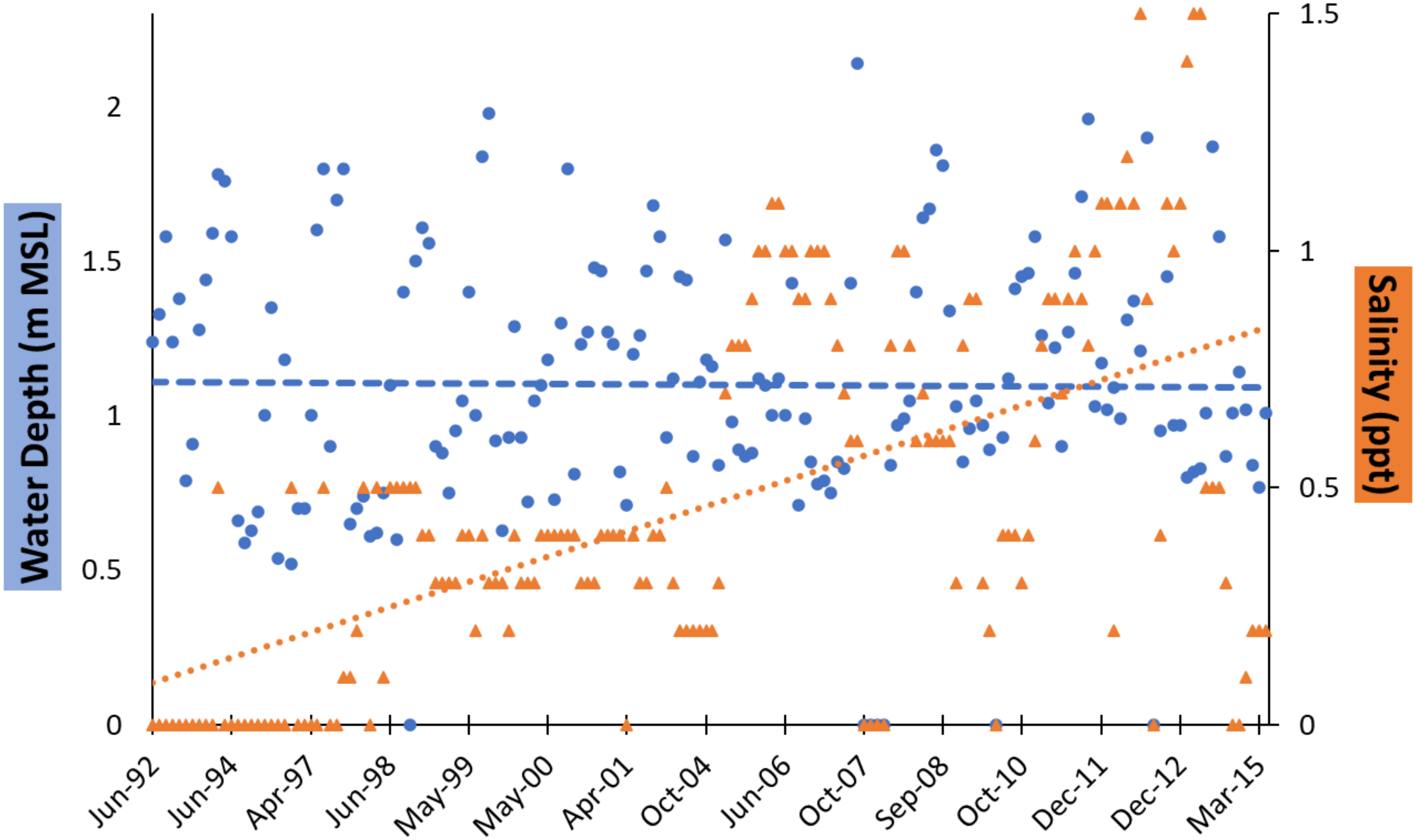


Figure 13. Measurements of groundwater depth (m; blue circle) and salinity (parts per thousand; orange triangles) in wells bordering a salt marsh within the Brownsville Preserve, Nassawadox, Virginia from 1992 to 2015(Brinson and Stasavich, 1997). Observations reflect a stable level of water depth and increasing salinity over the measurement period. This increase in salinity is one indicator of the transition of upland systems to coastal wetlands.

Figure 14. Experimental setup in a greenhouse in Painter, Virginia. Sixty pots were arranged randomly in a 10 x 12 grid pattern within a 105 cm x 130 cm frame and rearranged every two weeks.

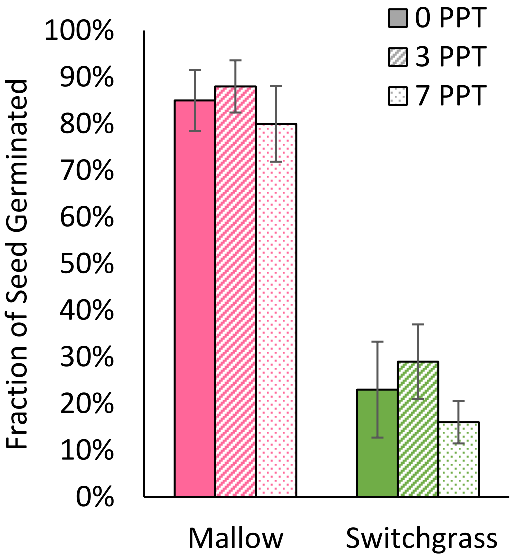


Figure 15. Germination efficiency expressed as the fraction of the number of seedlings that emerged from the potting compared to the number of seeds planted (Eq. 1). Bars are mean values ± SE (n=10 pots) of salt marsh mallow (*K. pentacarpos*) and switchgrass (*P. virgatum*) under three different treatments.

Table 5. ANOVA statistics for germination efficiency (arcsin transformed).

n=60	DF	Type III Sum of Squares	Mean Square	F Value	P Value (α=0.05)
Species	1	9.913	9.913	229.04	<0.0001
Salinity	2	0.143	0.072	1.66	0.2005
Species*Salinity	2	0.421	0.211	4.87	0.0114

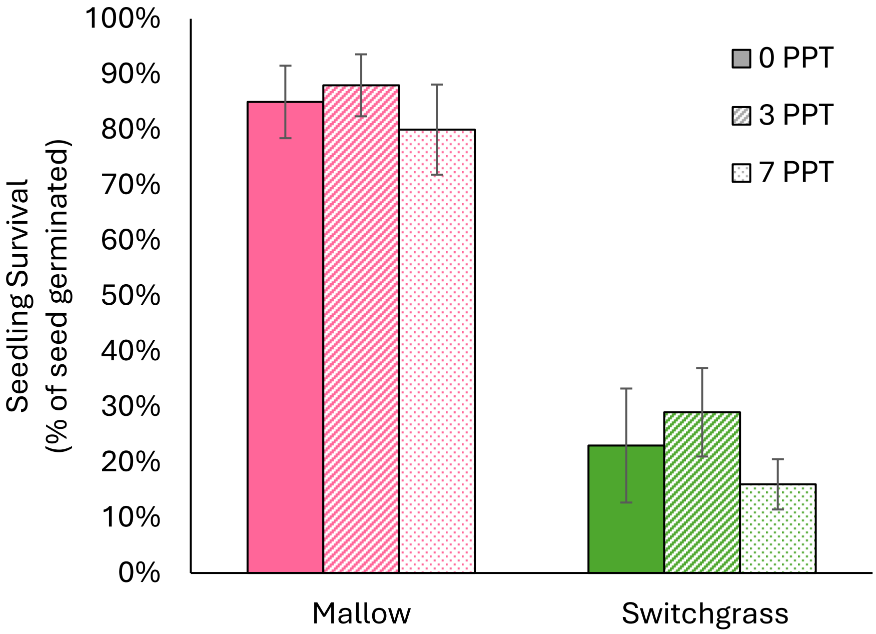


Figure 16. Effect of three salinity treatments on the survival to 116 days as a fraction of plants germinated for salt marsh mallow and switchgrass (mean ± SE).

Table 6. ANOVA statistics for survival (arcsin transformed); n=60.

	DF	Type III Sum of Squares	Mean Square	F Value	P Value (α=0.05)
Species	1	11.782	11.782	83.84	<0.0001
Salinity	2	0.148	0.074	0.53	0.5928
Species*Salinity	2	0.010	0.005	0.04	0.9638

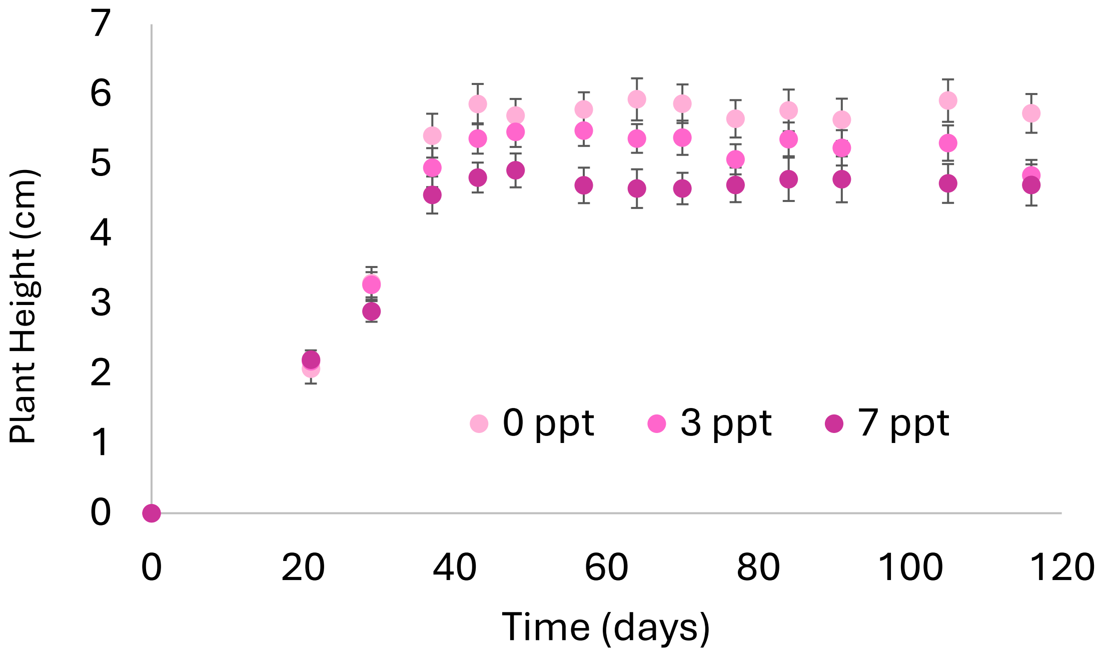


Figure 17. Effect of salinity on the growth of salt marsh mallow from the date of planting, December 15, 2016, to April 10, 2017. Error bars are ± standard error; n = 10.

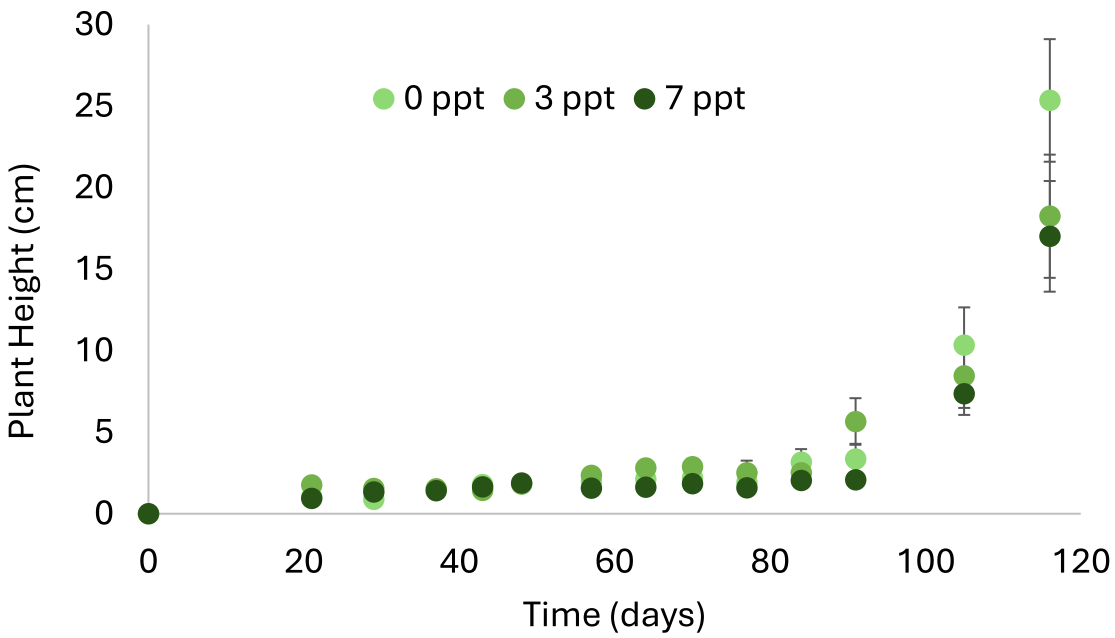


Figure 18. Effect of salinity on the growth of switchgrass from the date of planting, December 15, 2016 to April 10, 2017. Error bars are ± standard error; n = 10.

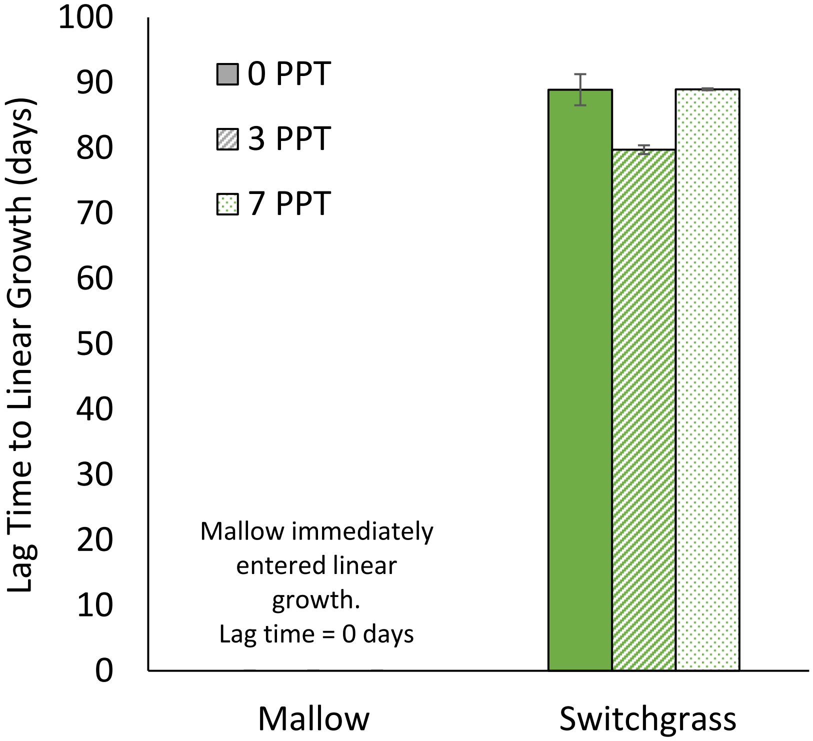


Figure 19. Effect of salinity on the time to initiation of rapid linear growth, the lag phase, for salt marsh mallow and switchgrass. Error bars for switchgrass are the 95% confidence intervals for the linear regression where the best fit line crossed the x-axis; n=10. See Appendix B.

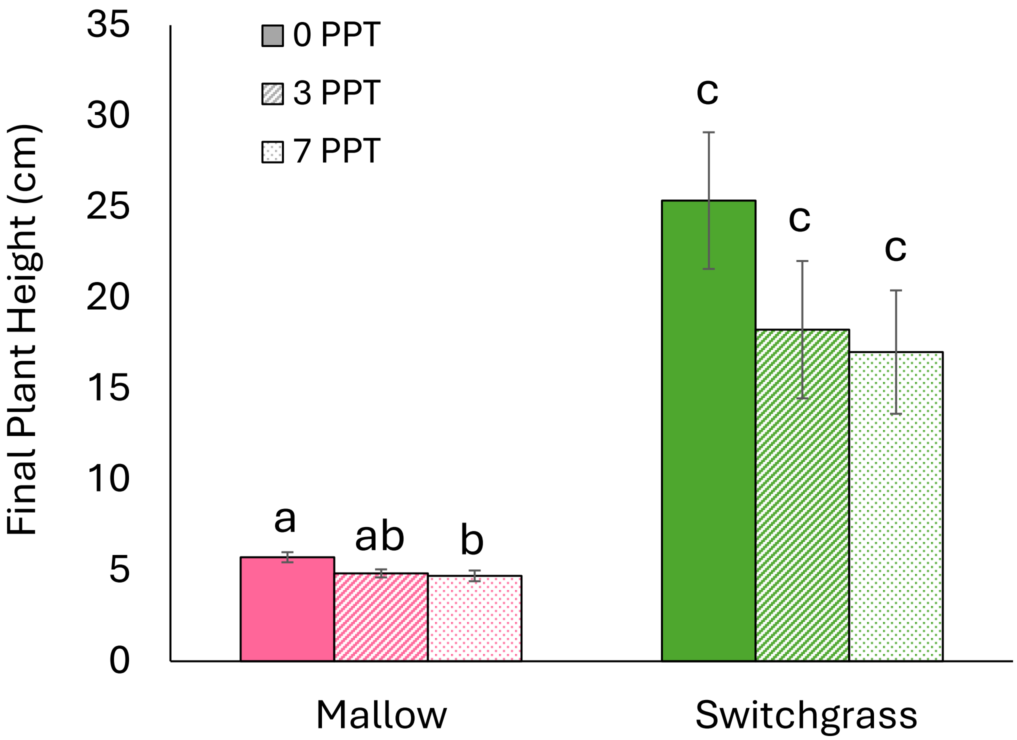


Figure 20. Effect of salinity on final plant height for *K. pentacarpos* and *P. virgatum*. Error bars show ± standard error of the mean; n=10.

Table 7. Full ANOVA statistics for testing the effects of species and salinity on final plant height.

Source	DF	Type III Sum of Squares	Mean Square	F Value	p value
species	1	2616.876	2616.876	81.23	<0.0001
salinity	2	182.4047	91.20236	2.83	0.0700
interaction	2	110.9930	55.49649	1.72	0.1907

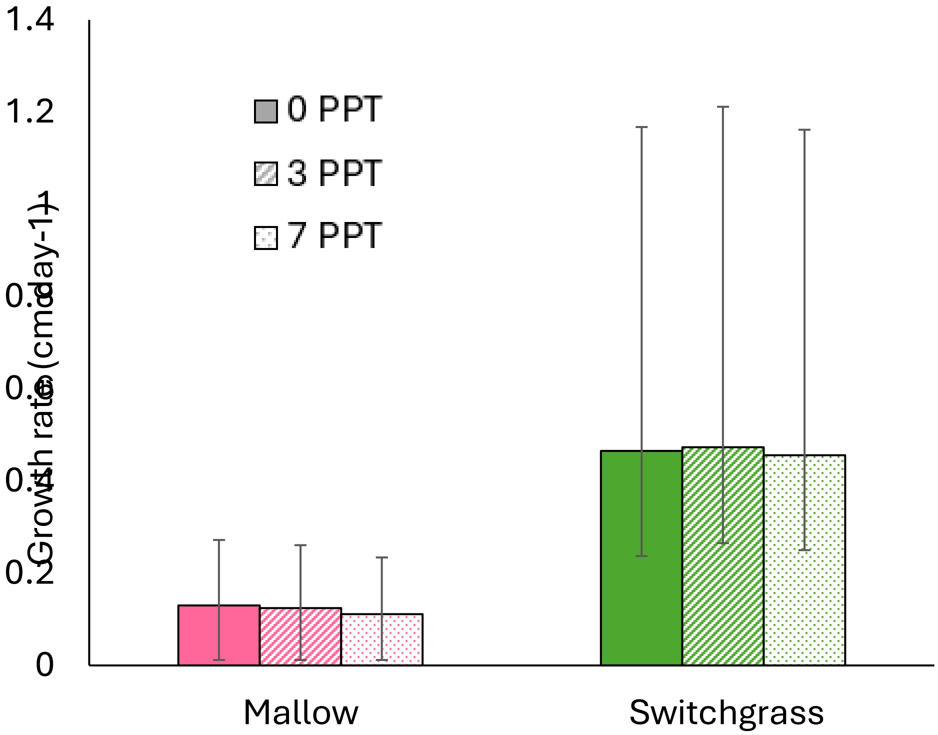


Figure 21. Effect of three salinity treatments on the growth rate (cm day^{-1}) of salt marsh mallow and switchgrass. Error bars show 95% confidence intervals; n=10.

Table 8. ANOVA table testing for the effect of three salinity treatments on the linear growth rate for salt marsh mallow and switchgrass.

Source	DF	Type III SS	Mean Square	F Value	p value
species	1	1.66302	1.66302	26.69	<0.0001
salinity	2	0.00273	0.00136	0.02	0.9784
interaction	2	0.00048	0.00024	0.00	0.9962

Table 9. Post-hoc least squares test of the effects of salinity on final plant height individually by species.

Species	DF	Type III Sum of Squares	Mean Square	F Value	p value
Mallow	2	6.1842	3.0921	4.35	0.0230
Switchgrass	2	224.805	112.403	1.32	0.2956

Chapter 4.

Effect of soil moisture on establishment and growth of two salt-tolerant species – salt marsh mallow (*Kosteletzkya* pentacarpos) and switchgrass (*Panicum virgatum*)

4.1. Abstract

Accelerated rates of sea level rise are threatening low-lying coastal farmlands where an increased frequency of flooding negatively impacts the suitability of farmland for the cultivation of traditional crops. In response, the cultivation of flood-tolerant species may be a suitable alternative to extend the viability of farming operations and preserve important ecosystem services during a period of transition. Salt marsh mallow (*Kosteletzkya pentacarpos*) and switchgrass *(Panicum virgatum*) are proposed crops for cultivation in wet and salinized farmland. To determine the effects of increased inundation frequency on the establishment and growth of monocultures and co-crops of mallow and switchgrass, a field experiment was conducted. Eight blocks of five plots were assigned to a wet or dry treatment (four wet, four dry), and each of the five plots was assigned one of five seeding treatment combinations of salt marsh mallow and switchgrass seeds. Percent cover was measured twice – two months after planting and 5 months after planting. Soil moisture was recorded before and after each watering event. T-tests were used to determine any significant effects of the watering treatment. An analysis of variance with a covariate was used to test for the effect of watering on final plant cover. Final percent cover of both mallow and switchgrass was consistent with the assigned seeding treatment. Mallow cover was higher than switchgrass in all combinations of the watering and seeding treatments. These results suggest that mallow may be more flood-tolerant than switchgrass and therefore a more suitable species for cultivation in agricultural lands experience increased frequencies of inundation.

4.2. Introduction

Rising sea level poses a risk to coastal areas as the frequency of flooding from storms, tides, and increased precipitation increases (Titus *et al.*, 2010), driving the process of ecosystem state change from upland to old field to salt marsh (Brinson *et al.*, 1995; Fagherazzi *et al.*, 2019a; Kearney *et al.*, 2019). Flooding or waterlogging events can change the environmental conditions (e.g. anoxic or hypoxic soils) that negatively affect species performance (Bertness, 1991; Corli *et al.*, 2023; Lenssen *et al.*, 2004; Watson *et al.*, 2015; Weiher & Keddy, 1995). Previous work suggests that in cases where severe flooding is expected, planting on elevated surfaces may ameliorate the stress of flooding (Doherty & Zedler, 2015). However, the burdensome cost for land managers associated with this option could be cost-prohibitive.

Alternatively, one solution may be the establishment of flood-tolerant species in areas that are expected to experience severe flooding. Two native perennial plants, salt marsh mallow (*Kosteletzkya pentacarpos*) and switchgrass (*Panicum virgatum*) have been identified as potential alternative crops for wet and salinized soils in coastal areas like the Eastern Shore of Virginia (Gallagher, 1985; Liu *et al.*, 2014). Currently, switchgrass is cultivated for biofuel production in the United States (Parrish & Fike, 2005) and salt marsh mallow has been identified as another plant source for biodiesel (Ruan *et al.*, 2012).

Salt marsh mallow is a perennial dicot native to high marshes along the Gulf and Atlantic coasts of the United States (Snell, 2018). Initially studied for its potential as a grain crop (Gallagher, 1985), mallow has also shown promise for the production of biodiesel and ethanol using the oil from pressed seeds (Moser *et al.*, 2013); as a feedstock for biodegradable absorbents, textile production (Vaughn *et al.*, 2013); and food production (Islam *et al.*, 1982). In addition to these commercial products, mallow also provides important ecosystem services including erosion mitigation, carbon sequestration, nutrient retention, and potential facilitation of inland marsh migration (Voutsina *et al.*, 2015a).

Switchgrass is a perennial grass native to most of the United States, except California and the Pacific Northwest. Switchgrass is currently grown as an agricultural commodity for biofuel production and hay for livestock in the United States (USDA NRCS, 2012). While some varieties of switchgrass are not very salt tolerant, native species can be found growing in the transition zone between high marsh and old agricultural fields. One cultivar in particular, Alamo, is a more salt-tolerant variety (Hu *et al.*, 2015; Zanetti *et al.*, 2019) and many upland and lowland ecotypes have exhibited tolerance to higher soil moisture conditions (Barney *et al.*, 2009). Similar to mallow, switchgrass also provides important ecosystem services, including erosion mitigation, and habitat and shelter for birds and small mammals (USDA NRCS, 2012).

As previously discussed, the Eastern Shore of Virginia is located in a hotspot of sea-level rise, making it a prime location for studies of the processes occurring in coastal environments undergoing community change. In areas that are experiencing a transition between ecosystem states driven by increased flooding, interactions between species can have a significant effect on the plant community. Lenssen *et al.*, (2004) found that longer flooding durations initially decreased competition, affecting both strong and weak competitors equally. A model proposed by Holmgren et. al. (1997) demonstrated that changes in water availability may shift interactions from competitive to facilitative or vice versa. There is a growing interest among ecologists to identify plant communities with built-in resilience, that is, a species composition that will persist in the face of sea level rise (Zedler, 2010).

Plant community composition results from a combination of positive and negative interactions among co-occurring plant species. The role of competition (negative interactions) in succession and community establishment is well documented within the literature for many plant communities (Bertness & Shumway, 1993; Brooker *et al.*, 2008; Brooker & Callaghan, 1998; Callaway & Walker, 1997; Connell & Slatyer, 1977; Hacker & Gaines, 1997; Holmgren *et al.*, 1997; Lenssen *et al.*, 2004; Merlin *et al.*, 2015; Sorrell *et al.*, 2012; Tilman, 1997). Co-cropping, or intercropping, is the process of growing two or more plant species simultaneously and has been extensively studied in agricultural and upland areas (Anil *et al.*, 1998 and the references therein). Similarly, plant-plant interactions of wetland species monocultures and mixed cultures along gradients of environmental disturbance have also been studied (Bertness, 1991; Luo *et al.*, 2016; J. Zhou *et al.*, 2018). However, I am not aware of any studies that focus on the eco-interactions of species from different habitats, for example, salt marsh mallow, a native species to coastal wetlands, and switchgrass, a common upland species.

As discussed in Chapter 2, an increase in the frequency of flooding events, whether from heavy precipitation or tidal flooding, is expected to promote plant community change from old-field to high marsh species (Brinson *et al.*, 1995). Wetland-adjacent agricultural fields will experience some rate of degradation as a result of the shifting hydrological regime under accelerated rates of sea-level rise. Planting flood-tolerant species could mitigate the effects of increased frequency of inundation and prolong a field's agricultural utility, while simultaneously allowing for the natural process of transition from upland fields to high marsh thus optimizing the tradeoffs between agriculture and the conversion to marsh.

As a native wetland species, mallow is considered to be more flood-tolerant than switchgrass. However, to my knowledge, the interaction of the two species under increased soil moisture conditions has not been well studied. One study examined the effect of waterlogging on *K. pentacarpos* seedlings and found higher rates of mortality associated with alternations of organelles (J. Zhou *et al.*, 2011). Another found evidence of a negative effect of waterlogging on *K. pentacarpos* performance (Corli *et al.*, 2023). To fill the knowledge gap pertaining to the suitability of cultivating mallow or switchgrass in old fields experiencing frequent inundation, it is critical to examine the tolerance of both species to variations in soil moisture. Therefore, a field experiment was carried out to determine the effect of increased soil moisture on the establishment of *K. pentacarpos* and *P. virgatum* in monocultures and mixed cultures. I hypothesized that mallow would outcompete switchgrass in the wet plots and switchgrass would outcompete mallow in the dry plots, regardless of the original seeding ratios. The outcome of this experiment will help improve the knowledge of the impact of freshwater inundation events on two species recommended for cultivation in old fields amid ecological transition.

4.3. Methods

4.3.1. Plant Materials

Salt marsh mallow seeds (*Kosteletzkya pentacarpos*) used for this experiment were collected from local, native populations on Virginia’s Eastern Shore. Seeds of switchgrass var. Alamo was purchased from a commercial seed source (Hancock Seed & Company, Inc., Dade City, FL USA). The Alamo cultivar was selected for its salinity tolerance and high biomass production (Hu *et al.*, 2015; J. Kim *et al.*, 2016; Liu *et al.*, 2014, 2015). Study site

The study was carried out on the Delmarva Peninsula at the Nature Conservancy’s Brownsville Preserve (located at 37.472318°N, 75.827455°W, https://goo.gl/maps/fTirW6yNvTPyVpBX7) which is near Nassawadox, Virginia. The Delmarva Peninsula extends from Delaware Bay southward along the seaside coast of Maryland to the mouth of the Chesapeake Bay in Virginia; it is bordered on the west by the Chesapeake Bay and on the east by the Atlantic Ocean (Figure 22).

The study site is situated in an upland field that is separated from a tidal creek and surrounding salt marsh by a failed dike system. The study site is flat with little topographic relief except for an irrigation pond built in the middle of the field (Figure 5). Excluding that pond and its mounded sides, and some depressions near the dike, elevations range from 0.65 m above msl at the edge of the field near the marsh to 1.37 m above msl near the road that provides a southern boundary of the field. The gentle slope across the field from north to south is approximately 0.9%.

4.3.2. Experimental Design

An 11 m x 7 m area was cleared and lightly tilled to remove the existing aboveground plant cover (Figure 23). The cleared area was divided into eight blocks of five 1 m x 1 m plots for a total of 40 experimental plots. One meter buffer separated each plot from neighboring plots and the surrounding community. Each block was assigned a watering treatment – wet or dry. Each of the five plots within a block was assigned one of five seeding ratios – 100% marsh mallow (*K. pentacarpos*), 75% marsh mallow and 25% switchgrass (*P. virgatum*), 50% marsh mallow and 50% switchgrass, 25% marsh mallow and 75% switchgrass, and 100% switchgrass.

The monoculture plots of *K. pentacarpos* were planted with 3.65 g of seed (~250 seeds m^{-2}) based on previous field experiment success. The monoculture plots of *P. virgatum* were planted with 0.56 g of seed based on the recommended seeding rate for switchgrass of 5 lbs $acre^{-1}$. All other seeding ratios were calculated based on the appropriate seeding rate for the species (Table 10). Seed mixtures were broadcast over the appropriate plots on May 29, 2019. All plots were watered by hand at the time of planting. Each plot received 3.8 liters of water dispersed from a standard watering can with a shower spray nozzle.

A gravity-fed irrigation system delivered the watering treatment. A 100-gallon (378-liter) cattle trough was placed on a 2.5-meter tall platform. A hole was drilled in the base of the trough to connect a 1 ½ inch (3.81 cm) PVC pipe that ran from the top of the tower to the ground surface and then branched into eight 0.45 m segments spanning the length of each block of five plots (two per plot) (Figure 23). Three holes were drilled on alternating sides of the PVC pipe as it passed through each plot within the block. On average, the irrigation system delivered 19 liters of water over 45 minutes to an hour to each plot. Beginning June 26, 2019, the wet treatment blocks were watered weekly until September 14, 2019. The dry plots received only rainwater; no supplemental water was added. Percent volumetric moisture content was measured in each plot using a Spectrum FieldScout TDR 300 soil moisture meter before and after each watering treatment. Average soil moisture measurements for each plot were calculated from the five measurements taken randomly in each plot.

4.3.3. Elevation

A detailed topographic survey of the study area was conducted using GPS Real Time Kinematic (RTK) measurements from high-resolution benchmarks established previously at Upper Phillip’s Creek in 1997 (BROWNSVILLE (+37° 27’ 38.4985028, -75° 50’ 4.961264)). All VCR permanent benchmarks are referenced to VCR1 (+37° 17' 42.156630", -75° 55' 59.492560", elevation = 8.7000 m), which is a benchmark that is part of the High Accuracy and Resolution Network (HARN). After the installation of VCR1, corrections were applied to the original data using the GEOID93 model and the GEOID12A model (Thomas & Carlson, 1999). Elevations in Figure 24 are based on this single point (VCR1) and referenced to NAVD88 where a value of zero corresponds to msl. Elevation was measured in each corner and the center of every plot (n=40) using Trimble R7 and Trimble R10.2 RTK survey equipment.

4.3.4. Percent Cover

Percent cover by species was estimated visually in each 1 m x 1 m plot. Because species cover was estimated independently, the total percent cover of all species could exceed 100% (Tilman, 1997). Percent cover by bare soil was also determined for each subplot. On June 15, 2019, seedlings were counted and classified by species (Table C 1). On July 24, 2019, the percent cover of the plots was measured and classified into four categories – salt marsh mallow, switchgrass, other, and bare (**Error! Reference source not found.**). Given the short time between planting and the July cover measurement, it was difficult to discern between switchgrass seedlings and other native grass species. Therefore, the percent cover measurement for switchgrass on July 24, 2019, may only be a measure of the total grass species cover.

On September 14, 2019, the final measurement of percent cover was recorded, and species cover was categorized into five categories – salt marsh mallow, switchgrass, grass, other, and bare. The relatively high percent cover of other grass species supported the idea of misidentification of switchgrass in the initial cover measurement on July 24, 2019. To account for this issue, the percent cover of switchgrass and grass on September 14, 2019, was summed and the average percent cover for switchgrass and grass was calculated to identify an adjustment rate for switchgrass (0.36) and other grass species (0.64). The switchgrass cover for July 24, 2019, was then multiplied by 0.36 and 0.64 to get the adjusted cover for switchgrass and other grass species, respectively. This measure of percent cover was used as the covariate in the statistical analysis.

To determine the change in percent cover from July 24 to September 14, 2019, the difference between the final percent cover for a given species or group and the adjusted initial cover was calculated.

4.3.5. Statistical Analysis

To determine if the addition of water made the plots wetter, paired t-tests were conducted using Microsoft Excel Data Analysis Tools. The effect of adding water was considered significant if $P>0.05$.

The effect of watering on species cover was analyzed by a split-plot analysis of variance with a covariate using Statistical Analysis Software version 9.4 (SAS Institute Inc., NC, USA). The analysis used the proc mixed procedure with species percent cover as the dependent variable, the watering treatment as a fixed effect, species base cover as measured on July 24, 2019, as a covariate, and a nested effect of block within the water treatment as a random effect. Main effects and interactions were considered significant if $P<0.05$.

4.4. Results

The results of this field experiment, described in detail below, indicate that there was a clear effect of watering on the soil moisture. However, no significant effect of watering on individual species cover was detected, although there were clear differences in establishment and growth response to increased soil moisture for both species. These differences are likely to affect the success of the two species under changing hydrologic conditions observed at the Brownsville field study site.

4.4.1. Elevation

The elevation across the plots was fairly uniform, ranging from 1.0 m to 1.10 m above msl (Figure 24). Elevation differences were negligible among the experimental plots and did not have an effect on soil moisture differences among or within blocks.

4.4.2. Soil Moisture

By measuring soil moisture throughout the experiment, it was confirmed that there was a significant effect of watering ($P<0.05$) in that adding water to the wet plots did increase the soil moisture (Table 11, Figure 25, Figure C 2). Average soil moisture was higher in the wet blocks than in the dry plots (Table 11, Figure C 2). Soil moisture increased after watering in the wet plots, and either stayed the same or decreased in the dry plots (Figure 25). This confirms that the experimental addition of water to the plots raised the soil moisture content of the soil (Table 11).

Annual precipitation for Northampton County in 2019 was 114.45 cm, slightly higher than the annual average of 107.44 cm (National Centers for Environmental Information, 2023). However, the summer of 2019 (June to September) had less precipitation (37.31 cm) than expected when compared to the average precipitation for those months (41.66 cm) (National Centers for Environmental Information, 2023). Three precipitation events coincided with scheduled watering treatments on July 24, August 5, and September 10, 2019 (Figure C 2) The rain events on July 24 and September 10, 2019, (8.25 cm and 6.5 cm of precipitation, respectively) resulted in standing water on the surface of the plots; consequently, the wet plots were not watered on these dates as planned. These precipitation events resulted in high soil moisture in all blocks (Figure C 2).

4.4.3. Percent Cover

Initial plant counts and percent cover were done on June 15, 2019 (Table C 1). Salt marsh mallow was present in all plots where it was planted. Switchgrass was present in all but five plots, even in the plots designated as monocultures of mallow. Percent cover was measured twice more on July 24, 2019, and September 14, 2019 (Figure 26). The July 24, 2019 cover was highly correlated with the final percent cover and represented a significant effect of the seeding ratio on the final percent cover of the plots for both *K. pentacarpos* and *P. virgatum* (Table 12, $F_{1,31}= 124.83$ and $17.58, P=<0.0001$ and 0.0002, respectively).

Switchgrass percent cover was higher in the dry plots than in the wet plots, while salt marsh mallow had a higher percent cover in the wet plots than the dry plots (Table 13). However, water had no effect on switchgrass cover ($F_{1,31}=17.58, P=0.3781$) and only a marginal effect on salt marsh mallow cover ($F_{1,6}=4.62, P=0.0751$) (Table 12). Because of the marginal effect of water in the analysis of covariance, interaction plots were graphed to examine the degree to which water may affect salt marsh mallow cover (Figure C 2). These graphs suggest that the addition of water does have a marginally positive effect on *K. pentacarpos* percent cover.

Overall, salt marsh mallow cover increased or stayed the same in the dry plots but always increased in the wet plots where it was planted (Figure 28) from July 24 to September 14, 2019. Over that same time, switchgrass cover tended to increase in the dry plots but decrease in the wet plots (Figure 27). When switchgrass was present in plots planted with 100% mallow seed, switchgrass percent cover also decreased between the initial and final measurements of percent cover (Figure 27). In the 50/50 mixed croppings of *K. pentacarpos* and *P. virgatum*, both mallow and switchgrass increased in the dry plots, however, mallow increased almost twice as much in the wet plots while switchgrass decreased after two months (Figure 27).

4.5. Discussion

The addition of water always increased the soil moisture content of the wet plots (Table 11, Figure 25, Figure C 2) However, the magnitude of the increase in the wet plots varied depending on the amount of rainfall immediately preceding an event. On September 10, 2019, 6.5 cm of rainfall was measured and saturated the soils as evidenced by standing water on the surface. The effect of this precipitation event persisted at least until September 14, 2019. During this time, measurements of volumetric moisture content exceeded 100% (Figure C 2). Because the soil was saturated, the watering treatment had a negligible effect on the moisture content of the wet plots (Table 11, Figure C 2). Based on the observations of the changes in the hydrology of the groundwater (Chapter 2), it is expected that the frequency of events resulting in increased soil moisture, either from flooding or poor soil drainage due to elevated water tables, will extend the duration of waterlogged conditions when compounded by more frequent, large precipitation events.

The habitats where mallow and switchgrass are likely to establish and grow are a reflection of their tolerance to higher soil moisture conditions. Corli *et al.* (2023) reported that *K. pentacarpos* does not perform well in flooded soils. This is contrary to personal observations of salt marsh mallow growing in saturated and frequently flooded soils in native high marsh habitats. This discrepancy is interesting in the context of the findings of this experiment where there was only a marginal effect of watering on the final percent cover (Figure 26, Figure C 2). Overall, when the higher percent cover of salt marsh mallow in the wet plots is compared to the dry plots, it appears that *K. pentacarpos* does benefit from the addition of supplemental water. Nonetheless, as the frequency and duration of flooding with seawater increases, mallow growth will be limited (Corli *et al.*, 2023).

Zhou *et al.* (2011) reported that *K. pentacarpos* had higher rates of mortality when experiencing prolonged periods of flooding and waterlogged soils. Periodic or prolonged periods of anoxia or hypoxia can have negative effects on the roots and rhizomes of plants resulting in decreased growth and performance (Corli *et al.*, 2023; Yordanova *et al.*, 2003). In the case of an extreme tide or high precipitation event, water may pond in areas of the field. Coupled with poor drainage from elevated water tables (Chapter 2), the ponded water may stress plants and restrict growth and various developmental processes including seed germination, vegetative growth, and reproduction (Blum & Christian, 2004; Pan *et al.*, 2021). When considered with the results of this study, mallow growth may be enhanced under more frequent flooding conditions initially, but growth will eventually be diminished depending on the timing and frequency of flooding events. The response of *K. pentacarpos* to these kinds of environmental changes will be further discussed in Chapter 5.

Switchgrass cover changed very little over the course of the experiment (Figure 27). This suggests that watering had no effect on switchgrass cover as it relates to establishment, survival, and growth. This is similar to the results discussed in Chapter 3 where watering with three different levels of salinity had no significant effect on the growth of switchgrass. A study of the effect of increased soil moisture conditions on transplants of switchgrass showed that some lowland ecotypes of *P. virgatum* produced more total biomass under higher soil moisture conditions (Barney *et al.*, 2009). However, Barney *et al.* (2009) conducted a greenhouse experiment, which may explain the difference in results between their study and the one reported here. Forero et. al. (2019) compared the results of greenhouse and field experiments measuring plant-soil feedbacks and found that greenhouse measurements appeared to overestimate field measurements of plant-soil feedbacks. Thus, it is reasonable to conclude that my findings differed from those reported by Barney *et al.* (2009) due to the difference in results between greenhouse and field experiments when examining plant community dynamics such as succession, abundance, coexistence, and species richness (Forero *et al.*, 2019 and the citations therein).

To my knowledge, there have been no studies of the soil moisture tolerance of switchgrass in a field experiment with co-cropping conditions. It is also possible that the length of both my greenhouse (4 months) and field experiment (5 months) was not enough time for the plants to establish. Furthermore, higher rates of establishment as demonstrated by percent cover in the field experiment, supports the idea that allowing more time for species establishment should have a positive impact on the establishment of *P. virgatum*.

The higher cover of salt marsh mallow relative to switchgrass within the monoculture treatments (Figure 26) and the marginally significant effect of water on *K. pentacarpos* cover (Table 12, Figure C 2) suggests that soils do not necessarily need to be saturated to favor mallow and that even a small increase in soil moisture can have a positive effect on establishment.

This study detected no evidence of a positive or negative interaction between salt marsh mallow and switchgrass. My finding is similar to those of Corli *et al.* (2023) who were unable to conclusively demonstrate evidence of competition between *K. pentacarpos* and co-existing species under varying soil moisture regimes. Regardless of the mixed-culture treatment, mallow cover was higher than switchgrass in both the wet and the dry plots (Figure 26). This may be the result of the difference in growth rates and lag time to linear growth between the two species reported in Chapter 3. The length of this experiment may not have allowed enough time for species establishment as plant community dynamics may vary between greenhouse and field experiments (Forero *et al.*, 2019). Alternatively, the higher percentage of salt marsh mallow relative to switchgrass in the monoculture treatments suggests that soil moisture may be more important than competition. Another study found that the interactions between species competition and flooding could result in changes in species abundance, however, the response was species-specific (Lenssen *et al.*, 2004). Poor establishment of switchgrass in my experiments does not allow me to distinguish between the effects of flooding or competition on the percent cover for *K. pentacarpos* or *P. virgatum*.

As coastal agricultural fields begin to experience increased frequency of flooding and prolonged periods of waterlogged soils, the ability of *K. pentacarpos* and *P. virgatum* to germinate and grow under elevated soil moisture conditions will be important for land management decisions. Mallow may be favored for cultivation in low-lying coastal fields because of its enhanced growth under increased soil moisture. Mallow's enhanced growth under wetter soil conditions provides evidence to suggest that it will establish more quickly in wet areas than switchgrass. While this work does not provide evidence to suggest either a beneficial or detrimental interaction of the species, it does support the ability of the two species to coexist, at least initially. This would allow land owners and managers to co-crop two potential salt-tolerant crops (Gallagher, 1985) could extend the economic viability of degraded farmland and retain important ecosystem services during the process of inland marsh migration into abandoned agricultural fields.

However, the lack of a developed market for the production and sale of alternative crops like *K. pentacarpos*, prevents farmers from utilizing these plants on a commercial scale. A more attenable option would be to cultivate mallow as a buffer crop in areas that are too wet for traditional crop cultivation. Planting perennial buffer crops like salt marsh mallow and switchgrass has the ability to boost carbon sequestration and nitrogen retention by 50% due to greater root depths and longer growing seasons (Glover *et al.*, 2007; Tolbert *et al.*, 2000). Perennial plants have the ability to store carbon in two ways, first in their plant structures that persist year to year, like roots, and secondly, in the creation of soil organic matter (Parrish & Fike, 2005) The accumulation of carbon and nitrogen in an upland field is a necessary precursor to the transition from upland to high marsh ecosystems (Brinson *et al.* 1995). Planting mallow in buffers or on degraded land may facilitate this transition while providing additional environmental and economic benefits (Figure 1).

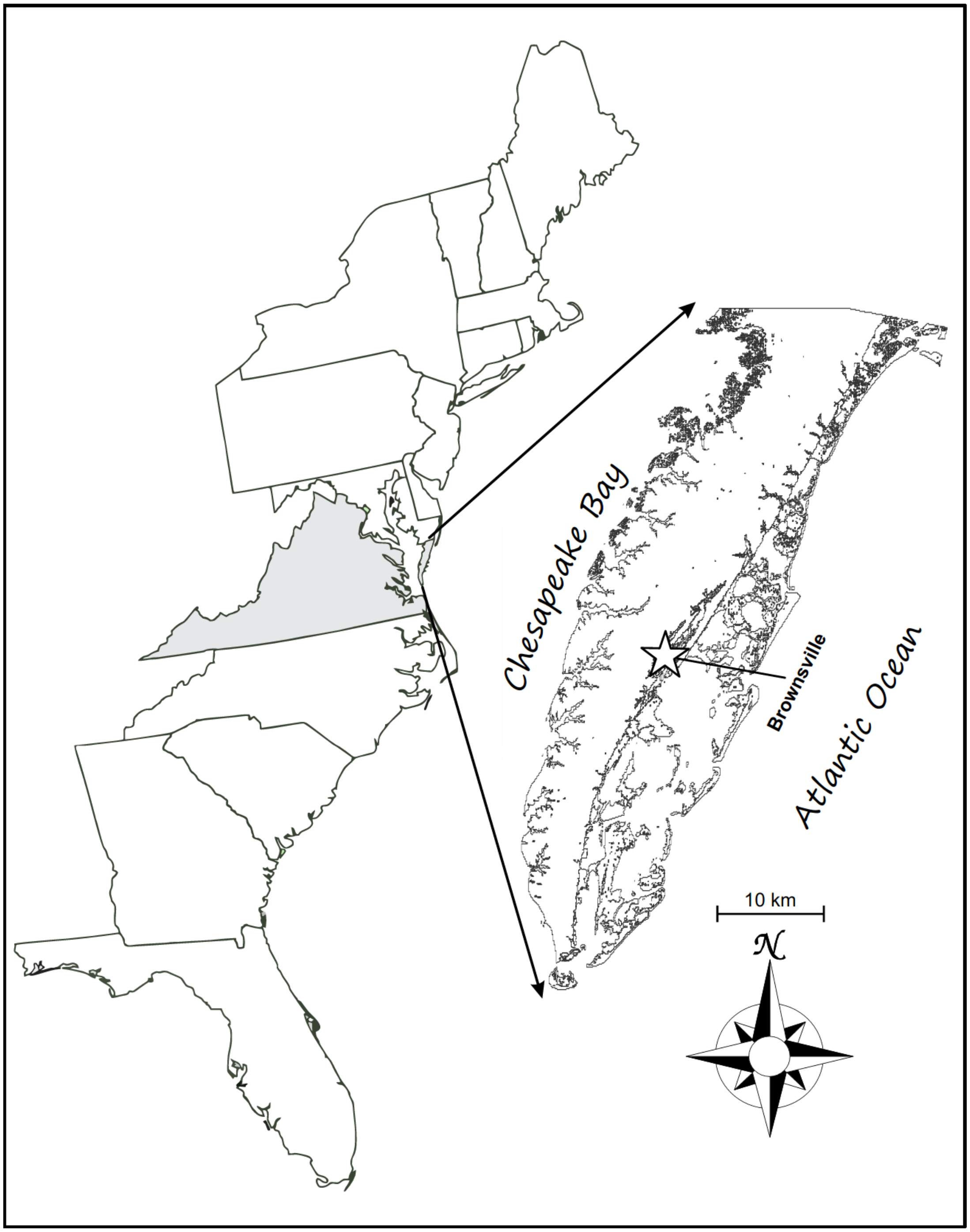


Figure 22. Brownsville Preserve field site location on the Eastern Shore of Virginia.

Table 10. Seeding treatment and corresponding target seed weights for salt marsh mallow (*Kosteletzkya pentacarpos*) and switchgrass (*Panicum virgatum*).

Seeding treatment	Mallow %	Mallow (g)	Switchgrass %	Switchgrass (g)
1	100	3.65	0	0
2	75	2.74	25	0.14
3	50	1.83	50	0.28
4	25	0.913	75	0.42
5	0	0	100	0.56

Figure 23. Water tower and irrigation system for the field experiment at the Brownsville Preserve in Nassawadox.

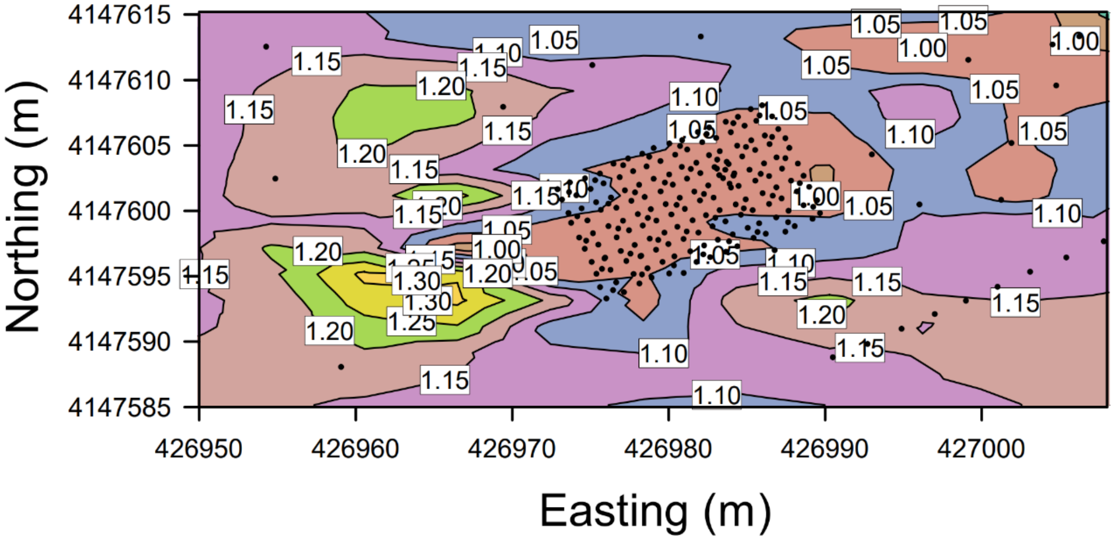


Figure 24. Topographic map of elevation relative to msl (NAVD 88) for the study area and surrounding field. Elevation ranges from 1-1.10 m above msl within the area of the experimental plots.

Table 11. Paired T-test means and p-values for measured percent volumetric moisture content (%VMC). Dashes represent days when no observations were made.

Date	**DRY**			**WET**		
	Pre (%VMC)	**Post (%VMC)**	***p-value (α=0.05)***	**Pre (%VMC)**	**Post (%VMC)**	***p-value (α=0.05)***
6/26/2019	-	-	-	81.298	101.638	*1.885E-07*
7/2/2019	65.0624	61.036	*0.0099374*	66.056	95.544	*7.707E-09*
7/11/2019	-	-	-	-	-	-
7/16/2019	75.659	71.257	*0.0222765*	73.139	88.828	*1.639E-08*
7/24/2019	-	-	-	-	-	-
7/30/2019	-	-	-	55.698	68.551	*1.209E-06*
8/5/2019	-	-	-	56.689	69.526	*4.998E-07*
8/13/2019	52.773	51.831	*0.6291497*	45.912	67.97	*1.884E-07*
8/27/2019	57.343	58.189	*0.6860455*	44.672	66.488	*3.371E-08*
9/3/2019	59.795	54.315	*0.017097*	43.516	58.828	*1.034E-07*
9/10/2019	-	-	-	-	-	-
9/14/2019	134.937	133.944	*0.5918359*	129.633	133.377	*0.0385276*

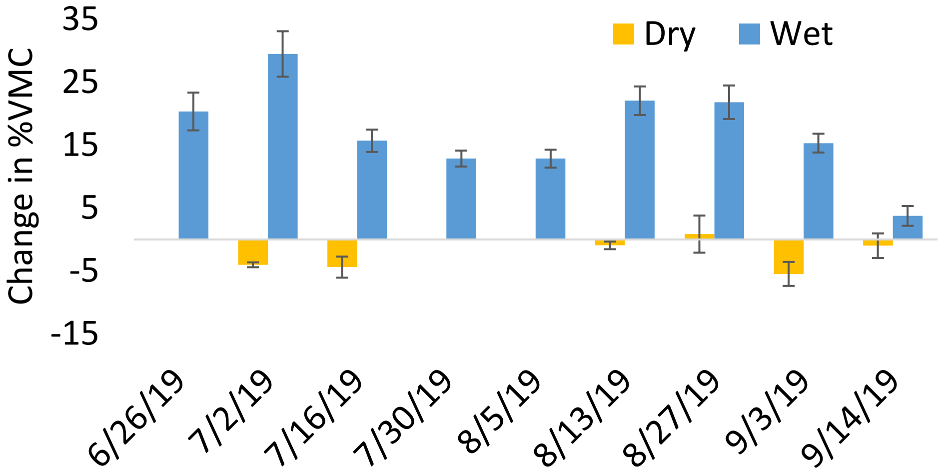


Figure 25. Average change in percent volumetric moisture content (%VMC) pre- and post-watering. Blue bars indicate the change in moisture content in the wet treatment plots. Gold bars indicate the change in moisture content in the dry treatment plots. Each bar is the mean of 20 plots. Error bars show standard error. Refer to Appendix for additional detail on each sampling date and plots.

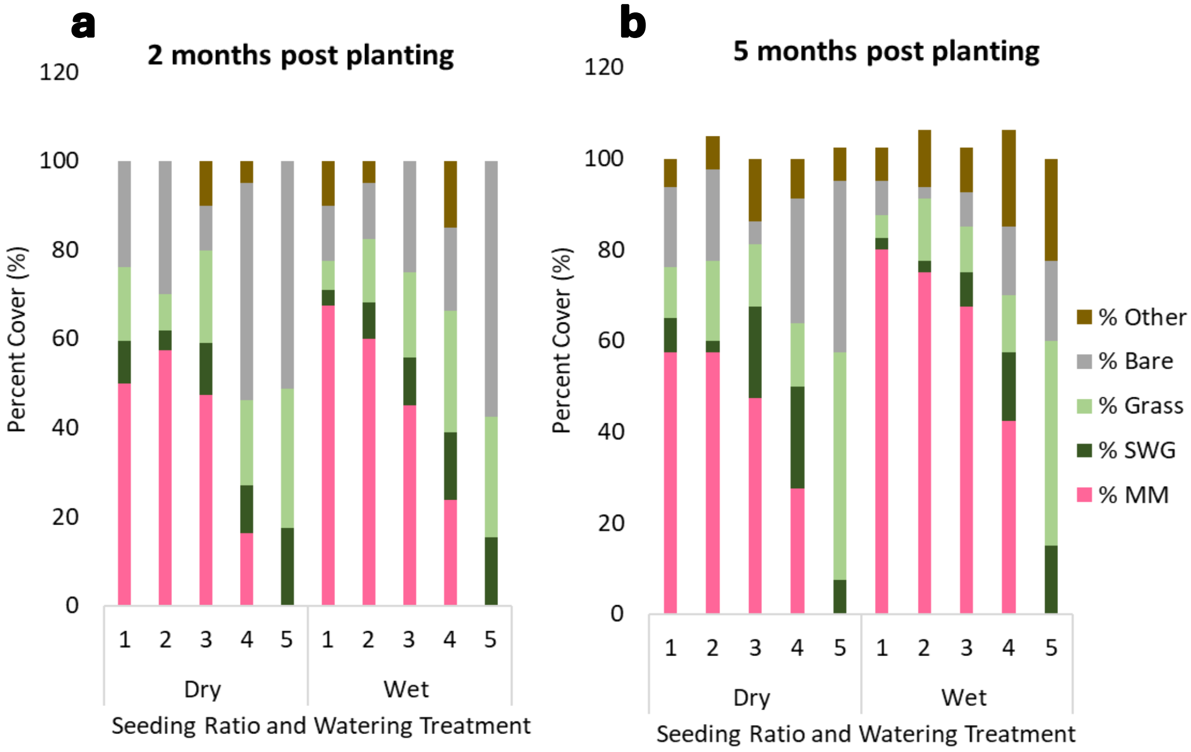


Figure 26. Percent cover (a) 2 months post planting on July 24, 2019, and (b) 5 months post planting on September 14, 2019. Cover was measured for 5 categories – *Kosteletzkya pentacarpos* (MM), *Panicum virgatum* (SWG), other grass species (Grass), bare, or other forbes and shrubs (other) for the wet and dry blocks, and for 5 seeding mixtures where 1= 100% MM, 2=75% MM, 25% SWG, 3=50% MM, 50% SWG, 4=25% MM, 75% SWG, 5=100% SWG.

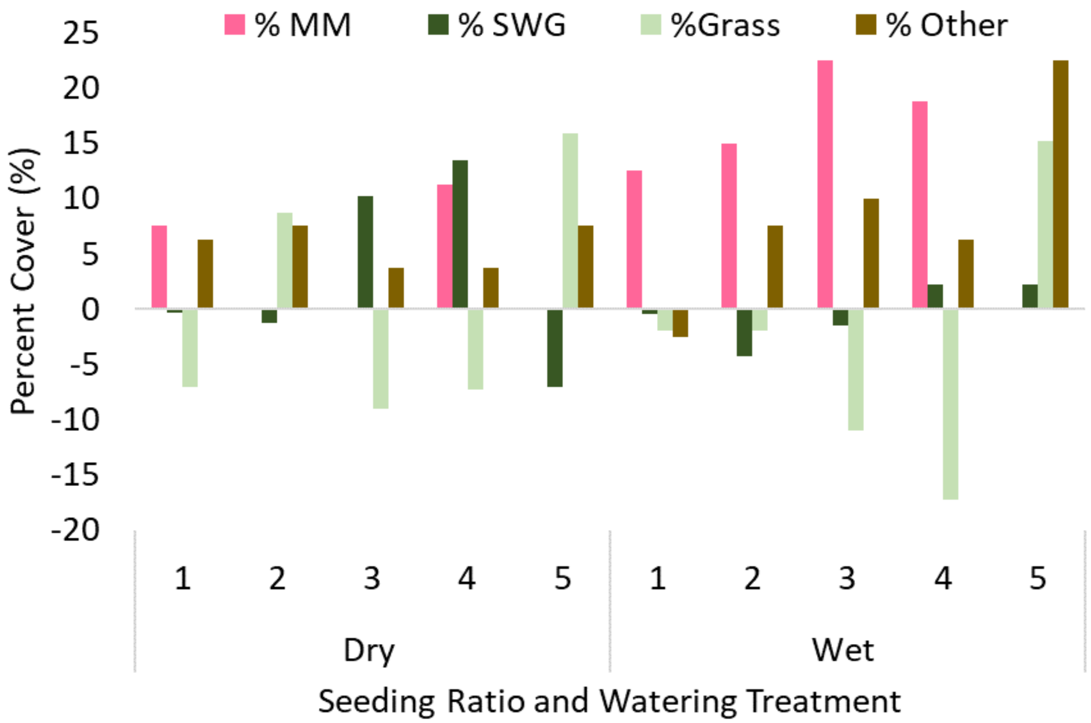


Figure 27. Change in the percent of plant cover between July 24 to September 14, 2019 for *Kosteletzkya pentacarpos* (MM), *Panicum virgatum* (SWG), other grass species (Grass), and other forbes and shrubs (Other) for the wet and dry blocks and the seeding mixtures where 1= 100% MM, 2=75% MM, 25% SWG, 3=50% MM, 50% SWG, 4=25% MM, 75% SWG, 5=100% SWG.

Table 12. Analysis of covariance statistics for the effects of watering and initial percent cover (base cover) on the percent cover of K. pentacarpos and P. virgatum; (α=0.05).

n=40	Effect	Num DF	Den DF	F Value	p-value
K. pentacarpos	water	1	6	4.62	0.0751
	base cover	1	31	124.83	<.0001
P. virgatum	water	1	6	0.91	0.3781
	base cover	1	31	17.58	0.0002

Table 13. Least squares means for species K. pentacarpos and P. virgatum percent cover in the dry and wet treatments.

n=40	Treatment	LS Means	Std Err	DF
K. pentacarpos	Dry	40.3713	3.3667	6
	Wet	50.6287	3.3667	6
P. virgatum	Dry	11.9261	2.4914	6
	Wet	8.5739	2.4914	6

Chapter 5.

Effect of disturbance and salt marsh mallow (*Kosteletzkya pentacarpos*) establishment on plant community composition of an old field

5.1. Abstract

Salt marsh mallow (*Kosteletzkya pentacarpos*) has been identified as a promising species for facilitating high marsh development in agricultural fields impacted by sea level rise. In 2015, locally collected mallow seeds were planted in an abandoned agricultural field experiencing frequent flooding with salt water. Plots (2 x 6 m) were established and divided in half with the midline marking the furthest expansion of *Distichlis spicata* communities in the field. One of four treatments was assigned to each half-plot without native marsh species and replicated in a three-block design. Treatments included tilled, tilled and drilled with *K. pentacarpos*, tilled and broadcasted with *K. pentacarpos*, and undisturbed control plots. Percent cover was measured at the end of the growing season. Observations of plant community composition focused on changes in the abundance of high marsh species, transition species, upland species, and *K. pentacarpos*. One year after the beginning of the experiment, the community composition was dominated by native grass populations, including *Panicum virgatum*. After two years, the percent cover of high marsh species, including *D. spicata*, and transition species, including mallow, increased in all treatment plots. Disturbance of the native plant community by tilling increased *D. spicata* cover in the experimental plots one year after the initial treatment. Changes in hydrological conditions in response to seawater flooding in three distinct zones within the field resulted in different plant communities. These results suggest that growing mallow in salinized agricultural fields may improve the natural recruitment of high marsh and transition plant species in coastal agricultural land experiencing sea-level rise.

5.2. Introduction

Accelerating rates of sea-level rise are resulting in the conversion of coastal agricultural land to salt marsh. The process of inland migration of coastal wetlands into farmland is starting to receive more attention (Fagherazzi *et al.*, 2019a; Gedan *et al.*, 2020; Gedan & Fernández-Pascual, 2019; Gewin, 2018; Tully *et al.*, 2019). Titus *et al.* (2010) estimated that Virginia loses 192 hectares of cropland to salt marsh annually. During the conversion of cropland to marsh, novel plant communities emerge as soils experience increasing frequencies of flooding due to sea-level rise (Gedan & Fernández-Pascual, 2019; Janousek & Folger, 2014).

The frequency and duration of storms, high tides, and extreme precipitation events can influence the timing of land conversion (Chapter 2). The impact of sea-level rise and storms varies across spatial and temporal scales in coastal uplands resulting in a cycle of chronic and acute environmental changes that drive plant community shifts (Brinson *et al.*, 1995; Fagherazzi *et al.*, 2019a; Guimond & Michael, 2021). Specifically, higher ground-water elevation and salinity will result in a shift from typical upland and old-field plant species to more flood- and salt-tolerant transition and high-marsh species (Allison, 1996; Brinson *et al.*, 1995; Hmieleski, 1994; Janousek & Folger, 2014). Temporal assessment of plant communities is the most effective way to document ecosystem shifts and understand land cover transitions, although, many studies use space-for-time substitutions (Pickett, 1989).

Anisfeld *et al.* (2017) used a space-for-time substitution experiment to examine the process of inland marsh migration into upland areas that were forest or lawn by assessing both biotic and abiotic indicators, including soil redox and salinity. They found that the location of the border between upland and marsh varied depending on which variable was examined and that different elements of marsh structure and function were likely to appear at different times based on elevation. Additionally, Anisfeld *et al.* (2017) reported changes to the plant community before changes in groundwater occurred. They suggested that individual storm events drove changes in species composition rather than edaphic conditions. Although analysis of the ground-water levels at the Brownsville study site did not show any diurnal tidal signal, salinization of ground-water by storm-surge flooding suggests storms can be important drivers of plant community change at Brownsville (Chapter 2).

While environmental disturbances change abiotic conditions, land managers also use disturbances such as tilling, mowing, burning, or herbicide application as a means of facilitating the establishment of desired species (Wheeler *et al.*, 2015 and citations therein). Bet-hedging approaches, such as tilling, may increase the success of restoration efforts in areas experiencing environmental unpredictability (Doherty & Zedler, 2015). Tilling can reduce competition from established plants and the seed bank and create open sites for new species establishment (Pywell *et al.*, 2002, 2007; Wheeler *et al.*, 2015; Wilson & Tilman, 1991). For example, native species richness and cover were increased in old fields when combining tilling and the addition of seeds of desired species when compared to other methods used to reduce pre-existing plant communities (Wheeler *et al.*, 2015). When applied to old fields, a combined approach of tilling and planting native species may speed up the conversion of upland to salt marsh plant communities.

Another management practice for restoration is the introduction of new species, especially nurse plants, to a plant community (Bertness & Callaway, 1994; Connell & Slatyer, 1977; Lundberg *et al.*, 2000; Wheeler *et al.*, 2015). The presence of a nurse plant species can facilitate the growth and establishment of other species by ameliorating environmental stress that would otherwise limit survival (Bertness & Hacker, 1994; Brooker *et al.*, 2008; Callaway & Walker, 1997; Egerova *et al.*, 2003; Filazzola & Lortie, 2014 and citations within; Padilla & Pugnaire, 2006; Voutsina, 2012). Nurse plants are also considered keystone species for their role in structuring communities (Filazzola & Lortie, 2014). Voutsina *et al.* (2015a) found that the presence of *Kosteletzkya pentacarpos,* a native high marsh species, improved the recruitment of two other native marsh species, *Spartina patens* and *Baccharus halimifolia*, without negatively affecting species richness, which suggests the potential for marsh mallow to serve as a nurse plant in coastal old fields.

The goal of this study was to test if planting salt marsh mallow in a coastal old field experiencing sea-level rise increases the recruitment of common marsh-upland transition species or high-marsh species into the upland plant community through a five-year study of plant community cover. Changes within the plant community can be an early sign of community transition to salt marsh (Anisfeld *et al.*, 2017; Brinson *et al.*, 1995). Specifically, I asked 1) if tilling the soil would facilitate the recruitment of transition species and/or high-marsh plant species, and 2) if seeding by either drilling or broadcasting in tilled plots would result in communities with similar composition at the end of the experiment. Understanding the interaction of the abiotic drivers of community change (*i.e.*, increased flooding and higher groundwater salinity) and management approaches to preserve ecosystem services will be important to land owners and managers in coastal areas.

5.3. Methods

5.3.1. Study Site

The study was carried out on the Delmarva Peninsula at the Nature Conservancy's Brownsville Preserve (located at 37.472318°N, 75.827455°W, https://goo.gl/maps/fTirW6yNvTPyVpBX7) which is near Nassawadox, Virginia. The Delmarva Peninsula extends from Delaware Bay southward along the seaside coast of Maryland to the mouth of the Chesapeake Bay in Virginia; it is bordered on the west by the Chesapeake Bay and on the east by the Atlantic Ocean (Figure 22).

The study site is situated in an upland field that is separated from a tidal creek and surrounding salt marsh by a failed dike system. The study site is flat with little topographic relief except for an irrigation pond built in the middle of the field (Figure 5) Excluding that pond and its mounded sides, and some depressions near the dike, elevations range from 0.65 m above msl at the edge of the field near the marsh to 1.37 m above msl near the road that provides a southern boundary of the field. The gentle slope across the field from north to south is approximately 0.9%.

5.3.2. Experimental Design

Three blocks of four 2 x 6 meter experimental paired plots were established in the field at Brownsville (Figure 28). To ensure that maximum variance within the plant community was captured, blocks were established approximately equidistant from a breach in the dike located near groundwater well 1 along three different compass directions (Figure 28). A line was walked approximately along cardinal directions (east, south, and west) until the community no longer contained *D. spicata*. Paired plots were established such that *D. spicata* was present in the undisturbed half of the plot, but had not yet spread into the experimental treatment half of the plot (Figure 29). The experimental portion of each paired plot was randomly assigned a treatment: 1) tilled, 2) tilled and drilled with *K. pentacarpos*, 3) tilled and broadcast with *K. pentacarpos*, or 4) left undisturbed (*i.e.* the treatment control).

Tilling is the agricultural practice of turning over the soil and disrupting the existing root system of the previous vegetation. Plots were tilled using a commercial landscape tiller (Model: LT118 manufactured by Caterpillar, Irving, Texas). Drilling is the seeding process of positioning seeds in a row and burying them to a uniform depth. Given the small plot size and limited availability of agricultural equipment, this process was done by hand using a garden hoe and string to dig the rows and cover the seed with 2.5 centimeters of soil. The method of broadcasting was used to mimic the natural seeding process of mallow and involves scattering the seed evenly across a specific area. Mallow seeds were sown using a hand-held broadcast spreader. An equal number of seeds (200) were drilled or broadcast in each plot (based on personal communication with J. Gallagher, University of Delaware). All mallow seeds were knicked before planting to increase germination efficiency (Poljakoff-Mayber *et al.*, 1994).

Recolonization of the unplanted tilled plots was allowed to occur by germination of seeds within the seed bank or clonal propagation by plants outside the plots, including the adjacent, undisturbed plots. Plots planted with *K. pentacarpos* were not weeded and colonization of plant species within the field occurred.

5.3.3. Percent Cover

Percent cover is commonly used as an estimate of species abundance (Tilman, 1997). Because species cover was estimated independently, the total cover of all species could exceed 100% (Tilman, 1997). Percent cover by bare soil or litter was also determined for each subplot. Measurements of cover were done each year between 2015 and 2019 in September when plant species diversity was highest. To estimate cover, each 2 x 3 meter half-plot was divided into six adjacent 1 x 1 meter plots that were visually examined to identify all plant species present and estimate the percent cover of each species in each 1 x 1 meter subplot. Species richness and relative abundance were estimated from the percent cover data.

5.3.4. Statistical Analysis

The effect of tilling and salt marsh mallow establishment and their interaction effects on the percent cover of wetland, transition, and upland plant species were analyzed by a repeated measures analysis of variance using Statistical Analysis Software version 9.4 (SAS Institute Inc., NC, USA). The analysis used the proc mixed procedure with species percent cover as the dependent variable; the plot treatment (undisturbed, tilled, tilled and drilled, or tilled and broadcast), sample year, and the plot treatment-year interaction as fixed effects; block and plot ID as random effects; and species base cover as a covariate. A repeated statement was used for the nested effect of plot ID within treatment. The analysis used a first-order autoregressive (AR(1)) correlation structure.

Main effects and interactions were considered significant if $P<0.05$. The percent covers of the undisturbed plots were used as a covariate to control for random effects. This analysis also assumed a fairly strong correlation between the percent cover from year to year. Post-hoc comparisons were conducted to determine if there was any effect of tilling (undisturbed v. all tilled) on percent cover or if there was a statistically significant difference in the effect of tilling or planting mallow (tilled v. drilled and broadcast) on percent cover.

5.4. Results

Plant community composition appeared to be uniform across the study site at the establishment of the experiment in 2015; however, later measurements of groundwater salinity showed that the communities in each block experienced different environmental conditions during this study (Chapter 2). The different environmental conditions included higher water table elevations, greater groundwater salinity, and more frequent and prolonged periods of flooding at the location of the proximal bloc. Water table elevations were lower, groundwater salinity decreased, and flood duration was shorter and less frequent at the medial block and even less at the distal block (Chapter 2).

5.4.1. All Blocks

5.4.1.1. *Percent Cover*

Tilling caused a disturbance in the plant community within the experimental plots that resulted in a species composition that differed from the undisturbed plots ($F_{1,31}=24.66, P=<0.0001$) (Table 14). However, no meaningful difference was observed between plots that were only tilled compared to the plots that were tilled and seeded with mallow ($F_{1,31}=0.25, P=0.6229$) (Table 14).

Tilling did result in low coverage of *D. spicata* in the tilled, drilled, and broadcast treatment plots in 2015, which then increased to a higher percentage in subsequent years compared to the undisturbed plot (Table 15, trt*year, $F_{12,30}=4.46, P=0.0004$) (Figure 30a). No treatment effect on *Phragmites australis* or the transition species group was observed (Table 14, Figure 30b, Figure 30c), even though there was a large increase in the coverage of the transition species in the broadcast treatment in 2019 (Figure 30c). Recall that *K. penatacarpos* is a transition species and was planted in the drilled and broadcast treatments; therefore mallow cover contributed to the transition species cover (Table 16, Figure 30c). All tilling treatments had a negative effect on the presence of upland species and switchgrass ($F_{3,31}=11.95, 8.24, P=<0.0001, 0.0004$, respectively) (Table 15, Figure 30c & Figure 30e). The effect of tilling on the upland group is likely due to the dominance of *P. virgatum* in the upland plant community (Table 16).

When the cover is compared between undisturbed and experimental paired plots, averaged across all blocks (Figure 31), there are three trends. First, mallow became an established part of the community where it was planted and persisted until the end of the study. In some cases, mallow colonized the undisturbed plots, spreading from planted populations over time (Figure 31). Second, in general, regardless of treatment, the abundance of transition species increased from 2015 to 2019 (Figure 31). Third, while some bare spots were observed in some plots throughout the experiment, they were a larger percent of the cover in the tilled, drilled, and broadcast plots at the end of the 2015 growing season, likely as a result of the tilling treatment. After 2015, bare soil was not an important cover class.

5.4.1.2. *Species richness*

In general, there was an increase in species richness in the experimental plots from 8 species in 2015 to 11 species in 2019 (Table 17). When new species colonized the plots, established species were not lost (Tabel 17). Instead, the relative abundance of the plant species shifted (Figure 31). A similar trend was observed in the undisturbed plots where species richness increased from 8 to 10 species from 2015 to 2019, and shifts in percent cover were observed (Table 17, Figure 31).

5.4.2. Proximal Block

The proximal block is located to the west of Well 1 (Figure 28) and has the lowest elevation of the three blocks (Figure 5). Here the groundwater was closest to the surface, experienced longer duration and more frequent flooding, and experienced the greatest change in groundwater salinity during the course of the experiments (Chapter 2).

5.4.2.1. *Percent Cover*

In these paired plots, tilling delayed colonization of high marsh species into the experimental plots (Figure 32). *D. spicata* was the only high marsh species present (Table 18) and generally accounted for 40% to 80% or more of the cover in the experimental half of the paired plots (Figure 32). *D. spicata* rapidly colonized the undisturbed control treatment although it was not present at the beginning of the experiment. By 2016, *D. spicata* cover caught up to the undisturbed experimental control and, in many cases, exceeded the cover in the undisturbed plots by 2019 (Figure 32).

Where mallow was planted, it was an important component of the transition species group in 2016 and 2017 (Figure 32, Table 18). *K. pentacarpos* cover declined from 2018 to 2019 (Table 18). *P. australis* was an equally important component of the transition group in the experimental plots and the dominant species in the undisturbed plots from 2015 to 2019 (Table 18). The most dominant species in the upland group was *P. virgatum* which was consistently between 11% to 40% of the community from 2015 to 2019 (Table 18).

5.4.2.2. *Species Richness and Abundance*

The proximal block had the highest abundance of *D. spicata* and the lowest relative cover of upland species across the three blocks (Table 18). The proximal block also had the fewest number of species present at the end of the study in 2019 (Table 18The high marsh species group included only one species, *D. spicata* (Table 18). There were six transition species present in the plant community throughout the study. Only three were present in the experimental half of the paired plots in 2019: *K. pentacarpos*, *P. australis*, and *Cyperus escuelentus* (Table 18). Of the four upland species observed in the plant community between 2015 and 2019, three were present in the experimental plots at the end of the study (Table 18).

5.4.3. Medial Block

The medial block is located to the south of Well 1 (Figure 28) and has an intermediate elevation compared to the other blocks (Figure 5, Chapter 2). Here the water table was farther from the surface, experienced shorter durations and less frequent flooding, and experienced a smaller change in groundwater salinity during the course of the experiments than the proximal block (Chapter 2).

5.4.3.1. *Percent Cover*

In the medial block, high marsh species cover was lowest in the experimental control half of the paired plot (Figure 33). In 2015, high marsh species accounted for less than five percent of the cover in the experimental plots (Table 19). Starting in year two (2016), *D. spicata* was the only high marsh species present and made up thirty to sixty percent of the plant community cover (Table 19, Figure 33). In the experimental control treatment, the upland plant group was the dominant group (Figure 33, Table 19).

Where *K. pentacarpos* was planted, it became an established part of the community after one year and spread to the undisturbed plots in year 3 (2017) (Figure 33). Mallow cover decreased from 2016 to 2019 in the drilled plots but increased in the broadcasted plots over the same period (Figure 33). Transition species cover increased from 2015 to 2019 in all undisturbed plots (Figure 33).

5.4.3.2. *Species Richness and Abundance*

In the undisturbed medial plots, the total number of species increased from 6 to 9 species from 2015 to 2019, while richness in the experimental plots increased from 5 to 10 species during the same time (Table 19). The medial block had the highest species richness in 2019 of all the blocks (Tables 18-20); the total number of species present in 2019 in the proximal, medial, and distal blocks was 7, 10, and 8 species, respectively.

When the average cover of each transition species (Tables 18-20) is summed for individual blocks, the total cover of transition species in the undisturbed plots was similar for the proximal (4.2) and medial blocks (4.4), and lower for the distal block (2.4). When the same is done for the experimental plots, the total cover of transition species was 7.2, 5.2, and 4.2 in the medial, proximal, and distal blocks, respectively.

5.4.4. Distal Block

The distal block is located to the east of Well 1 (Figure 28) and has the highest elevation of the three blocks (Figure 5, Chapter 2). Here the groundwater was furthest from the surface, experienced the shortest duration and least frequent flooding, and experienced the smallest change in groundwater salinity during the course of the experiments (Chapter 2).

5.4.4.1. *Percent Cover*

The bare class was a large percentage of the cover in the distal block in 2015 (Figure 34). High marsh species cover in this block was similar to the medial but lower than the proximal (Table 20). *D. spicata* was the only high marsh species present in the distal block except for 2017 when *Spartina patens* accounted for a small percent of the community cover (<5% to 10%) (Table 20).

There were no transition species present in the plant community in the tilled-only experimental plot from 2015 to 2019 (Figure 34). One year after planting, mallow covered 30% to 50% of the plots (Figure 34). From 2016 to 2019, *K. pentacarpos* decreased while other transition species increased in the drilled and broadcast plots (Figure 34). The increase in transition species cover in 2019 was the result of colonization by *Myrica cerifera*, a nitrogen-fixing, rapidly-growing, woody-plant species that has the ability to colonize areas experiencing rapid environmental change (Huang *et al.*, 2018) (Table 20).

Upland species cover was highest in the distal block of the three blocks (Figure 34).

5.4.4.2. *Species Richness and Abundance*

The upland species average cover was highest in the distal block (Table 20). Transition species abundance was lowest in the distal block (Table 20). One fewer species was present in the distal block than in the proximal block, and two fewer species were present in the distal block than in the medial block in 2019 (Table 20).

The sum of the average cover of upland species for each block (Tables 18-20) in the undisturbed plots was highest for the distal block (8), and lower for the medial (6.2) and proximal blocks (6.2). The total cover of upland species in the experimental plots was 7.8, 5.4, and 5.2 in the distal, medial, and proximal blocks, respectively.

5.5. Discussion

5.5.1. All blocks

Disturbances to the plant community, such as tilling (Wilson & Tilman, 1991), fire (Bowman *et al.*, 2009; Lynch, 1941), or floods (R. R. Christian *et al.*, 2000; Knowles *et al.*, 1991), can limit competition and create opportunities for species establishment. This study demonstrated that tilling had a significant effect on the structure of the old field plant community (Table 14). After one full growing season (2015), many bare areas remained. All tilling treatments resulted in a decrease in the presence of upland species including switchgrass (Table 15, Figure 30c, Figure 30e). *D. spicata* cover was also negatively impacted by tilling in the first year of the experiment but had a positive effect in subsequent years (Table 15). In an experiment that examined the role of increasing substrate heterogeneity on the establishment of fresh-water wetland plants, Doherty and Zedler (2015) found that disking the soil reduced plant cover initially but plant cover increased in subsequent years. Similarly, at the Brownsville study site, plant cover and species diversity increased in the years following tilling suggesting a beneficial effect on plant colonization.

The bare spots observed in the experimental plots in 2015 provided open space for the additional species to colonize the plots as suggested by Tilman (1997). In many cases, *D. spicata*, a rapid colonizer and pioneer species, was the principal species colonizing the bare areas (Figures 31-34). This response is consistent with what is known about *D. spicat*a (Brewer & Bertness, 1996; Lonard *et al.*, 2013). Previous studies found that *D. spicata* was an important colonizer in areas experiencing disturbances from storm surge (Allison, 1995, 1996), the driver of groundwater salinity changes in the field (Chapter 2).

This study also examined the impact of another kind of disturbance, the addition of a new species to the community (Bertness & Callaway, 1994; Connell & Slatyer, 1977; Lundberg *et al.*, 2000; Wheeler *et al.*, 2015). While no meaningful difference in plant cover was observed between plots that were only tilled and those that were tilled and planted with mallow, increasing species richness should have a positive impact on the resiliency of an ecosystem. Increased biodiversity within communities experiencing disturbances contributes to the plant community's resiliency and resistance to environmental changes (Isbell *et al.*, 2015; Mori, 2016; Oliver *et al.*, 2015). The conversion of upland areas to high marsh is not a slow, steady process. Ecosystems are generally more resilient to the gradual changes in environmental conditions that allow time for the plant communities to adapt. Rather, it is punctuated events, like storms and high tides, that result in sudden and extreme conditions that result in rapid transitions from one state to another (Brinson *et al.*, 1995; Kirwan & Gedan, 2019).

Measures of community cover showed an overall increase in the presence of transition species from 2015 to 2019 (Figure 31, Table 17). This shift in plant community cover coincides with a higher frequency and longer duration of flooding events within the old field. In gently sloping fields, like the study site, I hypothesized shifts in the plant community in response to sea-level rise (Fagherazzi *et al.*, 2019a) would be gradual as plants adapt to the *in situ* changes in environmental conditions as a consequence of the species' tolerance limits (Jump & Peñuelas, 2005).

Interannual community composition and cover did not change in a monotonic fashion. Instead, plant species popped into and were lost from the community, suggesting the importance of seed banks to community dynamics. Kiss *et al.* (2018) found that seed banks can support community resilience in habitats experiencing frequent disturbances. Plant species, like mallow, whose seeds persist in the seed bank, have a competitive advantage that will contribute to their resiliency in areas undergoing ecological transition.

In the plots where it was planted, *K. pentacarpos* became an established part of the community, persisted until the end of the study, and contributed to the overall increase in transition species (Figure 31, Table 17). However, seeding alone was not enough for the successful establishment of mallow within the community as demonstrated by the variations in cover across the planting treatments and blocks. This is consistent with personal observations and previous experiments which found that mallow had higher germination and survival rates in drier plots while plants grew larger and produced seed soon in wetter plots (Long, 2015). Mallow's dependence on suitable environmental conditions for successful establishment suggests that it is an opportunistic colonizer and not a highly competitive species, as suggested by Ruan et. al. (2008) who found that mallow did not displace native vegetation when introduced to an established plant community.

D. spicata was an established part of the plant community in the undisturbed paired plots at the start of the experiment and rapidly colonized the experimental paired plots one year after tilling. The mechanism behind the increased recruitment is not clear; however, the growth of *D. spicata* into open areas was likely by clonal expansion, rather than seed production and dispersal. The rapidly changing environmental conditions in the study site are potentially stressful to the existing plant community. Under stressful conditions, clonal plants often expand by clonal expansion rather than producing energetically demanding seeds (Chapin, 1987), thereby increasing their competitive advantage under shifting abiotic conditions. Alternatively, facilitation by the addition of a new species that altered the relationship among existing species, reduction of competition from the other species experiencing increased stress, or the inherent characteristics of *D. spciata* as a robust pioneer species could also explain the increase in *D. spicata* cover.

The original goal of this experiment was to understand plant community response to a combination of tilling, and drilling or broadcasting mallow seed. The experimental design was a completely randomized block with three replicates of four paired plots that were established along the leading edge of *D. spicata* growth at the study site intended to capture the maximum variance of plant community composition. However, groundwater analysis showed that each experimental block was experiencing different hydrologic conditions by the end of the experiment (see Chapter 2). Thus, the original experimental design lacks appropriate replication in each hydrologic zone to allow for statistical comparisons of the effect of salinity or seed-sowing approach on species cover as planned.

5.5.2. Individual blocks

The behavior of mallow in each block aligns with the three hydrologic zones discussed in Chapter 2. In the proximal block at the beginning of the experiment, soils were regularly saturated but not salty. Here, *K. pentacarpos* became a dominant species after planting in 2015 but had declined by the end of the experiment in 2019 when groundwater salinity was regularly above 20 parts per thousand (Chapter 2). As mallow declined, it was replaced by *D. spicata* (Figure 32, Table 18), likely due to the increased salinity.

At the beginning of this experiment, soils were saturated primarily by freshwater during high precipitation events in the medial zone. In this experimental block where mallow was broadcast, mallow cover increased from 2015 to 2019 and replaced upland species (Figure 33, Table 19). The behavior of mallow in the tilled and broadcast treatment plot of the medial block was similar to the behavior of the other transition species in the tilled-only treatment plots (Figure 33). The development of a robust *K. pentacarpos* population in the medial block reflects the intermediate conditions of the groundwater elevation and salinity compared to the proximal and distal blocks.

The soil moisture content and groundwater salinity in the distal zone were lower than in the other zones for the duration of the experiment. Mallow that was planted in the distal block was a larger proportion of the community one year after planting than in the other blocks. Subsequently, mallow became a smaller part of the plant community as upland and other transition species increased from 2017 to 2019 (Figure 34, Table 20). That mallow was initially more successful in the distal block than the other blocks may be due to the ability of mallow to capitalize on the drier conditions in bare spots (Long, 2015). Because bare spots ranged from 47% to 78% of the cover in the experimental plots that were tilled or tilled and planted with mallow, this allowed mallow to become a large proportion of the community in 2016.

Mallow persisted in the distal plant community even as the transition species *Iva frutescens* and *Baccharus hamlimifolia* became a small proportion of the community in 2017 and 2018 (Figure 34, Table 20). In 2019, however, *M. cerifera* became the dominant transition species, reducing the cover of all other transition species. *M. cerifera* is a rapid-growing, nitrogen-fixing, highly-competitive pioneer species (Huang *et al.*, 2018) which could account for its rapid expansion and displacement of the other transition species in 2019.

Of the three hydrologic zones within the field, the medial zone is where mallow is most likely to establish and persist. In this zone, the drier, low salinity conditions observed at the beginning of the experiment allowed mallow germination and seedling survival (Chapter 3, Poljakoff-Mayber *et al.*, 1992, 1994; Somers, 1982), and the wetter conditions at the end of the experiment were suitable for the growth of mature, seed-producing plants (Chapter 4). As sea level rises and more frequent flooding occurs in the distal zone, the plants in the medial zone would serve as a seed source to upland areas due to the structure of *K. pentacarpos* seeds that allow them to float in moving water (Poljakoff-Mayber *et al.*, 1992).

The shifts in plant community from the uniformity observed in 2015 across each block to those observed in 2019 match the expectations for species zonation across an environment experiencing inland marsh migration discussed in previous studies (Brinson *et al.*, 1995; Fagherazzi *et al.*, 2019a). In 2015, the only species identified as an indicator of transition between high marsh and uplands by Brinson *et al.* (1995) and Fagherazzi *et al.* (2019a) in the blocks was *D. spicata*. By the end of the experiment, transition indicator species identified by Brinson *et al.* (1995) were common in all blocks (Tables 18-20), but transition species cover was highest in the medial and distal blocks (Tables 18-20). The rapid changes in plant communities reported in this study are likely due to the low slope of the study site and the proximity of the blocks to the tidal creek that allowed spatial zonation of three species groups in only five years.

The groundwater elevation and salinity observations discussed in Chapter 2 support the presence of transitional areas within the study site; although, it is not possible to determine if the plant community change is driven by saturated soils or salinity, or a combination thereof, without experimental replication. This study found that plants well-suited to the emerging environmental conditions took advantage when the community was disturbed (Figure 31-34). For example, the highest abundance of high marsh species, including *D. spicata*, was found in the proximal block, where groundwater elevation and salinity were the highest (Table 18). The medial block has the highest species richness and abundance of transition species (Table 19), which aligns with the expectation of a plant community in transition (Brinson *et al.*, 1995; Costa *et al.*, 2003; Fagherazzi *et al.*, 2019a; Hmieleski, 1994; Huang *et al.*, 2018; Janousek & Folger, 2014). The distal block had the highest upland species cover, although transition species did increase in abundance in the later years of the experiment (Table 20). Conceptual models suggest that shifts from upland to transition species should continue as the groundwater elevation and salinity increase with rising sea levels (Brinson *et al.*, 1995; Fagherazzi *et al.*, 2019a) (see Chapter 6).

5.5.3. Applications

Understanding community disturbance is necessary to determine best management practices for environments experiencing shifting hydrologic regimes resulting from sea-level rise. As more agricultural land is abandoned due to increased frequency of flooding and prolonged periods of soil saturation, knowledge of the plant community response is crucial to achieving land management and restoration goals in changing ecosystems. Introduction of a new species (Amsberry *et al.*, 2000; Bertness & Shumway, 1993; Connell & Slatyer, 1977; McIntire & Fajardo, 2014), flooding (R. R.

Christian *et al.*, 2000; Kang *et al.*, 2016; Knowles *et al.*, 1991), increased salinity (Brinson *et al.*, 1995; Fagherazzi *et al.*, 2019a; Janousek & Folger, 2014; Kearney *et al.*, 2019; Nordio & Fagherazzi, 2022; Raposa *et al.*, 2017; Taillie *et al.*, 2019; Tully *et al.*, 2019; Wasson *et al.*, 2013), fire (Bowman *et al.*, 2009; Lynch, 1941), and mowing (Wilson & Tilman, 1991) are common disturbances in coastal areas and some are used as management tools.

Short-term effects of tilling and long-term effects of establishing *K. pentacarpos* may disturb the plant community in such a way that provides important ecosystem services that would not be realized as rapidly if fields were left to transition without any intervention. The data presented here suggests that planting mallow increased biodiversity within the plant community (Tables 17-20). Additionally, other ecosystem services could include increased overall extent of marshes, wildlife habitat, carbon and nitrogen sequestration, and minimization of erosion and invasive species colonization (Figure 1)(Ruan *et al.*, 2008; Thuma *et al.*, 2020; Voutsina *et al.*, 2015a).

Agricultural fields that are just beginning to experience poor drainage, prolonged periods of waterlogged soils, or increased frequencies of flooding with seawater may be best suited for the cultivation of mallow. Despite not having an established economic market, for farmers looking to extend the life of their agricultural land, a minimal investment of tilling and broadcasting mallow seed would provide ecosystem services that make salt marsh mallow a good "crop of last resort."

Figure 28. Paired-plot locations at the Brownsville Preserve in Nassawadox, Virginia. The three blocks align with the proximal (A), medial (B), and distal (C) groups associated with groundwater salinity discussed in Chapter 2.

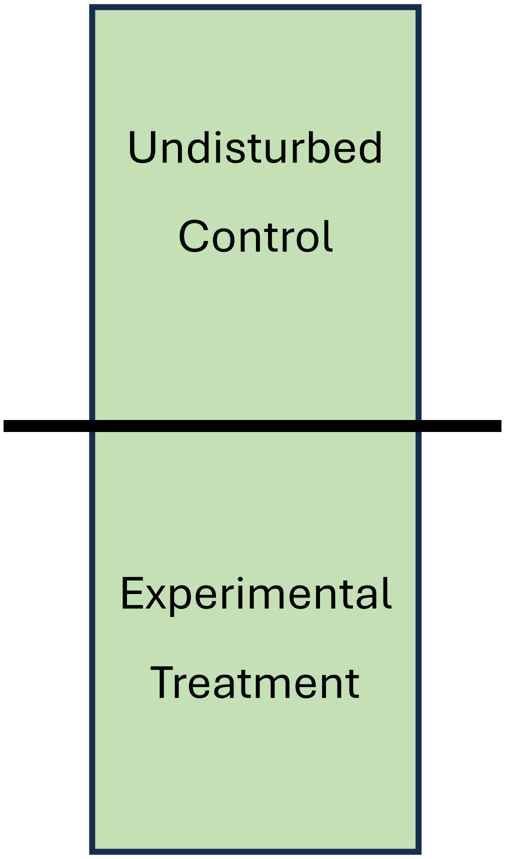


Figure 29. Paired-plot design of 2 x 6 meter experimental plots. Three blocks of four plots were established along the furthest extent of *D. spicata* colonization within the study area in Spring 2015 (shown by the thick black line). The “undisturbed control” is the half of the paired plot where *D. spicata* was present and was not treated. The “experimental treatment” half of the paired plot, which contained no *D. spicata*, was randomly assigned one of 4 treatments – undisturbed, tilled, tilled and drilled with *K. pentacarpos*, and tilled and broadcast with *K. pentacarpos*.

Table 14. Comparison statistics to test for 1) the effect of tilling and 2) a difference in effect between tilling and planting salt marsh mallow. (α=0.05)

Contrast	Num DF	Den DF	F Value	Pr > F
undisturbed v. all tilled	1	31	24.66	<.0001
tilled v. planted mallow	1	31	0.25	0.6229

Table 15. Analysis of covariance results for the effect of tilling and planting mallow, time, the interaction of the treatment and time, and the covariate base cover on percent cover of *Distichlis spicata*, *Phragmites australis*, transitions species group, upland species group, and *Panicum virgatum.* (α=0.05)

n= 30	Effect	Num df	Den df	F Value	p-value
D. spicata	treatment	3	30	0.21	0.8908
	year	4	30	16.74	<.0001
	trt*year	12	30	4.46	0.0004
	base cover	1	30	4.28	0.0474
P. australis	treatment	3	31	0.61	0.6159
	year	4	31	1.08	0.3828
	trt*year	12	31	0.74	0.7033
	base cover	1	31	3.23	0.0822
Transition species	treatment	3	31	0.58	0.6326
	year	4	31	1.22	0.3218
	trt*year	12	31	0.71	0.7314
	base cover	1	31	6.68	0.0147
Upland species	treatment	3	31	11.95	<.0001
	year	4	31	2.51	0.0623
	trt*year	12	31	3.42	0.0028
	base cover	1	31	4.1	0.0516
P. virgatum	treatment	3	31	8.24	0.0004
	year	4	31	3.21	0.0257
	trt*year	12	31	3.42	0.0029
	base cover	1	31	3.21	0.083

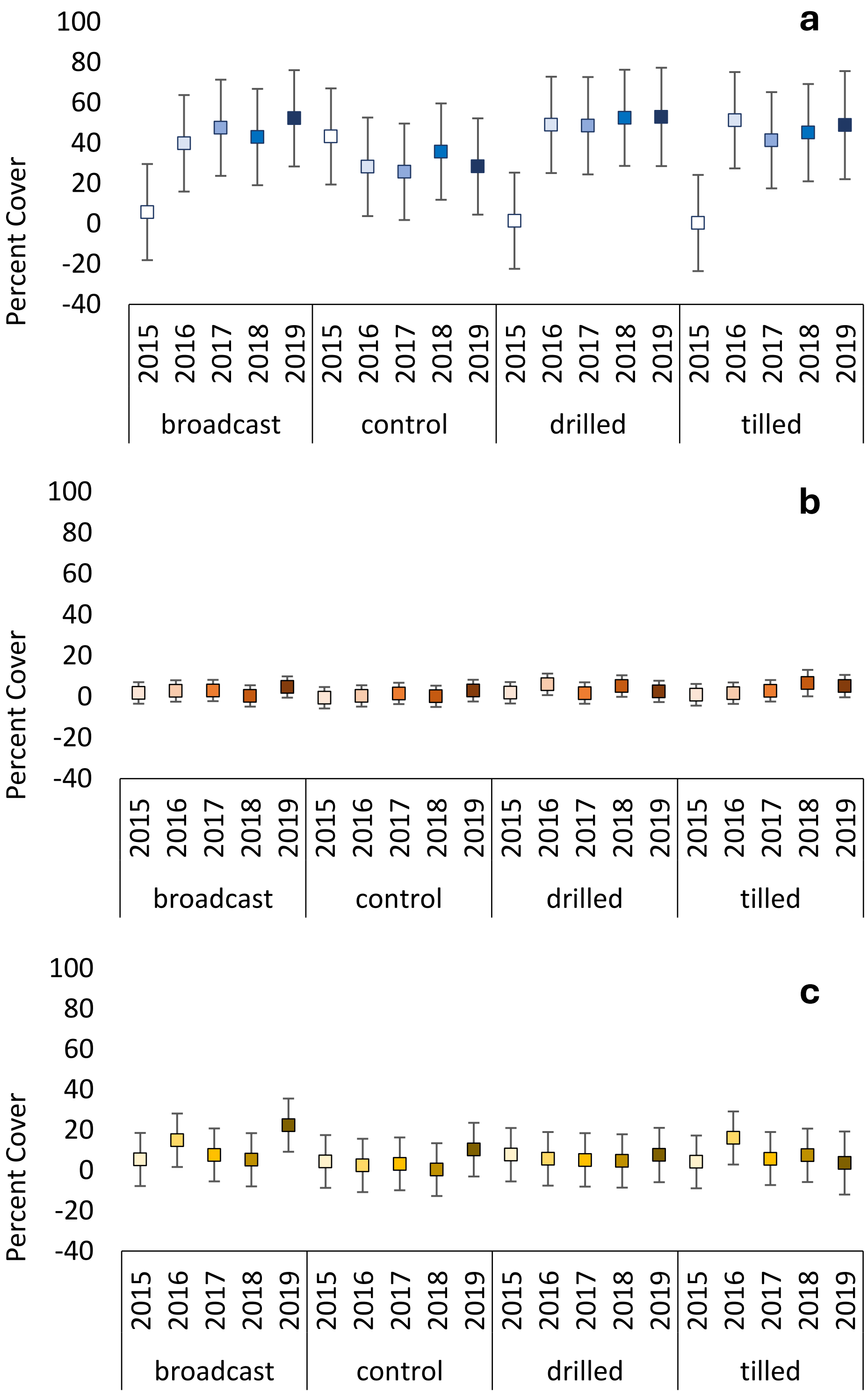
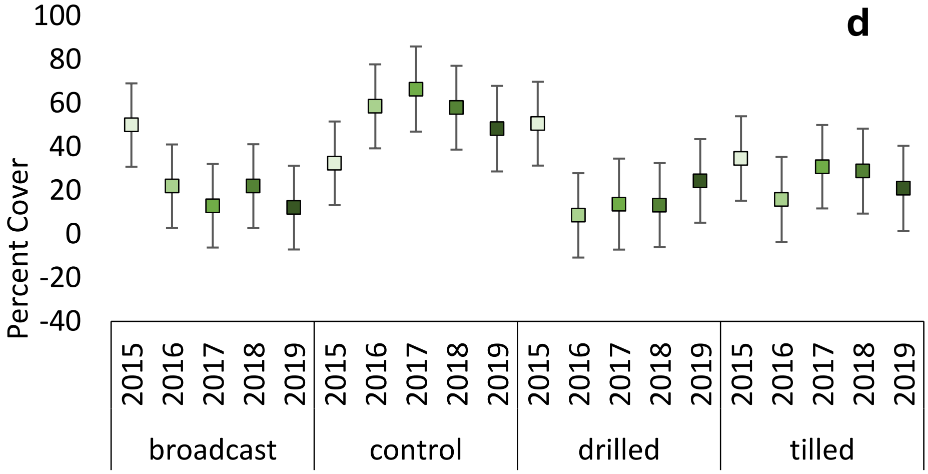


Figure 30. Percent cover change from 2015 to 2019 for all four treatments in the experimental half of the paired plots for (a) *D. spicata*, (b) *P. australis*, (c) transition species, (d) *P. virgatum*, and (e) upland species percent cover. Boxes show least squares means estimates (n=3). Bars show standard error. Figure continues on next page. See Table 15 for treatment comparisons. See Table 16 for a list of species included in the upland and transition classifications.


d
Percent Cover
100
80
60
40
20
0
-20
-40
2015
2016
2017
2018
2019
broadcast
control
drilled
tilled

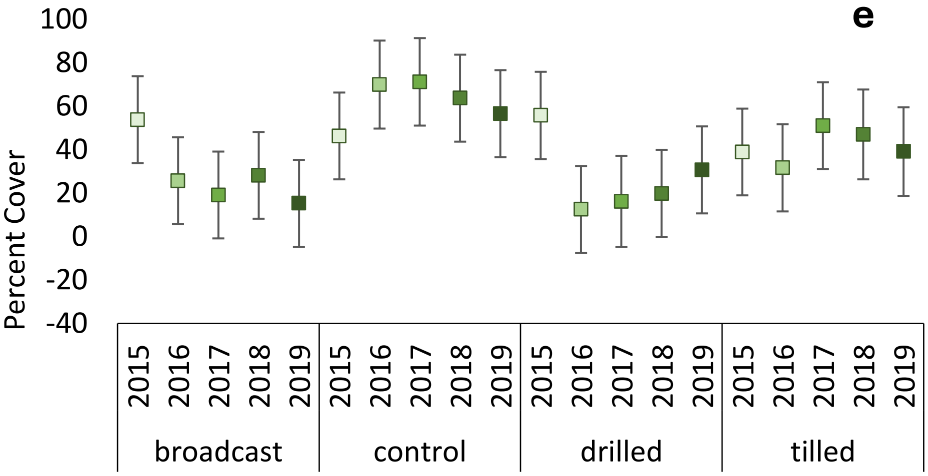

e
Percent Cover
100
80
60
40
20
0
-20
-40
2015
2016
2017
2018
2019
broadcast
control
drilled
tilled

Table 16. Group classification of species present in experimental plots. Classification scheme used was based on Hmieleski (1994).

Upland	Transition	High Marsh
Panicum virgatum	*Kosteletzkya pentacarpos*	*Distichlis spicata*
Asclepias incarnata	*Cyperus esculentus*	*Spartina patens*
Setaria parviflora	*Phragmites australis*	
Eupatorium perfoliatum	*Aster pilosus*	
Foeniculum vulgare	*Myrica cerifera*	
Solanum ptycanthum	*Scirpus sp.*	
	Iva frutescens	
	Limonium carolinium	
	Baccharus halimifolia	
	Juncus gerardii	

Figure 31. Percent cover for each plant group for each paired plot treatment averaged for the proximal, medial, and distal blocks from 2015 to 2019 (n=3). The experimental half of each pair is shown in the top row, while the undisturbed half of each pair is shown in the bottom row of bar graphs. Before K. pentacarpos seeds were drilled or broadcast, plots were tilled. See Table 16 for species classification for the high marsh, transition, and upland plant groups.

Table 17. Species presence and average abundance for all blocks in years 2015 – 2019. Dark blue indicates high marsh species. Light blue indicates transition plant species. Green indicates upland plant species. Presence and relative abundance is indicated by (•). •••• = >40%, ••• = 11% to 40%, •• = 5% to 10%, and • = <5%. The average cover was calculated by summing the number of (•) and dividing by the number of years. The sum of the average cover for each plant group is reported at the bottom of each category in bold. Species order is based on the average cover across all years.

ALL BLOCKS	Undisturbed Plots						Experimental Plots					
Species	2015	2016	2017	2018	2019	*AVG cover*	2015	2016	2017	2018	2019	*AVG cover*
D. spicata	••••	••••	••••	••••	••••	*4*	•••	••••	•••	••••	••••	*3.6*
S. patens			•			*0.2*			•			*0.2*
SUM						***4.2***						***3.8***
K. pentacarpos			•	•	•	*0.6*		•••	•••	•••	••	*2.2*
C. esculentus	••				•••	*1*	•	••	•		••	*1.2*
P. australis	•	•	•	•	•	*1*	•	•	•	••	•	*1.2*
A. pilosus		•	•			*0.4*		••	•			*0.6*
M. cerifera		•			•	*0.4*					•••	*0.6*
Scirpus sp.	•			•	•	*0.6*	•		•	•		*0.6*
I. frutescens			•	•		*0.4*			•	•		*0.4*
L. carolinianum		••		•		*0.6*				•		*0.2*
Baccharus halimifolia				•		*0.2*				•		*0.2*
J. gerardii				•		*0.2*						*0*
SUM						***5.4***						***7.2***
P. virgatum	•••	•••	•••	•••	•••	*3*	••••	•••	•••	•••	•••	*3.2*
A. incarnata	••	••	••	••	••	*2*	••	•	•	••	••	*1.6*
S. parviflora	•	•	•	•	•	*1*	•	••	••	•	••	*1.6*
Eupatorium perfoliatum	••				•	*0.6*	•				•	*0.4*
Foeniculum vulgare						*0*					•	*0.2*
Solanum ptycanthum						*0*					•	*0.2*
SUM						***6.6***						***7.2***
Total # of Species	**8**	**8**	**9**	**11**	**10**		**8**	**8**	**11**	**10**	**11**	

Figure 32. Percent cover for each plant group for each paired plot treatment in the proximal block from 2015 to 2019 (n=1). The experimental half of each pair is show in the top row, while the undisturbed half of each pair is shown in the bottom row of bar graphs. Before *K. pentacarpos* seeds were drilled or broadcast, plots were tilled. See Table 16 for species classification for the high marsh, transition, and upland plant groups.

Table 18. Species presence and average abundance for the proximal block (A) in years 2015 – 2019. Dark blue indicates high marsh species. Light blue indicates transition plant species. Green indicates upland plant species. Presence and relative abundance is indicated by (•). •••• = >40%, ••• = 11% to 40%, •• = 5% to 10%, and • = <5%. The average cover was calculated by summing the number of (•) and dividing by the number of years. The sum of the average cover for each plant group is reported at the bottom of each category in bold. Species order is based on the average cover across all years.

PROXIMAL	Undisturbed Plots						Experimental Plots					
Species	2015	2016	2017	2018	2019	*AVG cover*	2015	2016	2017	2018	2019	*AVG cover*
D. spicata	••••	••••	••••	••••	••••	*4*	•••	••••	••••	••••	••••	*3.8*
S. patens						*0*						*0*
SUM						***4***						***3.8***
K. pentacarpos					•	*0.2*		••	•••	•••	•	*1.8*
P. australis	•	•	•	••	••	*1.4*	•	••	•	•••	••	*1.8*
A. pilosus		•	••			*0.6*		•••	•			*0.8*
C. esculentus	•••		•			*0.8*	••				•	*0.6*
L. carolinianum		•••		•		*0.8*				•		*0.2*
J. gerardii				••		*0.4*						*0*
Baccharus halimifolia						*0*						*0*
I. frutescens						*0*						*0*
M. cerifera						*0*						*0*
Scirpus sp.						*0*						*0*
SUM						***4.2***						***5.2***
P. virgatum	•••	•••	•••	•••	•••	*3*	•••	•••	•••	•••	•••	*3*
A. incarnata	•••	•••	••	••	•	*2.2*	•	••	•	•	•	*1.2*
Eupatorium perfoliatum	•••					*0.6*	•••					*0.6*
S. parviflora			•	•		*0.4*		•			•	*0.4*
Foeniculum vulgare						*0*						*0*
Solanum ptycanthum						*0*						*0*
SUM						***6.2***						***5.2***
Total # of Species	**6**	**6**	**7**	**7**	**5**		**6**	**7**	**6**	**6**	**7**	

Figure 33. Percent cover for each plant group for each paired plot treatment in the medial block from 2015 to 2019 (n=1). The experimental half of each pair is show in the top row, while the undisturbed half of each pair is shown in the bottom row of bar graphs. Before *K. pentacarpos* seeds were drilled or broadcast, plots were tilled. See Table 16 for species classification for the high marsh, transition, and upland plant groups.

Table 19. Species presence and average abundance for the medial block (B) in years 2015 – 2019. Dark blue indicates high marsh species. Light blue indicates transition plant species. Green indicates upland plant species. Presence and relative abundance is indicated by (•). •••• = >40%, ••• = 11% to 40%, •• = 5% to 10%, and • = <5%. The average cover was calculated by summing the number of (•) and dividing by the number of years. The sum of the average cover for each plant group is reported at the bottom of each category in bold. Species order is based on the average cover across all years.

MEDIAL	Undisturbed Plots						Experimental Plots					
Species	2015	2016	2017	2018	2019	*AVG cover*	2015	2016	2017	2018	2019	*AVG cover*
D. spicata	••••	••••	••••	••••	•••	*3.8*	•	••••	••••	•••	••••	*3.2*
S. patens						*0*						*0*
SUM						***3.8***						***3.2***
K. pentacarpos			••	•	••	*1*		•••	•••	•••	•••	*2.4*
C. esculentus	••				•••	*1*	•••	•••	•		•••	*2*
P. australis	•	••	•	••	••	*1.6*		••	•	•••	••	*1.6*
Scirpus sp.				•	•	*0.4*			•	•		*0.4*
A. pilosus			•			*0.2*		•	•			*0.4*
I. frutescens						*0*			•	•		*0.4*
Baccharus halimifolia						*0*						*0*
J. gerardii						*0*						*0*
L. carolinianum				•		*0.2*						*0*
M. cerifera						*0*						*0*
SUM						***4.4***						***7.2***
P. virgatum	•••	•••	•••	•••	•••	*3*	••••	•••	••••	•••	•••	*3.4*
A. incarnata	••	•	••	••	•••	*2*	••	•	•	•	••	*1.4*
S. parviflora	•	•	•	•	•	*1*	••		•	•	•	*1*
Eupatorium perfoliatum					•	*0.2*					•	*0.2*
Foeniculum vulgare						*0*					•	*0.2*
Solanum ptycanthum						*0*					•	*0.2*
SUM						***6.2***						***6.4***
Total # of Species	**6**	**5**	**7**	**8**	**9**		**5**	**7**	**10**	**8**	**10**	

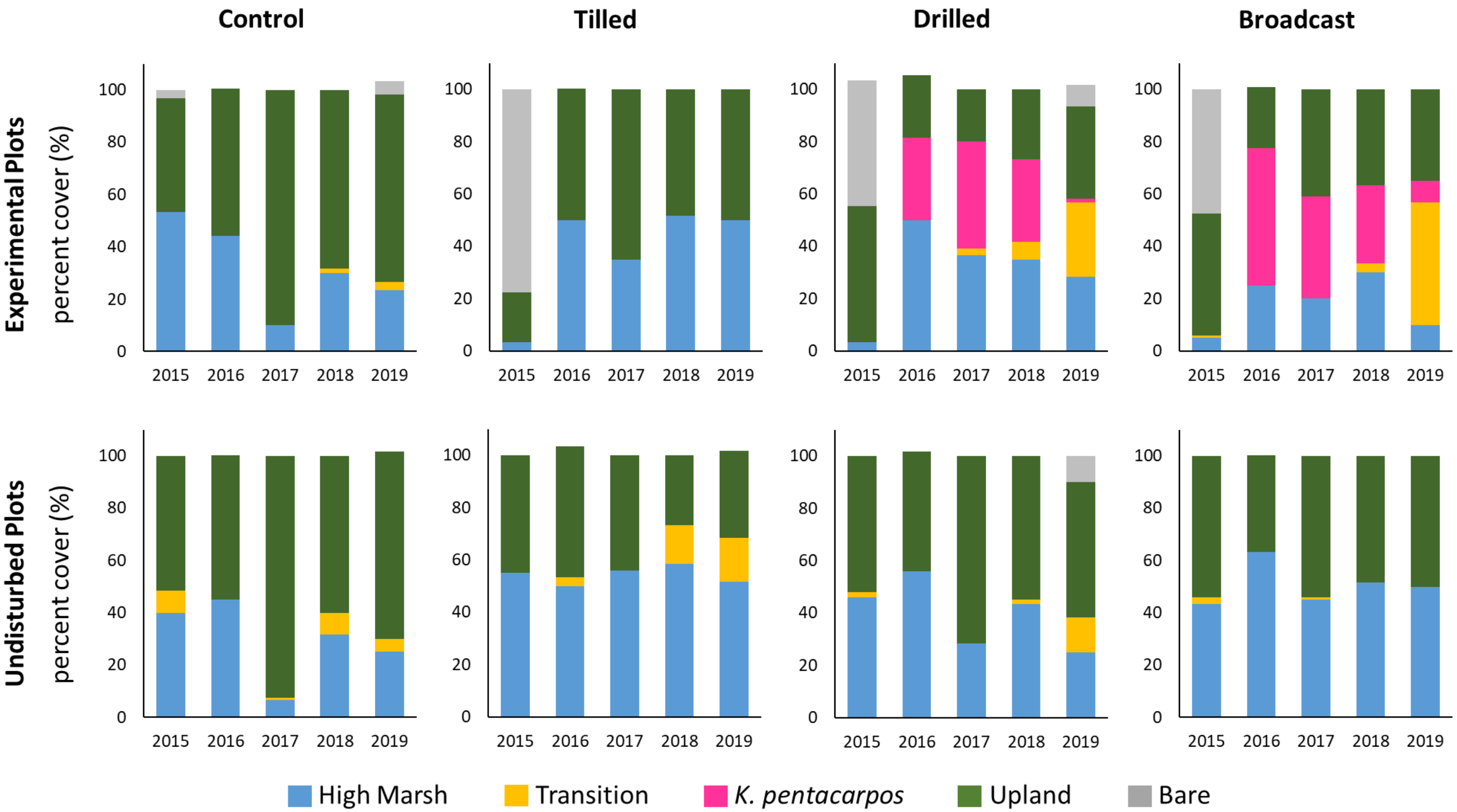


Figure 34. Percent cover for each plant group for each paired plot treatment in the distal block from 2015 to 2019 (n=1). The experimental half of each pair is show in the top row, while the undisturbed half of each pair is shown in the bottom row of bar graphs. Before *K. pentacarpos* seeds were drilled or broadcast, plots were tilled. See Table 16 for species classification for the high marsh, transition, and upland plant groups.

Table 20. Species presence and average abundance for the distal block (C) in years 2015 – 2019. Dark blue indicates high marsh species. Light blue indicates transition plant species. Green indicates upland plant species. Presence and relative abundance is indicated by (•). •••• = >40%, ••• = 11% to 40%, •• = 5% to 10%, and • = <5%. The average cover was calculated by summing the number of (•) and dividing by the number of years. The sum of the average cover for each plant group is reported at the bottom of each category in bold. Species order is based on the average cover across all years.

DISTAL	Undisturbed Plots						Experimental Plots					
Species	2015	2016	2017	2018	2019	*AVG cover*	2015	2016	2017	2018	2019	*AVG cover*
D. spicata	••••	••••	•••	••••	•••	*3.6*	•••	••••	•••	•••	•••	*3.2*
S. patens			•			*0.2*			••			*0.4*
SUM						***3.8***						***3.6***
K. pentacarpos						*0*		••••	•••	•••	••	*2.4*
M. cerifera		•			•••	*0.8*					•••	*0.6*
I. frutescens			•	•		*0.4*			•	••		*0.6*
C. esculentus					•	*0.2*					•	*0.2*
Scirpus sp.	•					*0.2*	•					*0.2*
Baccharus halimifolia						*0*				•		*0.2*
P. australis	•			••		*0.6*						*0*
A. pilosus			•			*0.2*						*0*
J. gerardii						*0*						*0*
L. carolinianum						*0*						*0*
SUM						***2.4***						***4.2***
P. virgatum	•••	•••	••••	•••	•••	*3.2*	•••	•••	•••	•••	•••	*3*
S. parviflora	••	•••	•••	••	••	*2.4*	•	•••	•••	•••	•••	*2.6*
A. incarnata	••	••	•••	•••	••	*2.4*	••	•	••	••	••	*1.8*
Eupatorium perfoliatum					•••	*0*					•	*0.2*
Foeniculum vulgare						*0*						*0*
Solanum ptycanthum						*0*						*0*
SUM						***8***						***7.6***
Total # of Species	**6**	**5**	**7**	**6**	**7**		**5**	**5**	**7**	**7**	**8**	

Chapter 6.

Synthesis and Significance

1.1 Synthesis and Significance

The results of this dissertation provide a better understanding of the response of old field plant communities to increased flooding and higher groundwater salinity resulting from the interaction of storm surge and precipitation that is exacerbated by sea level rise. The rate of sea-level rise on Virginia's Eastern shore is 5.63 mm yr-1 between 1978-2023 (NOAA, 2023 "Tides and Currents"), corresponding to an increase of 4.5 cm from 2012 to 2020, the timeframe of water table elevation measurements. Increases in sea level of this magnitude have pronounced effects on the groundwater elevation and salinity at the study site due to the low elevation (≤1 meter msl) and shallow slope (0.002) (Chapter 2).

The field site at the Brownsville Preserve was farmed from 1652 (Whitelaw, 1951) until the early 2000s when it was planted in warm seasonal grasses (personal communication with Barry Truitt) after the dike system failed resulting in increased flooding from the nearby tidal marsh (Figure 5). In 2012, when the first groundwater well was installed, the plant community was dominated by switchgrass (*Panicum virgatum*) but included common old field species such as *Asclepias incarnata*, *Setaria parviflora*, *Eupatorium perfoliatum*, *Aster sp*, and *Phragmites australis*. Additionally, common high marsh species, *Distichlis spicata* and *Spartina patens*, colonized the low-elevation areas near breaches in the dike.

The results of my work show that plant communities within the old field resist change associated with more frequent seawater flooding increase and that disturbance is a catalyst for state change (*sensu* Brinson *et al.*, 1995)**.** In this chapter, I discuss a revised conceptual model of the changes in groundwater elevation, salinity, and precipitation that lead to marsh migration into old fields, building on the work of Brinson *et al.* (1995) and Fagherazzi *et al.* (2019a).

Brinson *et al.*(1995) examined how salt marsh migration inland occurs but limited the scope to the salt marsh and upland forest interface (Figure 3). They described an upland forest that is resistant to the chronic environmental impacts of sea-level rise until abrupt disturbances to the forest initiate species change to organic high marsh. My observations of the groundwater elevation from 2012 to 2017 suggested a gradual rise in the water table in upland areas adjacent to the salt marsh and are consistent with rising sea level. Therefore, our expectation was that the fresh- and saltwater interface would rise gradually toward the surface as the water table rose and the entire water column became salinized (Fagherazzi *et al.*, 2019a, Figure 4). With the expected changes in the depth to the fresh-saltwater interface, we predicted that the species composition would also shift gradually but lag salinization of the root zone.

The field at Brownsville presented an opportunity to look at the environmental changes in an old field transitioning to high marsh and test our conceptual model (Fagherazzi *et al.*, 2019a, Figure 4). At this site, overland flooding with saline water from the nearby tidal creek provided a source of salinity to the groundwater. However, the salinizing effect from storm surge was mitigated by flooding with freshwater from large precipitation events (Chapter 2). As sea level continues to rise, the expected increase in frequency of tide-dominated high-water events will result in a shallower water-table, and, in the absence of precipitation, a permanent increase in groundwater salinity. Therefore, understanding the plant species' responses to increased inundation frequency with both salt- and freshwater was important.

To understand the effects of salinity on species establishment and persistence in the community, I carried out a greenhouse experiment to test the tolerance of *Kosteletzkya pentacarpos* and *Panicum virgatum* under three different levels of salinity (Chapter 3). Switchgrass was selected because it was the dominant plant in the old field. Salt marsh mallow has been identified as a potential nurse crop to increase carbon and nutrient sequestration, and mitigate erosion in salinized agricultural fields (Voutsina *et al.*, 2015b) and is a resource to important pollinator species, Figure 1). Malllow exhibited a higher tolerance than switchgrass with more individuals growing faster sooner and surviving to the end of the experiment in the higher salinity treatments (Chapter 3). For this reason, mallow would be better suited than switchgrass for establishment in salinized fields where disturbance has created an opportunity for colonization. Although established switchgrass exhibits tolerance to increases in salinity (Carson *et al.*, 2016; Hu *et al.*, 2015, 2015, 2018; J. Kim *et al.*, 2016; S. Kim *et al.*, 2012; Liu *et al.*, 2014; Schmer *et al.*, 2012; Shrestha *et al.*, 2022; Sun *et al.*, 2018; Zanetti *et al.*, 2019), I expect it would be limited in its ability to propagate and spread in salinized fields, eventually disappearing from the plant community. Additionally, perennials like switchgrass with deep tap roots will be affected sooner by groundwater salinization than shallow-rooted annuals. In contrast, mallow has both deep and shallow root structures that allow for efficient water uptake throughout the soil profile. Thus, when considered with its higher salinity tolerance, mallow will persist in the community after salinization of the groundwater and soil.

In addition to increased salinity, higher water table elevations will lead to longer periods of waterlogged soils when flooding does occur. This increase in soil moisture will impact the existing plant community and result in a shift to species more tolerant of saturated soils. Therefore, I tested the effect of increased soil moisture on the establishment of *K. pentacarpos* and *P. virgatum* in an old field undergoing ecological transition (Chapter 4). While increased soil moisture had no effect on switchgrass cover, mallow cover was enhanced by increased soil moisture. This result confirms that mallow would be a better option than switchgrass for land managers seeking to establish a native species population on land with higher water table elevations and increased flooding frequency. While mature switchgrass plants do exhibit tolerance to soil saturation (Barney *et al.*, 2009), germination of seeds and survival of seedlings was lower for switchgrass than mallow.

Regardless of moisture content, mallow cover was higher than switchgrass at the end of the experiment in both the wet and dry plots. Mallow's increased performance was likely due to its higher germination efficiency and faster growth rates than switchgrass (Chapter 3) which allowed for rapid establishment in the disturbed plots over the duration of the experiment (Chapter 4). Species that can quickly establish within a community may increase or sustain ecosystem services in rapidly degrading land. Fast-growing perennials, like mallow, provide peak ecological benefits, such as mitigation of erosion and carbon and nutrient sequestration, sooner than annual species or slower-growing perennials.

Ultimately, accelerating rates of sea-level rise will impact larger areas of coastal lands, resulting in more frequent flooding and higher groundwater salinity that drive plant community change. Facilitating the transition between upland and high marsh environments can preserve important ecosystem functions that would otherwise be diminished (citation). Disturbing the existing plant community creates open areas for species colonization and increases species diversity. In abandoned agricultural fields, tilling may increase the recruitment of high marsh species, thereby promoting inland marsh migration as a consequence of the negative effect of disturbance on upland species cover (Chapter 5).

Despite evidence within the literature showing that disturbance in combination with planting hastens restoration efforts (Pywell *et al.*, 2002, 2002; Wheeler *et al.*, 2015), and recommendations to plant nurse crops in degrading agricultural fields (Voutsina *et al.*, 2015b), here planting mallow had no detectable effect on the recruitment of the pioneer high-marsh species, *D. spicata*, or other high marsh plants into an old field (Chapter 5). Instead, where mallow was planted, it became an established part of the plant community but had no detectable impact on the presence or cover of other species.

In all experimental treatments, including the unmanipulated control, the half of the paired plots where *D. spicata* was not present at the beginning of the experiment were colonized by *D. spicata* by the end of the experiment. The presence of *D. spicata* only one year after tilling suggests that the conversion of upland old fields was not a gradual process. Rather, these observations imply that the abiotic and biotic conditions at this site were poised for *D. spicata* to spread throughout the field at the time the experimental blocks were established. For example, the failure of the dike at the study site increased the frequency of flooding, introduced salt into the groundwater, and provided a pathway for the spread of species from the salt marsh ecosystem. As the groundwater elevation and salinity continued to rise over the study period, the number of transition species increased. Based on these observations, I conclude that although the presence of one wetland species (*D. spicata*) may be a leading indicator of community change, it is the presence of transition species that indicates a threshold has been reached, and the community will no longer recover to that of an old field.

The work present here suggests the need to refine the model we proposed in Fagherazzi *et al.* (2019a) model. My research shows that the observed changes in salinity, as well as the response of the plant community, do not occur in a slow, monotonic progression as previously hypothesized. Instead, the development of plant community zonation is better described by a press-pulse model like that proposed by Cahoon *et al.* (1998). Similarly, Flester and Blum (2020) reported that as salt marsh migrate into uplands, coastal plant communities resist change until there is a disturbance which provides an opportunity for species better suited to the environmental conditions to colonize.

In the revised model, which focuses only on the transition from abandoned agricultural fields with an established plant community to high marsh (Figure 35), the groundwater elevation and salinity are decoupled and the effect of precipitation on both is emphasized. Changes in the water table elevation are largely a function of sea-level rise relative to the ground surface elevation and the slope of the coastal old field. Overall, the upward trend of water table elevation appears monotonic during nine years of observations (2012-2020); however, at shorter scales such as daily, weekly, monthly, or seasonally, water table variability can be high. Precipitation also causes temporary increases in groundwater elevation and affects groundwater salinity. Depending on the source of the flood waters, salinity can increase or decrease. For example, flooding with seawater from storm surge increases groundwater salinity; likewise, extended periods of drought increase salinity through evaporation. Conversely, large precipitation events decrease groundwater salinity, if only temporarily, by the addition of freshwater. Changes in salinity occur at different rates and time scales than changes in groundwater elevation (Chapter 2). In some cases, individual flooding events can have much larger effects on salinity than on the elevation of the water table. Precipitation can cause dramatic decreases in salinity that persist until the next saltwater flooding event. A major finding of my work is that the magnitude and timing of precipitation events can delay salinization of old fields experiencing high rates of sea-level rise by reducing salinity stress to the plant community (Rubin *et al.*, 2024).

While Figure 35 may suggest a linear change in the plant community from upland to old field to wetland species, the progression is not unidirectional. For instance, a transition species may appear in the upland community but in the following year are lost from the community just to reappear in subsequent years (Tables 17-20, Chapter 5). This type of interannual variation in species composition at a location likely reflects short-term variation in groundwater elevation and salinity. Likewise, small differences in land surface elevation (12 cm) had a disproportionate effect on the rate of plant community change. Changes in the spatial distribution of species varied greatly at small scales reflecting the specific hydrologic conditions related to ground surface elevation. Although plant community composition at the start of the experiment was similar across the experimental sites, I observed the development of three distinct hydrologic zones (Chapter 2) that align with three plant communities, which appear to be in different stages of transition (Chapter 5). Thus, it is clear that the rate of inland marsh migration is dependent upon the abiotic conditions at a given site and the resiliency of the plant community to environmental change and varies at different spatial and temporal scales.

As the sea level continues to rise, abandoned agricultural fields experience increased frequency of flooding and higher groundwater salinity that drive the transition of the plant community from that of an old field to a salt marsh. The time to transition is likely dependent on the elevation and slope of the land, as well as the frequency of inundation and source of floodwater. In fields experiencing high rates of salinization, disturbance can facilitate the transition from upland to salt marsh ecosystems. The addition of new species, which thrive under the dynamic environmental conditions, may have the added benefit of increasing important ecosystem services that otherwise may be lost temporarily during transition. This body of work suggests the suitability of *K. pentacarpos* cultivation in old fields, not as a facilitator of ecosystem change, but as a placeholder to provide ecosystem services during periods of rapid transition.

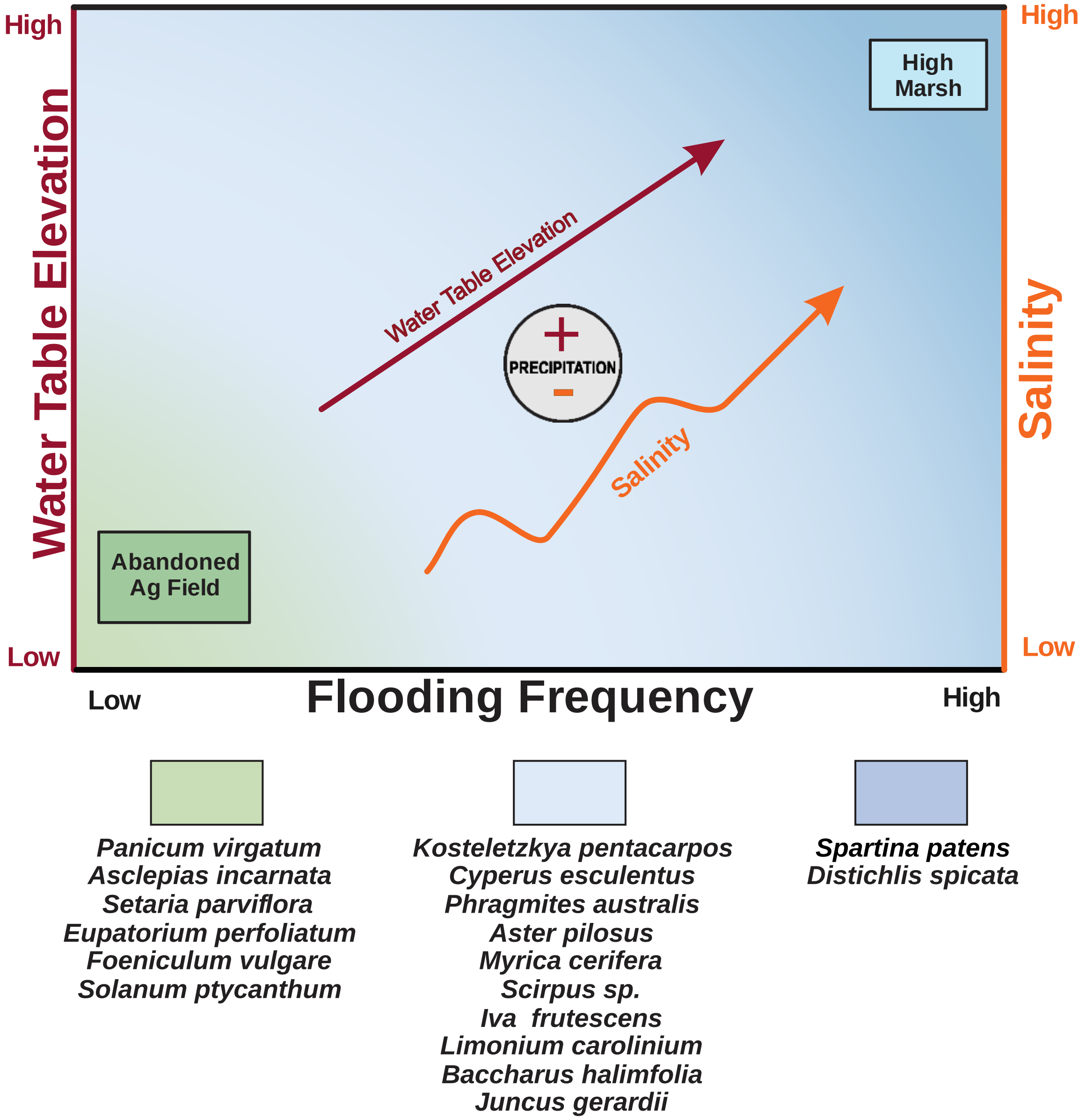


Figure 35. Conceptual model (revised from Fagherazzi *et al.* (2019a)) of changes in plant community composition in abandoned coastal agricultural fields experiencing inland marsh migration due to sea-level rise. Drivers of community change include flooding frequency (x-axis) and precipitation (gray circle). Response variables include water table elevation (dark red line), salinity (orange line), and plant community composition (green to blue gradient). Precipitation increases water table elevation (plus sign), whereas precipitation decreases salinity (minus sign). Observed plant community composition is listed by community type: abandoned agricultural field (light green), transition (light blue), and high marsh (dark blue).

RESOURCES

Accomack County. (2014). *Respecting the Past, Creating the Future: Accomack County Comprehensive Plan*. Accomack County Planning Commission.

Accomack-Northampton Planning District Commission. (2012). *Eastern Shore of Virginia Comprehensive Economic Development Strategy*.

Allison, S. K. (1995). Recovery From Small-Scale Anthropogenic Disturbances by Northern California Salt Marsh Plant Assemblages. *Ecological Applications*, *5*(3), 693–702. https://doi.org/10.2307/1941978

Allison, S. K. (1996). Recruitment and Establishment of Salt Marsh Plants Following Disturbance by Flooding. *The American Midland Naturalist*, *136*(2), 232–247. https://doi.org/10.2307/2426728

Amsberry, L., Baker, M. A., Ewanchuk, P. J., & Bertness, M. D. (2000). Clonal Integration and the Expansion of Phragmites Australis. *Ecological Applications*, *10*(4), 1110–1118. https://doi.org/10.1890/1051-0761(2000)010[1110:CIATEO]2.0.CO;2

Andrea, P., Carla, L., & Monti, A. (2018). Areas with Natural Constraints to Agriculture: Possibilities and Limitations for The Cultivation of Switchgrass (Panicum Virgatum L.) and Giant Reed (Arundo Donax L.) in Europe. In R. Li & A. Monti (Eds.), *Land Allocation for Biomass Crops: Challenges and Opportunities with Changing Land Use* (pp. 39–63). Springer International Publishing. https://doi.org/10.1007/978-3-319-74536-7_3

Anil, Park, Phipps, & Miller. (1998). Temperate intercropping of cereals for forage: A review of the potential for growth and utilization with particular reference to the UK. *Grass and Forage Science*, *53*(4), 301–317. https://doi.org/10.1046/j.1365-2494.1998.00144.x

Anisfeld, S. C., Cooper, K. R., & Kemp, A. C. (2017). Upslope development of a tidal marsh as a function of upland land use. *Global Change Biology*, *23*(2), 755–766. https://doi.org/10.1111/gcb.13398

Baart, F., van Gelder, P. H. A. J. M., de Ronde, J., van Koningsveld, M., & Wouters, B. (2012). The Effect of the 18.6-Year Lunar Nodal Cycle on Regional Sea-Level Rise Estimates. *Journal of Coastal Research*, *28*(2), 511–516.

Bailey, R. T., & Jenson, J. W. (2014). Effects of Marine Overwash for Atoll Aquifers: Environmental and Human Factors. *Groundwater*, *52*(5), 694–704. https://doi.org/10.1111/gwat.12117

Barlow, P. M., & Reichard, E. G. (2010). Saltwater intrusion in coastal regions of North America. *Hydrogeology Journal*, *18*(1), 247–260. https://doi.org/10.1007/s10040-009-0514-3

Barney, J. N., Mann, J. J., Kyser, G. B., Blumwald, E., Van Deynze, A., & DiTomaso, J. M. (2009). Tolerance of switchgrass to extreme soil moisture stress: Ecological implications. *Plant Science*, *177*(6), 724–732. https://doi.org/10.1016/j.plantsci.2009.09.003

Bertness, M. D. (1991). Interspecific Interactions among High Marsh Perennials in a New England Salt Marsh. *Ecology*, *72*(1), 125–137. https://doi.org/10.2307/1938908

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(5), 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Bertness, M. D., & Hacker, S. D. (1994). Physical Stress and Positive Associations Among Marsh Plants. *The American Naturalist*, *144*(3), 363–372. https://doi.org/10.1086/285681

Bertness, M. D., & Leonard, G. H. (1997). The Role of Positive Interactions in Communities: Lessons from Intertidal Habitats. *Ecology*, *78*(7), 1976–1989. https://doi.org/10.1890/0012-9658(1997)078[1976:TROPII]2.0.CO;2

Bertness, M. D., & Shumway, S. W. (1993). Competition and Facilitation in Marsh Plants. *The American Naturalist*, *142*(4), 718–724. https://doi.org/10.1086/285567

Blits, K. C., & Gallagher, J. L. (1990a). Salinity tolerance of Kosteletzkya virginica. I. Shoot growth, ion and water relations. *Plant, Cell & Environment*, *13*(5), 409–418.

Blits, K. C., & Gallagher, J. L. (1990b). Salinity tolerance of Kosteletzkya virginica. II. Root growth, lipid content, ion and water relations. *Plant, Cell & Environment*, *13*(5), 419–425.

Blum, L. K., & Christian, R. R. (2004). Belowground Production and Decomposition Along a Tidal Gradient in a Virginia Salt Marsh. In *The Ecogeomorphology of Tidal Marshes* (pp. 47–73). American Geophysical Union (AGU). https://doi.org/10.1029/CE059p0047

Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D’Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., … Pyne, S. J. (2009). Fire in the Earth System. *Science*, *324*(5926), 481–484. https://doi.org/10.1126/science.1163886

Brewer, J. S., & Bertness, M. D. (1996). Disturbance and Intraspecific Variation in the Clonal Morphology of Salt Marsh Perennials. *Oikos*, *77*(1), 107–116. https://doi.org/10.2307/3545590

Brinson, M. M., Christian, R. R., & Blum, L. K. (1995). Multiple states in the sea-level induced transition from terrestrial forest to estuary. *Estuaries*, *18*(4), 648–659. https://doi.org/10.2307/1352383

Brinson, M. M., & Stasavich, L. (1997). *Brownsville and Hog Island Surficial Well Data at the Virginia Coast Reserve 1990-present.* (Publication knb-lter-vcr.58.21) [dataset]. Virginia Coast Reserve Long-Term Ecological Research Project Data. http://www.vcrlter.virginia.edu/cgi-bin/showDataset.cgi?docid=knb-lter-vcr.58

Brinson, M. M., & Stasavich, L. (2015a). *Brownsville and Hog Island Surficial Well Data at the Virginia Coast Reserve 1990-2015* (knb-lter-vcr.58.23) [dataset]. [object Object]. https://doi.org/10.6073/PASTA/A40DA2D531099D355A984810EEA379A6

Brinson, M. M., & Stasavich, L. (2015b). *Brownsville and Hog Island surficial well data at the Virginia Coast Reserve 1997-2009* (knb-lter-vcr.171.22) [dataset]. [object Object]. https://doi.org/doi:10.6073/pasta/c3d63f52c49715cd4f4d4001a62183ec

Brooker, R. W., & Callaghan, T. V. (1998). The Balance between Positive and Negative Plant Interactions and Its Relationship to Environmental Gradients: A Model. *Oikos*, *81*(1), 196–207. https://doi.org/10.2307/3546481

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C. L., … Michalet, R. (2008). Facilitation in Plant Communities: The Past, the Present, and the Future. *Journal of Ecology*, *96*(1), 18–34.

Cahoon, D. R., Day Jr., J. W., Reed, D. J., & Young, R. S. (1998). *Global climate change and sea-level rise: Estimating the potential for submergence of coastal wetlands* (Vulnerability of Coastal Wetlands in the Southeastern United States, pp. 19–32) [USGS Biological Science Report].

Callaway, R. M., & Walker, L. R. (1997). Competition and Facilitation: A Synthetic Approach to Interactions in Plant Communities. *Ecology*, *78*(7), 1958–1965. https://doi.org/10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2

Campbell, A. D., Fatoyinbo, L., Goldberg, L., & Lagomasino, D. (2022). Global hotspots of salt marsh change and carbon emissions. *Nature*, *612*(7941), Article 7941. https://doi.org/10.1038/s41586-022-05355-z

Cantelon, J. A., Guimond, J. A., Robinson, C. E., Michael, H. A., & Kurylyk, B. L. (2022). Vertical Saltwater Intrusion in Coastal Aquifers Driven by Episodic Flooding: A Review. *Water Resources Research*, *58*(11), e2022WR032614. https://doi.org/10.1029/2022WR032614

Carson, M. A., Bachle, S., & Morris, A. N. (2016). Germination and Growth of Panicum virgatum Cultivars in a NaCl Gradient. In M. A. Khan, B. Boër, M. Ȫzturk, M. Clüsener-Godt, B. Gul, & S.-W. Breckle (Eds.), *Sabkha Ecosystems: Volume V: The Americas* (pp. 287–297). Springer International Publishing. https://doi.org/10.1007/978-3-319-27093-7_16

Chambers, R. M., Havens, K. J., Killeen, S., & Berman, M. (2008). Common reed Phragmites australis occurrence and adjacent land use along estuarine shoreline in Chesapeake Bay. *Wetlands*, *28*(4), 1097–1103. https://doi.org/10.1672/07-61.1

Chapin, F. S. (1987). Environmental Controls over Growth of Tundra Plants. *Ecological Bulletins*, *38*, 69–76.

Chen, J. L., Shum, C. K., Wilson, C. R., Chambers, D. P., & Tapley, B. D. (2000). Seasonal sea level change from TOPEX/Poseidon observation and thermal contribution. *Journal of Geodesy*, *73*(12), 638–647. https://doi.org/10.1007/s001900050002

Christian, R. (2014). *End of Year Biomass in marsh transition plots in Upper Phillips Creek marsh 1999-2014* (knb-lter-vcr.171.22) [dataset]. [object Object]. https://doi.org/10.6073/PASTA/C3D63F52C49715CD4F4D4001A62183EC

Christian, R. R., Stasavich, L. E., Thomas, C. R., & Brinson, M. M. (2000). References is a Moving Target in Sea-Level Controlled Wetlands. In M. P. Weinstein & D. A. Kreeger (Eds.), *Concepts and Controversies in Tidal Marsh Ecology* (pp. 805–825). Springer Netherlands. https://doi.org/10.1007/0-306-47534-0_35

Christiansen, T. (1998). *Sediment deposition on a tidal salt marsh* [Ph.D. Dissertation]. University of Virginia.

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. *The American Naturalist*, *111*(982), 1119–1144.

Corli, A., Gerdol, R., Orsenigo, S., Rossi, G., Abeli, T., Iacumin, P., Marchesini, R., & Brancaleoni, L. (2023). Relative importance of site selection and aftercare for successful reintroduction of the policy species Kosteletzkya pentacarpos. *Plant Biosystems - An International Journal Dealing with All Aspects of Plant Biology*, *157*(1), 80–88. https://doi.org/10.1080/11263504.2022.2089762

Costa, C. S. B., Marangoni, J. C., & Azevedo, A. M. G. (2003). Plant zonation in irregularly flooded salt marshes: Relative importance of stress tolerance and biological interactions. *Journal of Ecology*, *91*(6), 951–965. https://doi.org/10.1046/j.1365-2745.2003.00821.x

Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., Guo, H., & Machmuller, M. (2009). Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. *Frontiers in Ecology and the Environment*, *7*(2), 73–78. https://doi.org/10.1890/070219

Diamond, D. D., & Smeins, F. E. (1985). Composition, Classification and Species Response Patterns of Remnant Tallgrass Prairies in Texas. *The American Midland Naturalist*, *113*(2), 294–308. https://doi.org/10.2307/2425575

Doherty, J. M., & Zedler, J. B. (2015). Increasing substrate heterogeneity as a bet-hedging strategy for restoring wetland vegetation. *Restoration Ecology*, *23*(1), 15–25. https://doi.org/10.1111/rec.12154

Egerova, J., Proffitt, C. E., & Travis, S. E. (2003). Facilitation of survival and growth of Baccharis halimifolia L. by Spartina alterniflora Loisel. In a created Louisiana salt marsh. *Wetlands*, *23*(2), 250–256. https://doi.org/10.1672/4-20

Fagherazzi, S., Anisfeld, S. C., Blum, L. K., Long, E. V., Feagin, R. A., Fernandes, A., Kearney, W. S., & Williams, K. (2019a). Sea Level Rise and the Dynamics of the Marsh-Upland Boundary. *Frontiers in Environmental Science*, *7*. https://www.frontiersin.org/articles/10.3389/fenvs.2019.00025

Fagherazzi, S., Nordio, G., Munz, K., Catucci, D., & Kearney, W. S. (2019b). Variations in Persistence and Regenerative Zones in Coastal Forests Triggered by Sea Level Rise and Storms. *Remote Sensing*, *11*(17). https://doi.org/10.3390/rs11172019

Feng, A., Gao, J., Wu, S., Liu, L., Li, Y., & Yue, X. (2018). Assessing the inundation risk resulting from extreme water levels under sea-level rise: A case study of Rongcheng, China. *Geomatics, Natural Hazards and Risk*, *9*(1), 456–470. https://doi.org/10.1080/19475705.2018.1447026

Filazzola, A., & Lortie, C. J. (2014). A systematic review and conceptual framework for the mechanistic pathways of nurse plants. *Global Ecology and Biogeography*, *23*(12), 1335–1345. https://doi.org/10.1111/geb.12202

Flester, J. A., & Blum, L. K. (2020). Rates of Mainland Marsh Migration into Uplands and Seaward Edge Erosion are Explained by Geomorphic Type of Salt Marsh in Virginia Coastal Lagoons. *Wetlands*, *40*(6), 1703–1715. https://doi.org/10.1007/s13157-020-01390-6

Flewelling, S. A., Hornberger, G. M., Herman, J. S., Mills, A. L., & Robertson, W. M. (2014). Diel patterns in coastal-stream nitrate concentrations linked to evapotranspiration in the riparian zone of a low-relief, agricultural catchment: EVAPOTRANSPIRATION AND DIEL PATTERNS IN STREAM NO3−. *Hydrological Processes*, *28*(4), 2150–2158. https://doi.org/10.1002/hyp.9763

Flowers, T. J., & Colmer, T. D. (2015). Plant salt tolerance: Adaptations in halophytes. *Annals of Botany*, *115*(3), 327–331. https://doi.org/10.1093/aob/mcu267

Forero, L. E., Grenzer, J., Heinze, J., Schittko, C., & Kulmatiski, A. (2019). Greenhouse- and Field-Measured Plant-Soil Feedbacks Are Not Correlated. *Frontiers in Environmental Science*, *7*. https://www.frontiersin.org/articles/10.3389/fenvs.2019.00184

Gallagher, J. L. (1985). Halophytic crops for cultivation at seawater salinity. *Plant and Soil*, *89*(1), 323–336. https://doi.org/10.1007/BF02182251

Gedan, K. B., Epanchin-Niell, R., & Qi, M. (2020). Rapid Land Cover Change in a Submerging Coastal County. *Wetlands*, *40*(6), 1717–1728. https://doi.org/10.1007/s13157-020-01328-y

Gedan, K. B., & Fernández-Pascual, E. (2019). Salt marsh migration into salinized agricultural fields: A novel assembly of plant communities. *Journal of Vegetation Science*, *30*(5), 1007–1016. https://doi.org/10.1111/jvs.12774

Gewin, V. (2018, March 2). *The Slow-Motion Catastrophe Threatening America's 350-Year-Old Farms*. The Atlantic. https://www.theatlantic.com/science/archive/2018/03/maryland-salt-farms/554663/

Gittman, R. K., Scyphers, S. B., Smith, C. S., Neylan, I. P., & Grabowski, J. H. (2016). Ecological Consequences of Shoreline Hardening: A Meta-Analysis. *BioScience*, *66*(9), 763–773. https://doi.org/10.1093/biosci/biw091

Glenn, E. P., Anday, T., Chaturvedi, R., Martinez-Garcia, R., Pearlstein, S., Soliz, D., Nelson, S. G., & Felger, R. S. (2013). Three halophytes for saline-water agriculture: An oilseed, a forage and a grain crop. *Environmental and Experimental Botany*, *92*, 110–121. https://doi.org/10.1016/j.envexpbot.2012.05.002

Glover, J., Cox, C., & Reganold, J. (2007). Future Farming: A Return to Roots? *Scientific American*, *297*, 82–89. https://doi.org/10.1038/scientificamerican0807-82

Gori, A., Lin, N., & Smith, J. (2020). Assessing Compound Flooding From Landfalling Tropical Cyclones on the North Carolina Coast. *Water Resources Research*, *56*(4), e2019WR026788. https://doi.org/10.1029/2019WR026788

Grabowski, J., Douglas, J., Lang, D., Meints, P., & Watson, C. (n.d.). *Response of Two Switchgrass (Panicum virgatum L.) Ecotypes to Seed Storage Environment, Storage Duration, and Prechilling*.

Guimond, J. A., & Michael, H. A. (2021). Effects of Marsh Migration on Flooding, Saltwater Intrusion, and Crop Yield in Coastal Agricultural Land Subject to Storm Surge Inundation. *Water Resources Research*, *57*(2), e2020WR028326. https://doi.org/10.1029/2020WR028326

Hacker, S. D., & Gaines, S. D. (1997). Some Implications of Direct Positive Interactions for Community Species Diversity. *Ecology*, *78*(7), 1990–2003. https://doi.org/10.1890/0012-9658(1997)078[1990:SIODPI]2.0.CO;2

Hallett, L. M., Stein, C., & Suding, K. N. (2017). Functional diversity increases ecological stability in a grazed grassland. *Oecologia*, *183*(3), 831–840. https://doi.org/10.1007/s00442-016-3802-3

Hamlington, B. D., Piecuch, C. G., Reager, J. T., Chandanpurkar, H., Frederikse, T., Nerem, R. S., Fasullo, J. T., & Cheon, S.-H. (2020). Origin of interannual variability in global mean sea level. *Proceedings of the National Academy of Sciences*, *117*(25), 13983–13990. https://doi.org/10.1073/pnas.1922190117

Hingst, M. C., McQuiggan, R. W., Peters, C. N., He, C., Andres, A. S., & Michael, H. A. (2023). Surface Water-Groundwater Connections as Pathways for Inland Salinization of Coastal Aquifers. *Groundwater*, *61*(5), 626–638. https://doi.org/10.1111/gwat.13274

Hmieleski, J. I. (1994). *High Marsh-Forest Transitions in a Brackish Marsh: The Effects of Slope* [East Carolina University]. https://www.vcrlter.virginia.edu/thesis/Hmieleski94/Hmieleski.html

Holmgren, M., Scheffer, M., & Huston, M. A. (1997). The Interplay of Facilitation and Competition in Plant Communities. *Ecology*, *78*(7), 1966–1975. https://doi.org/10.1890/0012-9658(1997)078[1966:TIOFAC]2.0.CO;2

Hu, G., Liu, Y., Duo, T., Zhao, B., Cui, G., Ji, J., Kuang, X., Ervin, E. H., & Zhang, X. (2018). Antioxidant metabolism variation associated with alkali-salt tolerance in thirty switchgrass (Panicum virgatum) lines. *PLOS ONE*, *13*(6), e0199681. https://doi.org/10.1371/journal.pone.0199681

Hu, G., Liu, Y., Zhang, X., Yao, F., Huang, Y., Ervin, E. H., & Zhao, B. (2015). Physiological Evaluation of Alkali-Salt Tolerance of Thirty Switchgrass (Panicum virgatum) Lines. *PLOS ONE*, *10*(7), e0125305. https://doi.org/10.1371/journal.pone.0125305

Huang, H., Zinnert, J. C., Wood, L. K., Young, D. R., & D'Odorico, P. (2018). Non-linear shift from grassland to shrubland in temperate barrier islands. *Ecology*, *99*(7), 1671–1681. https://doi.org/10.1002/ecy.2383

Huizer, S., Karaoulis, M. C., Oude Essink, G. H. P., & Bierkens, M. F. P. (2017). Monitoring and simulation of salinity changes in response to tide and storm surges in a sandy coastal aquifer system. *Water Resources Research*, *53*(8), 6487–6509. https://doi.org/10.1002/2016WR020339

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., De Luca, E., Ebeling, A., Griffin, J. N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., … Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, *526*(7574), 574–577. https://doi.org/10.1038/nature15374

Islam, M. N., Wilson, C. A., & Watkins, T. R. (1982). Nutritional evaluation of seashore mallow seed, Kosteletzkya virginica. *Journal of Agricultural and Food Chemistry*, *30*(6), 1195–1198. https://doi.org/10.1021/jf00114a048

Janousek, C. N., & Folger, C. L. (2014). Variation in tidal wetland plant diversity and composition within and among coastal estuaries: Assessing the relative importance of environmental gradients. *Journal of Vegetation Science*, *25*(2), 534–545. https://doi.org/10.1111/jvs.12107

Jobe IV, J. G. D., & Gedan, K. (2021). Species-specific responses of a marsh-forest ecotone plant community responding to climate change. *Ecology*, *102*(4), e03296. https://doi.org/10.1002/ecy.3296

Jump, A. S., & Peñuelas, J. (2005). Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecology Letters*, *8*(9), 1010–1020. https://doi.org/10.1111/j.1461-0248.2005.00796.x

Kang, L., Ma, L., & Liu, Y. (2016). Evaluation of farmland losses from sea level rise and storm surges in the Pearl River Delta region under global climate change. *Journal of Geographical Sciences*, *26*(4), 439–456. https://doi.org/10.1007/s11442-016-1278-z

Kastler, J. A., & Wiberg, P. L. (1996). Sedimentation and Boundary Changes of Virginia Salt Marshes. *Estuarine, Coastal and Shelf Science*, *42*(6), 683–700. https://doi.org/10.1006/ecss.1996.0044

Kearney, W. S., Fernandes, A., & Fagherazzi, S. (2019). Sea-level rise and storm surges structure coastal forests into persistence and regeneration niches. *PLOS ONE*, *14*(5), e0215977. https://doi.org/10.1371/journal.pone.0215977

Kim, J., Liu, Y., Zhang, X., Zhao, B., & Childs, K. L. (2016). Analysis of salt-induced physiological and proline changes in 46 switchgrass (Panicum virgatum) lines indicates multiple response modes. *Plant Physiology and Biochemistry*, *105*, 203–212. https://doi.org/10.1016/j.plaphy.2016.04.020

Kim, S., Rayburn, A. L., Voigt, T., Parrish, A., & Lee, D. K. (2012). Salinity Effects on Germination and Plant Growth of Prairie Cordgrass and Switchgrass. *BioEnergy Research*, *5*(1), 225–235. https://doi.org/10.1007/s12155-011-9145-3

Kirwan, M. L., & Gedan, K. B. (2019). Sea-level driven land conversion and the formation of ghost forests. *Nature Climate Change*, *9*(6), 450–457. https://doi.org/10.1038/s41558-019-0488-7

Kiss, R., Deák, B., Török, P., Tóthmérész, B., & Valkó, O. (2018). Grassland seed bank and community resilience in a changing climate. *Restoration Ecology*, *26*(S2), S141–S150. https://doi.org/10.1111/rec.12694

Knowles, D. B., Bryant, Jr., W. B., & Pendleton, E. C. (1991). *Wrack as an agent of disturbance in an irregularly flooded marsh* (Open-File Report 91–03; M.M. Brinson, Ecology of a Nontidal Brackish Marsh in Coastal North Carolina, pp. 147–186). United States Fish and Wildlife Service.

Kuchler, A. W. (1964). *Manual to accompany the map of potential vegetation of the conterminous United States* (Vol. 77). American Geological Society. https://www.fs.usda.gov/database/feis/plants/graminoid/panvir/all.html#DISTRIBUTION%20AND%20OCCURRENCE

Kulp, S., & Strauss, B. H. (2017). Rapid escalation of coastal flood exposure in US municipalities from sea level rise. *Climatic Change*, *142*(3), 477–489. https://doi.org/10.1007/s10584-017-1963-7

Lenssen, J. P. M., van de Steeg, H. M., & de Kroon, H. (2004). Does Disturbance favour weak competitors? Mechanisms of changing plant abundance after flooding. *Journal of Vegetation Science*, *15*(3), 305–314. https://doi.org/10.1111/j.1654-1103.2004.tb02229.x

Liu, Y., Zhang, X., Miao, J., Huang, L., Frazier, T., & Zhao, B. (2014). Evaluation of Salinity Tolerance and Genetic Diversity of Thirty-Three Switchgrass (Panicum virgatum) Populations. *BioEnergy Research*, *7*(4), 1329–1342. https://doi.org/10.1007/s12155-014-9466-0

Liu, Y., Zhang, X., Tran, H., Shan, L., Kim, J., Childs, K., Ervin, E. H., Frazier, T., & Zhao, B. (2015). Assessment of drought tolerance of 49 switchgrass (Panicum virgatum) genotypes using physiological and morphological parameters. *Biotechnology for Biofuels*, *8*(1), 152. https://doi.org/10.1186/s13068-015-0342-8

Lonard, R. I., Judd, F. W., & Stalter, R. (2013). The Biological Flora of Coastal Dunes and Wetlands: Distichlis spicata (C. Linnaeus) E. Greene. *Journal of Coastal Research*, *29*(1), 105–117. https://doi.org/10.2112/JCOASTRES-D-12-00018.1

Long, E. V. (2015). *Establishment Practices and Monitoring of Seashore Mallow (Kosteletzkya pentacarpos) In Low-Lying Coastal Fields* [Senior Thesis]. University of Virginia.

Lundberg, P., Ranta, E., & Kaitala, V. (2000). Species loss leads to community closure. *Ecology Letters*, *3*(6), 465–468. https://doi.org/10.1111/j.1461-0248.2000.00170.x

Luo, F.-L., Jiang, X.-X., Li, H.-L., & Yu, F.-H. (2016). Does hydrological fluctuation alter impacts of species richness on biomass in wetland plant communities? *Journal of Plant Ecology*, *9*(4), 434–441. https://doi.org/10.1093/jpe/rtv065

Lyddon, C., Robins, P., Lewis, M., Barkwith, A., Vasilopoulos, G., Haigh, I., & Coulthard, T. (2023). Historic Spatial Patterns of Storm-Driven Compound Events in UK Estuaries. *Estuaries and Coasts*, *46*, 30–56. https://doi.org/10.1007/s12237-022-01115-4

Lynch, J. J. (1941). The Place of Burning in Management of the Gulf Coast Wildlife Refuges. *The Journal of Wildlife Management*, *5*(4), 454–457. https://doi.org/10.2307/3795690

McIntire, E. J. B., & Fajardo, A. (2014). Facilitation as a ubiquitous driver of biodiversity. *New Phytologist*, *201*(2), 403–416. https://doi.org/10.1111/nph.12478

McSteen, P. (2010). Auxin and Monocot Development. *Cold Spring Harbor Perspectives in Biology*, *2*(3), a001479–a001479. https://doi.org/10.1101/cshperspect.a001479

Merlin, A., Bonis, A., Damgaard, C. F., & Mesléard, F. (2015). Competition Is a Strong Driving Factor in Wetlands, Peaking during Drying Out Periods. *PLOS ONE*, *10*(6), e0130152. https://doi.org/10.1371/journal.pone.0130152

Molino, G. D., Carr, J. A., Ganju, N. K., & Kirwan, M. L. (2022). Variability in marsh migration potential determined by topographic rather than anthropogenic constraints in the Chesapeake Bay region. *Limnology and Oceanography Letters*, *7*(4), 321–331. https://doi.org/10.1002/lol2.10262

Mori, A. S. (2016). Resilience in the Studies of Biodiversity–Ecosystem Functioning. *Trends in Ecology & Evolution*, *31*(2), 87–89. https://doi.org/10.1016/j.tree.2015.12.010

Moser, B. R., Dien, B. S., Seliskar, D. M., & Gallagher, J. L. (2013). Seashore mallow (Kosteletzkya pentacarpos) as a salt-tolerant feedstock for production of biodiesel and ethanol. *Renewable Energy*, *50*, 833–839. https://doi.org/10.1016/j.renene.2012.08.016

Myhre, G., Alterskjær, K., Stjern, C. W., Hodnebrog, Ø., Marelle, L., Samset, B. H., Sillmann, J., Schaller, N., Fischer, E., Schulz, M., & Stohl, A. (2019). Frequency of extreme precipitation increases extensively with event rareness under global warming. *Scientific Reports*, *9*(1), 16063. https://doi.org/10.1038/s41598-019-52277-4

Najjar, R. G., Walker, H. A., Anderson, P. J., Barron, E. J., Bord, R. J., Gibson, J. R., Kennedy, V. S., Knight, C. G., PatrickMegonigal, J., O^{1}Connor, R. E., Polsky, C. D., Psuty, N. P., Richards, B. A., Sorenson, L. G., Steele, E. M., & Swanson, R. S. (2000). The potential impacts of climate change on the mid-Atlantic coastal region. *Climate Research*, *14*(3), 219–233. https://doi.org/10.3354/cr014219

National Centers for Environmental Information, N. O. and A. A. (2023, October). *County Mapping | Climate at a Glance | National Centers for Environmental Information (NCEI)*. Climate at a Glance: Country Mapping. https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/county/mapping

Nelissen, H., Gonzalez, N., & Inzé, D. (2016). Leaf growth in dicots and monocots: So different yet so alike. *Current Opinion in Plant Biology*, *33*, 72–76. https://doi.org/10.1016/j.pbi.2016.06.009

Neumann, B., Vafeidis, A. T., Zimmermann, J., & Nicholls, R. J. (2015). Future Coastal Population Growth and Exposure to Sea-Level Rise and Coastal Flooding—A Global Assessment. *PLOS ONE*, *10*(3), e0118571. https://doi.org/10.1371/journal.pone.0118571

Nicholls, R. J., & Leatherman, S. P. (1995). Global sea-level rise. In *K.M. Strzepek (ed.), As Climate Changes: International Impacts and Implication* (pp. 92–123). Cambridge University Press.

NOAA. (2023). *Sea Level Trends—NOAA Tides & Currents*. Sea Level Trends. https://tidesandcurrents.noaa.gov/sltrends/sltrends_station.shtml?id=8631044

NOAA US Department of Commerce. (2015). *What is a Nor'easter?* NOAA's National Weather Service. https://www.weather.gov/safety/winter-noreaster

Nordio, G., & Fagherazzi, S. (2022). Salinity increases with water table elevation at the boundary between salt marsh and forest. *Journal of Hydrology*, *608*. https://doi.org/10.1016/j.jhydrol.2022.127576

Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L., Petchey, O. L., Proença, V., Raffaelli, D., Suttle, K. B., Mace, G. M., Martín-López, B., Woodcock, B. A., & Bullock, J. M. (2015). Biodiversity and Resilience of Ecosystem Functions. *Trends in Ecology & Evolution*, *30*(11), 673–684. https://doi.org/10.1016/j.tree.2015.08.009

Padilla, F. M., & Pugnaire, F. I. (2006). The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and the Environment*, *4*(4), 196–202. https://doi.org/10.1890/1540-9295(2006)004[0196:TRONPI]2.0.CO;2

Pan, J., Sharif, R., Xu, X., & Chen, X. (2021). Mechanisms of Waterlogging Tolerance in Plants: Research Progress and Prospects. *Frontiers in Plant Science*, *11*. https://www.frontiersin.org/articles/10.3389/fpls.2020.627331

Parrish, D. J., & Fike, J. H. (2005). The Biology and Agronomy of Switchgrass for Biofuels. *Critical Reviews in Plant Sciences*, *24*(5–6), 423–459. https://doi.org/10.1080/07352680500316433

Pennings, S. C., Grant, M.-B., & Bertness, M. D. (2005). Plant Zonation in Low-Latitude Salt Marshes: Disentangling the Roles of Flooding, Salinity and Competition. *Journal of Ecology*, *93*(1), 159–167.

Pickett, S. T. A. (1989). *Long-Term Studies in Ecology* (pp. 110–135). https://doi.org/10.1007/978-1-4615-7358-6_5

Poiré, R., Wiese-Klinkenberg, A., Parent, B., Mielewczik, M., Schurr, U., Tardieu, F., & Walter, A. (2010). Diel time-courses of leaf growth in monocot and dicot species: Endogenous rhythms and temperature effects. *Journal of Experimental Botany*, *61*(6), 1751–1759. https://doi.org/10.1093/jxb/erq049

Poljakoff-Mayber, A., Somers, G. F., Werker, E., & Gallagher, J. L. (1992). Seeds of Kosteletzkya virginica (Malvaceae): Their Structure, Germination, and Salt Tolerance. I. Seed Structure and Germination. *American Journal of Botany*, *79*(3), 249–256. https://doi.org/10.2307/2445012

Poljakoff-Mayber, A., Somers, G. F., Werker, E., & Gallagher, J. L. (1994). Seeds of Kosteletzkya virginica (Malvaceae): Their structure, germination, and salt tolerance. II. Germination and salt tolerance. *American Journal of Botany*, *81*(1), 54–59. https://doi.org/10.1002/j.1537-2197.1994.tb15408.x

Pywell, R. F., Bullock, J. M., Hopkins, A., Walker, K. J., Sparks, T. H., Burke, M. J. W., & Peel, S. (2002). Restoration of species-rich grassland on arable land: Assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology*, *39*(2), 294–309. https://doi.org/10.1046/j.1365-2664.2002.00718.x

Pywell, R. F., Bullock, J. M., Tallowin, J. B., Walker, K. J., Warman, E. A., & Masters, G. (2007). Enhancing diversity of species-poor grasslands: An experimental assessment of multiple constraints. *Journal of Applied Ecology*, *44*(1), 81–94. https://doi.org/10.1111/j.1365-2664.2006.01260.x

Raposa, K. B., Weber, R. L. J., Ekberg, M. C., & Ferguson, W. (2017). Vegetation Dynamics in Rhode Island Salt Marshes During a Period of Accelerating Sea Level Rise and Extreme Sea Level Events. *Estuaries and Coasts*, *40*(3), 640–650. https://doi.org/10.1007/s12237-015-0018-4

Reed, D. J., Bishara, D. A., Cahoon, D. R., Donnelly, J., Kearney, M., Kolker, A. S., Leonard, L. L., Orson, R. A., & Stevenson, J. C. (2008). *Site-Specific Scenarios for Wetlands Accretion as Sea Level Rises in the Mid-Atlantic Region* (EPA Report No. 430R07004). EPA.

Rinehart, L. (2006). Switchgrass as a Bioenergy Crop. *National Center for Appropriate Technology*. http://attra. ncat. org/attra-pub/PDF/switchgrass. pdf (2006).

Ruan, C.-J., Li, H., Guo, Y.-Q., Qin, P., Gallagher, J. L., Seliskar, D. M., Lutts, S., & Mahy, G. (2008). Kosteletzkya virginica, an agroecoengineering halophytic species for alternative agricultural production in China's east coast: Ecological adaptation and benefits, seed yield, oil content, fatty acid and biodiesel properties. *Ecological Engineering*, *32*(4), 320–328. https://doi.org/10.1016/j.ecoleng.2007.12.010

Ruan, C.-J., Xing, W.-H., & Teixeira da Silva, J. A. (2012). Potential of five plants growing on unproductive agricultural lands as biodiesel resources. *Renewable Energy*, *41*, 191–199. https://doi.org/10.1016/j.renene.2011.10.022

Rubin, E. V. L., Blum, L. K., & Mills, A. L. (2024). Effect of Flooding on Water-Table Elevation and Salinity in an Abandoned Coastal Agricultural Field. *Journal of Coastal Research*. https://doi.org/10.2112/JCOASTRES-D-23-00071.1

Sallenger, A. H., Doran, K. S., & Howd, P. A. (2012). Hotspot of accelerated sea-level rise on the Atlantic coast of North America. *Nature Climate Change*, *2*(12), 884–888. https://doi.org/10.1038/nclimate1597

Sanderson, M. A., Reed, R. L., McLaughlin, S. B., Wullschleger, S. D., Conger, B. V., Parrish, D. J., Wolf, D. D., Taliaferro, C., Hopkins, A. A., Ocumpaugh, W. R., Hussey, M. A., Read, J. C., & Tischler, C. R. (1996). Switchgrass as a sustainable bioenergy crop. *Bioresource Technology*, *56*(1), 83–93. https://doi.org/10.1016/0960-8524(95)00176-X

Schieder, N. W., Walters, D. C., & Kirwan, M. L. (2018). Massive Upland to Wetland Conversion Compensated for Historical Marsh Loss in Chesapeake Bay, USA. *Estuaries and Coasts*, *41*(4), 940–951. https://doi.org/10.1007/s12237-017-0336-9

Schmer, M. R., Xue, Q., & Hendrickson, J. R. (2012). Salinity effects on perennial, warm-season (C_4) grass germination adapted to the northern Great Plains. *Canadian Journal of Plant Science*, *92*(5), 873–881. https://doi.org/10.4141/cjps2012-001

Shiflett, S. A. (2013). Changes in plant community composition and structure following restoration of maritime communities1. *The Journal of the Torrey Botanical Society*, *140*(1), 89–100. https://doi.org/10.3159/TORREY-D-12-00008.1

Shrestha, S. L., Sams, C., & Allen, F. (2022). Genotypic Variation for Salt Tolerance within and between 'Alamo' and 'Kanlow' Switchgrass (Panicum virgatum L.) Cultivars. *Agronomy*, *12*(4), Article 4. https://doi.org/10.3390/agronomy12040973

Snell, S. C. (2018). *Plant Guide for Virginia saltmarsh mallow (Kosteletzkya virginica)*. USDA-Natural Resources Conservation Service, Cape May Plant Materials Center, Cape May, NJ. https://plants.usda.gov/DocumentLibrary/plantguide/pdf/pg_kovi.pdf

Somers, G. F. (1982). Food and economic plants: General review. *Biosaline Research*, 127–148.

Sorrell, B. K., Tanner, C. C., & Brix, H. (2012). Regression analysis of growth responses to water depth in three wetland plant species. *AoB PLANTS*, *2012*, pls043. https://doi.org/10.1093/aobpla/pls043

Sun, Y., Niu, G., Ganjegunte, G., & Wu, Y. (2018). Salt Tolerance of Six Switchgrass Cultivars. *Agriculture*, *8*(5), Article 5. https://doi.org/10.3390/agriculture8050066

Sweet, W., Park, J., Marra, J., Zervas, C., & Gill, S. (2014). *Sea level rise and nuisance flood frequency changes around the United States* (Technical Report NOS CO-OPS 073). NOAA. https://repository.library.noaa.gov/view/noaa/30823

Taillie, P. J., Moorman, C. E., Poulter, B., Ardón, M., & Emanuel, R. E. (2019). Decadal-Scale Vegetation Change Driven by Salinity at Leading Edge of Rising Sea Level. *Ecosystems*, *22*(8), 1918–1930. https://doi.org/10.1007/s10021-019-00382-w

Thomas, C., & Carlson, C. R. (1999). *VCR LTER Dataset VCR99060—GPS Elevations of VCR/LTER Marshes* (VCR99060) [dataset]. Virginia Coast Reserve Long-Term Ecological Research Project Data Publication. https://www.vcrlter.virginia.edu/data/query/text/datasets/VCR99060.html

Thuma, J., Roulston, T., & Blum, L. (2020). Implications of Sea Level Rise for Bee Communities in Rural Eastern Virginia Coastal Habitats. *Journal of the Kansas Entomological Society*, *92*(4), 602–616. https://doi.org/10.2317/0022-8567-92.4.602

Tilman, D. (1997). Community Invasibility, Recruitment Limitation, and Grassland Biodiversity. *Ecology*, *78*(1), 81–92. https://doi.org/10.1890/0012-9658(1997)078[0081:CIRLAG]2.0.CO;2

Titus, J. G., Hudgens, D., Hershner, C., Kasskian, J. M., Penumalli, P. R., Berman, M., & Nuckols, W. H. (2010). *Virginia: The Likelihood of Shore Protection*. *1*. http://risingsea.net/ERL/VA.html

Tolbert, V. R., Joslin, J. D., Bock, B. R., Bandaranayake, W., Houston, A. E., & Tyler, D. D. (2000). Increasing below-ground carbon sequestration with conversion of agricultural lands to production of bio-energy crops. *New Zealand Journal of Forestry Science*, *30*(1/2), 138–149.

Tully, K., Gedan, K., Epanchin-Niell, R., Strong, A., Bernhardt, E. S., BenDor, T., Mitchell, M., Kominoski, J., Jordan, T. E., Neubauer, S. C., & Weston, N. B. (2019). The Invisible Flood: The Chemistry, Ecology, and Social Implications of Coastal Saltwater Intrusion. *BioScience*, *69*(5), 368–378. https://doi.org/10.1093/biosci/biz027

USDA NRCS. (2012). *Release Brochure for Switchgrass (Panicum virgatum)*. James E. “Bud” Smith Plant Materials Center, Knox City, TX. https://www.nrcs.usda.gov/plantmaterials/txpmcrb11189.pdf

USGS Water Resources Mission Area. (2019, March 2). *Saltwater Intrusion*. Saltwater Intrusion | U.S. Geological Survey. https://www.usgs.gov/mission-areas/water-resources/science/saltwater-intrusion#overview

Vaughn, S. F., Moser, B. R., Dien, B. S., Iten, L. B., Thompson, A. R., Seliskar, D. M., & Gallagher, J. L. (2013). Seashore mallow (Kosteletzkya pentacarpos) stems as a feedstock for biodegradable absorbents. *Biomass and Bioenergy*, *59*, 300–305. https://doi.org/10.1016/j.biombioe.2013.06.010

Voutsina, N. (2012). *SEASHORE MALLOW (KOSTELETZKYA PENTACARPOS) AS AN ECOSYSTEM ENGINEER: COMMUNITY DYNAMICS AND GROWTH*. University of Delaware.

Voutsina, N., Seliskar, D. M., & Gallagher, J. L. (2015a). The Facilitative Role of Kosteletzkya pentacarpos in Transitioning Coastal Agricultural Land to Wetland During Sea Level Rise. *Estuaries and Coasts*, *38*(1), 35–44. https://doi.org/10.1007/s12237-014-9795-4

Voutsina, N., Seliskar, D. M., & Gallagher, J. L. (2015b). The Facilitative Role of Kosteletzkya pentacarpos in Transitioning Coastal Agricultural Land to Wetland During Sea Level Rise. *Estuaries and Coasts*, *38*(1), 35–44. https://doi.org/10.1007/s12237-014-9795-4

Wahl, T., Jain, S., Bender, J., Meyers, S. D., & Luther, M. E. (2015). Increasing risk of compound flooding from storm surge and rainfall for major US cities. *Nature Climate Change*, *5*(12), 1093–1097. https://doi.org/10.1038/nclimate2736

Wasson, K., Woolfolk, A., & Fresquez, C. (2013). Ecotones as Indicators of Changing Environmental Conditions: Rapid Migration of Salt Marsh–Upland Boundaries. *Estuaries and Coasts*, *36*(3), 654–664. https://doi.org/10.1007/s12237-013-9601-8

Watson, E. B., Wigand, C., Cencer, M., & Blount, K. (2015). Inundation and precipitation effects on growth and flowering of the high marsh species Juncus gerardii. *Aquatic Botany*, *121*, 52–56. https://doi.org/10.1016/j.aquabot.2014.10.012

Weiher, E., & Keddy, P. A. (1995). The Assembly of Experimental Wetland Plant Communities. *Oikos*, *73*(3), 323–335. https://doi.org/10.2307/3545956

Wheeler, M. M., Neill, C., Loucks, E., Weiler, A., Von Holle, B., Pelikan, M., & Chase, T. (2015). Vegetation removal and seed addition contribute to coastal sandplain grassland establishment on former agricultural fields. *Restoration Ecology*, *23*(5), 539–547. https://doi.org/10.1111/rec.12253

White, E., & Kaplan, D. (2017). Restore or retreat? Saltwater intrusion and water management in coastal wetlands. *Ecosystem Health and Sustainability*, *3*(1), e01258. https://doi.org/10.1002/ehs2.1258

Whitelaw, R. T. (1951). *Virginia's Eastern Shore: A History of Northampton and Accomack Counties* (Vol. 1). Virginia Historical Society.

Wilson, S. D., & Tilman, D. (1991). Interactive Effects of Fertilization and Disturbance on Community Structure and Resource Availability in an Old-Field Plant Community. *Oecologia*, *88*(1), 61–71.

Yordanova, R. Y., Alexieva, V. S., & Popova, L. P. (2003). Influence of Root Oxygen Deficiency on Photosynthesis and Antioxidant Status in Barley Plants1. *Russian Journal of Plant Physiology*, *50*(2), 163–167. https://doi.org/10.1023/A:1022908811211

Zanetti, F., Zegada-Lizarazu, W., Lambertini, C., & Monti, A. (2019). Salinity effects on germination, seedlings and full-grown plants of upland and lowland switchgrass cultivars. *Biomass and Bioenergy*, *120*, 273–280. https://doi.org/10.1016/j.biombioe.2018.11.031

Zedler, J. B. (2010). How frequent storms affect wetland vegetation: A preview of climate-change impacts. *Frontiers in Ecology and the Environment*, *8*(10), 540–547. https://doi.org/10.1890/090109

Zhang, S., Sun, F., Wang, W., Yang, G., Zhang, C., Wang, Y., Liu, S., & Xi, Y. (2019). Comparative transcriptome analysis provides key insights into seedling development in switchgrass (Panicum virgatum L.). *Biotechnology for Biofuels*, *12*(1), 193. https://doi.org/10.1186/s13068-019-1534-4

Zhou, G., Xia, Y., Ma, B. L., Feng, C., & Qin, P. (2010). Culture of Seashore Mallow under Different Salinity Levels Using Plastic Nutrient-Rich Matrices and Transplantation. *Agronomy Journal*, *102*(2), 395–402. https://doi.org/10.2134/agronj2009.0274

Zhou, J., Wan, S. W., Li, G., & Qin, P. (2011). Ultrastructure changes of seedlings of Kosteletzkya virginica under waterlogging conditions. *Biologia Plantarum*, *55*(3), 493–498. https://doi.org/10.1007/s10535-011-0115-6

Zhou, J., Zheng, L.-D., Pan, X., Li, W., Kang, X.-M., Li, J., Ning, Y., Zhang, M.-X., & Cui, L.-J. (2018). Hydrological Conditions Affect the Interspecific Interaction between Two Emergent Wetland Species. *Frontiers in Plant Science*, *8*. https://www.frontiersin.org/articles/10.3389/fpls.2017.02253

zu Ermgassen, P. S. E., Baker, R., Beck, M. W., Dodds, K., zu Ermgassen, S. O. S. E., Mallick, D., Taylor, M. D., & Turner, R. E. (2021). Ecosystem Services: Delivering Decision-Making for Salt Marshes. *Estuaries and Coasts*, *44*(6), 1691–1698. https://doi.org/10.1007/s12237-021-00952-z

APPENDIX A

Table A 1. Summary of weather events from January 2016 to November 2019. Table continues on the next page. (Source: NOAA Tides and Currents, Weather Underground Historical Data)

Event Number	Date	Type	Measured Maximum Tide (m)	Predicted Maximum Tide (M)	Difference in Measured and Predicted Tide (m)	Maximum Wind Gust (m/s)	Wind Direction	Precipitation (cm)
1	January 22-24, 2016	Tide	1.986	0.649	0.83	29.7	NE	0
2	February 8-10, 2016	Tide	1.56	0.711	0.69	6.7	NE	0.1
3	April 28 – May 9, 2016	Both	1.511	0.863	0.44	11.6	NNW	5.8
4	September 19-22, 2016	Precipitation	1.061	0.904	0.17	13.6	ENE	5.1
5	September 29 – October 4, 2016	Tide	1.41	0.715	0.56	13.4	ENE	0.5
6	October 8-10, 2016	Both	1.068	0.405	.44	24.6	N	14.7
7	April 23-27, 2017	Precipitation	1.237	0.818	0.32	16..7	NE	2.5
8	May 5-8, 2017	Precipitation	0.862	0.525	0.19	11.1	S	4.9
9	May 23-30, 2017	Precipitation	1.313	0.903	0.37	11.6	NE	8.1
10	July 6-8, 2017	Both	0.838	0.681	0.15	9.7	SW	1.2
11	July 28-30, 2017	Both	1.21	0.483	0.56	14.1	NE	3.9
12	September 17-21, 2017	Tide	1.498	0.808	0.53	9.5	NE	0
13	October 12-14, 2017	Tide	1.414	0.753	0.661	17.1	NE	0.43
14	November 4-10, 2017	Tide	1.398	0.817	0.39	10.2	NE	0.56
15	December 3-5, 2017	Tide	1.165	0.874	0.29	5.2	NE	0
16	January 4-5, 2018	Both	0.977	0.779	-0.01	23.5	NNW	1.7
17	March 3-8, 2018	Tide	1.41	0.63	0.65	18.3	W	1.4
18	March 20-22, 2018	Both	1.368	0.66	0.52	19.1	NE	3.3

Event Number	Date	Type	Measured Maximum Tide (m)	Predicted Maximum Tide (M)	Difference in Measured and Predicted Tide (m)	Maximum Wind Gust (m/s)	Wind Direction	Precipitation (cm)
19	June 10-13, 2018	Precipitation	1.21	0.747	0.34	17	NE	8.7
20	July 7-16, 2018	Both	1.16	0.898	0.15	9.1	NE	1.1
21	July 21-26, 2018	Precipitation	1.055	0.614	0.21	11.1	WSW	8.2
22	August 30 - September 2, 2018	Precipitation	0.919	0.659	0.103	3.1	W	3.5
23	September 8-12, 2018	Tide	1.762	0.9	0.51	16.7	NE	0.8
24	October 11-13, 2018	Tide	1.245	0.649	0.38	17.9	SE	0.3
25	October 26-27, 2018	Tide	1.341	0.811	0.47	15.2	E	0
26	November 13-16, 2018	Both	0.954	0.473	0.52	18.6	ENE	6.4
27	November 25-27, 2018	Tide	1.257	0.78	0.39	14	SSE	0.3
28	January 19-20, 2019	Tide	1.31	0.742	0.4	5.7	NE	1.2
29	July 1-5, 2019	Tide	1.118	0.84	0.25	6.3	N	0
30	July 7-9, 2019	Precipitation	1.035	0.615	0.31	9.1	SW	14
31	August 25-28, 2019	Tide	1.3	0.739	0.45	14.4	NE	0.1
32	September 6-7, 2019	Both	1.493	0.724	0.61	19.5	NE	6.4
33	September 29-30, 2019	Tide	1.255	0.936	0.45	11.8	NE	0
34	October 8-12, 2019	Tide	1.524	0.662	0.63	15.5	NE	1.2
35	October 15-17, 2019	Precipitation	1.053	0.729	0.21	13.7	S	3.9
36	October 20-23, 2019	Precipitation	1.125	0.656	0.32	10.3	E	12
37	October 27-31, 2019	Tide	1.34	0.952	0.3	9.6	NE	0
38	November 16-19, 2019	Tide	1.403	0.624	0.68	15.8	NE	0.2

APPENDIX B

Table B 1. Dry weight biomass of *K. pentacarpos* seed per individual plant collected at three different site types. Number of seeds produced by each plant was calculated based on the dry weight of seed for each field type ($y=0.0143x+0.0411$, $r^2=0.9997$). On average, every flower produces a capsule with five seeds.

Site Type	**Seed (g)**	**# of Seed**	**# of Flowers**
Farm	0.6374	64.557692	12.91153846
Marsh	4.055526	393.22368	78.64473684
Old Field	4.056333	393.30128	78.66025641

Table B 2. Post-hoc ANOVA statistics for testing the effects of salinity on growth rate within species.

Species	DF	Type III Sum of Squares	Mean Square	F Value	p value
Mallow	2	0.00188	0.00094	2.84	0.0757
Switchgrass	2	0.00128	0.00064	0.00	0.9951

Table B 3. Post-hoc comparison of least squares means p-values for the slope of K. pentacarpos ($\alpha=0.05$) using Tukey's adjustment for multiple comparisons.

Salinity	0 ppt	3 ppt	7 ppt
0 ppt		0.7587	0.0690
3 ppt	0.7587		0.2566
7 ppt	0.0690	0.2566	

Table B 4. Post-hoc comparison of least squares means p-values for the slope of P. virgatum (α=0.05) using Tukey's adjustment for multiple comparisons.

Salinity	0 ppt	3 ppt	7 ppt
0 ppt		0.9988	0.9983
3 ppt	0.9988		0.9947
7 ppt	0.9983	0.9947	

Table B 5. Mean plant height, percent germination, and survival of salt marsh mallow and switchgrass for three salinity treatments (mean ± standard error).

Salinity (ppt)	Height (cm)		Expected Germination (%)		Survival (%)	
	Mallow	Switchgrass	Mallow	Switchgrass	Mallow	Switchgrass
0	5.27 ± 0.12	3.31 ± 0.537	125.0 ± 5.27	62 ± 9.17	85.0 ± 6.5	22.8 ± 10.3
3	4.86 ± 0.10	4.39 ± 0.53	100.0 ± 5.27	84 ± 14.24	87.5 ± 5.6	29.0 ± 8.0
7	4.39 ± 0.10	3.11 ± 0.48	115.0 ± 10.0	69 ± 12.86	80.2 ± 8.1	16.0 ± 4.5

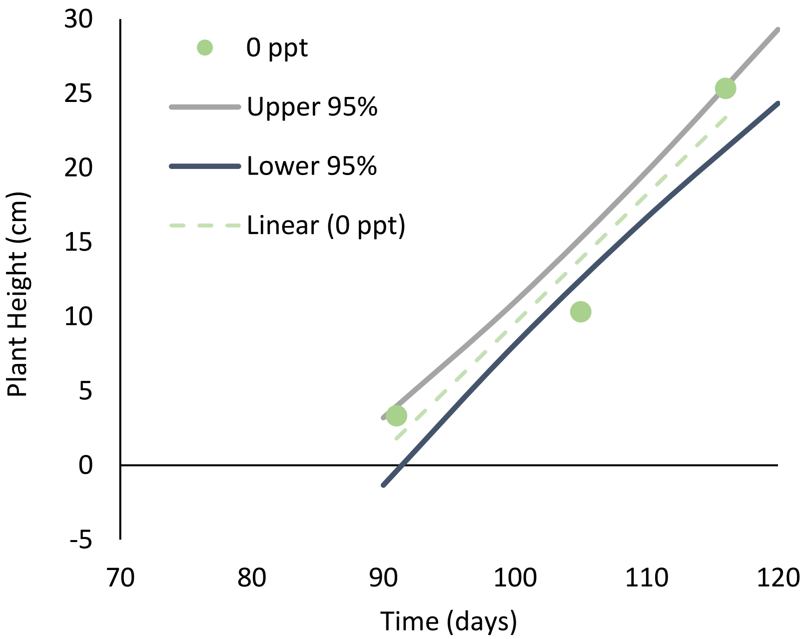


Figure B 1. Linear regression and 95% confidence intervals for the last three measures of mean plant height (cm) as a function of time (days) for switchgrass at 0 parts per thousand salinity treatment. $y=0.8628x – 76.722$, $R^2 = 0.9253$

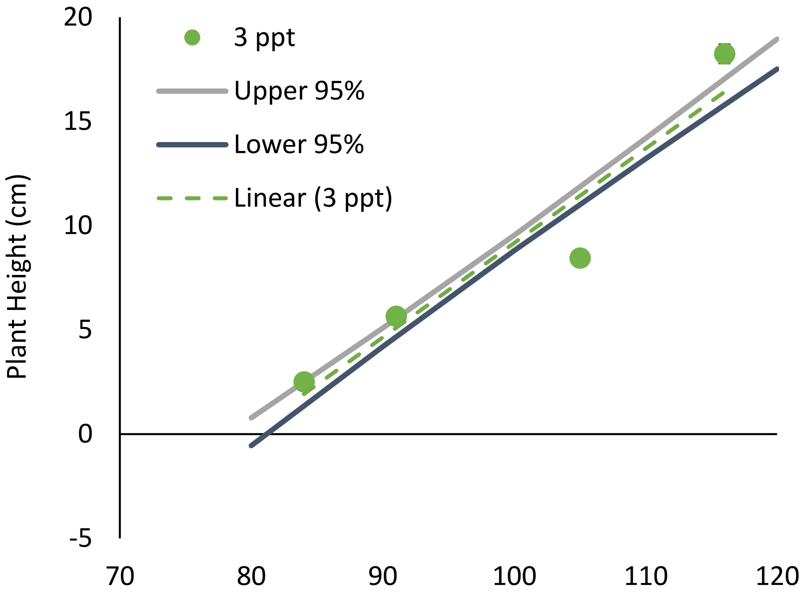


Figure B 2. Linear regression and 95% confidence intervals for the last three measures of mean plant height (cm) as a function of time (days) for switchgrass at 3 parts per thousand salinity treatment. $y=0.4529x - 36.117$, $R^2 = 0.9072$

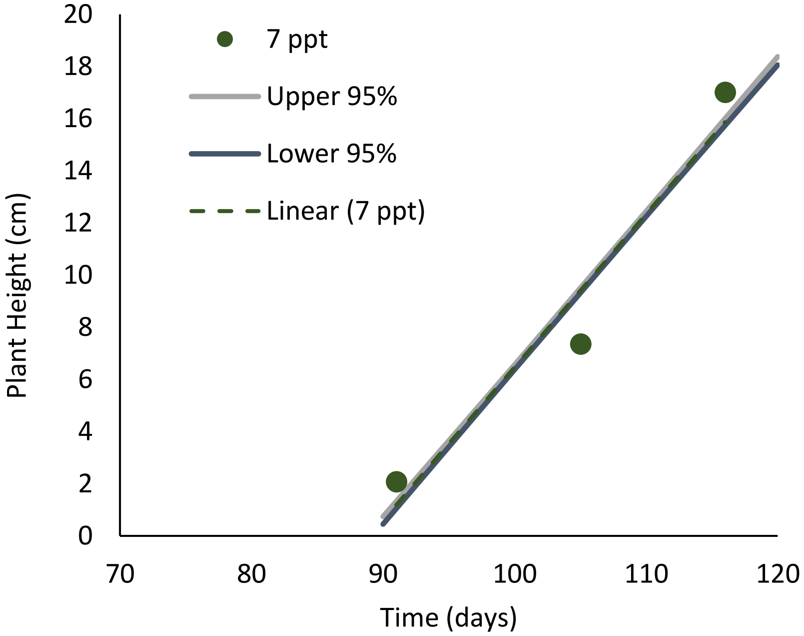


Figure B 3. Linear regression and 95% confidence intervals for the last three measures of mean plant height (cm) as a function of time (days) for switchgrass at 7 parts per thousand salinity treatment. $y=0.5874x - 52.271$, $R^2 = 0.9448$

APPENDIX C

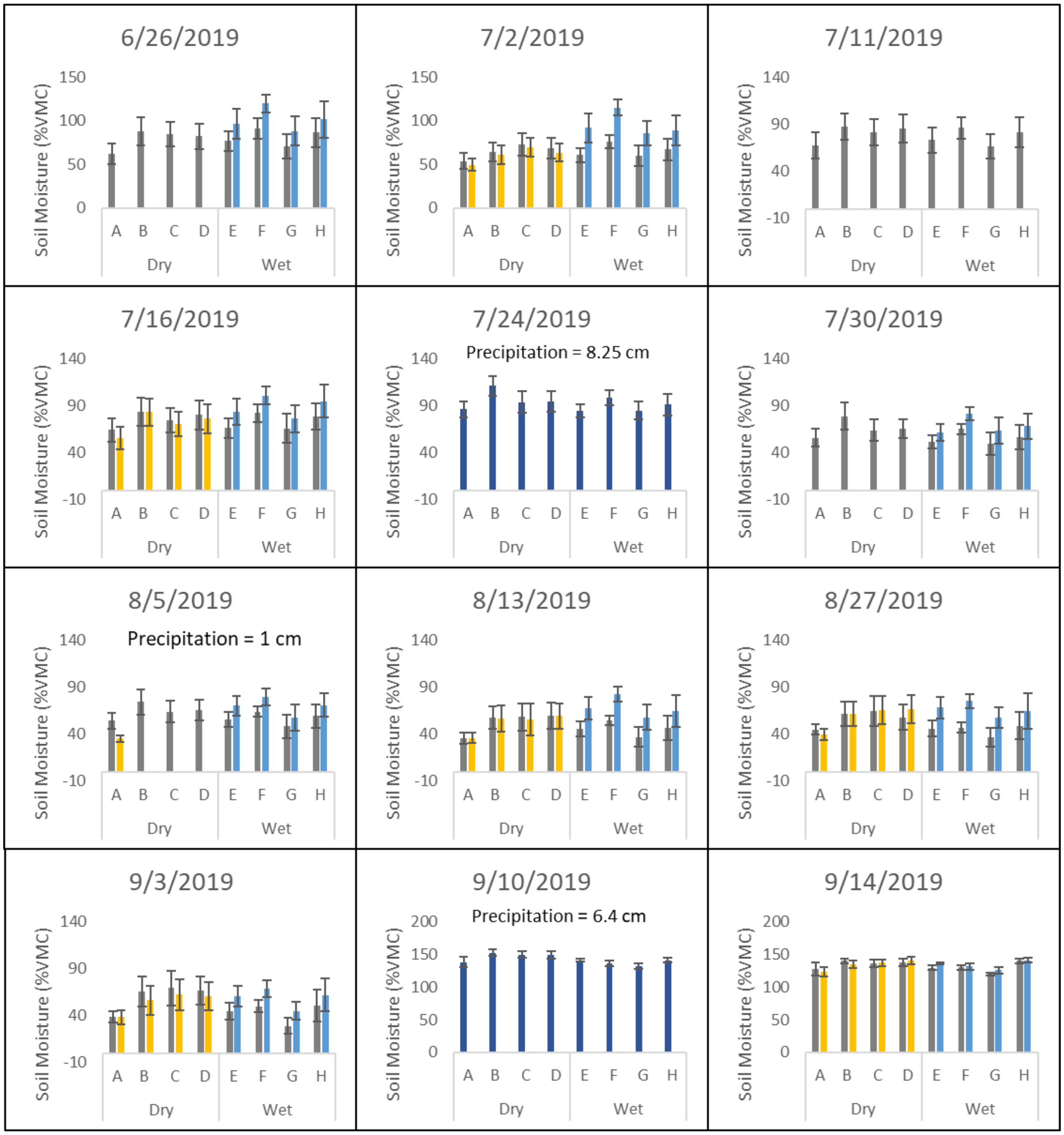


Figure C 1. Effect of the addition of water for the duration of the field experiment (June 26 – September 14, 2019). Gray bars show the initial soil moisture (%VMC); gold bars show the soil moisture in the dry plots after the watering treatment; light blue bars show the soil moisture of the wet plots after the watering treatment; dark blue bars show soil moisture measurements after recorded precipitation events when no watering treatment was applied. Bars show the standard error of the mean (n=5). Watering almost always made the plots wetter, whereas the dry plots remained the same or got drier.

Table C 1. Initial percent cover and number of plants present in watering experiment plots two weeks after planting on June 15, 2019. The low percent cover reflects the age and maturity of the seedlings. The estimation of percent cover and number of plants for switchgrass may be artificially high due to the inability to distinguish switchgrass from other grass species at such a young age. Multiple grass species were likely present in the seed bank.

Water Treatment	Plot ID	Seeding Treatment	% Cover Mallow	% Cover Switchgrass	# of Mallow plants	# of Switchgrass plants
Dry	A1	2	5	2	36	16
Dry	A2	1	5	15	28	53
Dry	A3	4	<1	5	6	30
Dry	A4	5	-	2	-	22
Dry	A5	3	3	-	21	-
Dry	B1	3	3	2	20	20
Dry	B2	2	3	4	23	42
Dry	B3	5	-	2	-	24
Dry	B4	1	<1	<1	26	6
Dry	B5	4	<1	-	3	-
Dry	C1	1	5	<1	26	6
Dry	C2	2	4	2	27	15
Dry	C3	3	1	1	11	8
Dry	C4	4	<1	<1	4	1
Dry	C5	5	-	2	-	16
Dry	D1	3	<1	<1	9	5
Dry	D2	5	-	2	-	20
Dry	D3	1	6	<1	41	3
Dry	D4	2	2	-	14	-
Dry	D5	4	<1	1	5	12
Wet	E1	4	<1	<1	4	3
Wet	E2	2	1	2	12	17
Wet	E3	5	-	3	-	22
Wet	E4	3	2	<1	13	2
Wet	E5	1	4	2	24	16
Wet	F1	2	7	5	45	42
Wet	F2	5	-	-	-	-
Wet	F3	4	<1	4	3	33
Wet	F4	3	3	<1	22	3
Wet	F5	1	2	1	12	11
Wet	G1	4	<1	3	8	22
Wet	G2	1	3	<1	16	6
Wet	G3	2	3	1	15	8
Wet	G4	5	-	<1	-	4
Wet	G5	3	3	1	14	12
Wet	H1	1	5	5	31	39
Wet	H2	2	3	1	23	8
Wet	H3	5	-	2	-	12
Wet	H4	4	2	<1	12	3
Wet	H5	3	1	2	8	17

Figure C 2. Interaction plots for the variables base cover (%) and final cover (%) and the wet and dry treatments for two species, *Kosteletzkya penatacarpos* (a) and *Panicum virgatum* (b). A marginally significant interaction is observed for *K. pentacarpos*, implying an effect of watering on percent cover. No interaction is observed for *P. virgatum*.

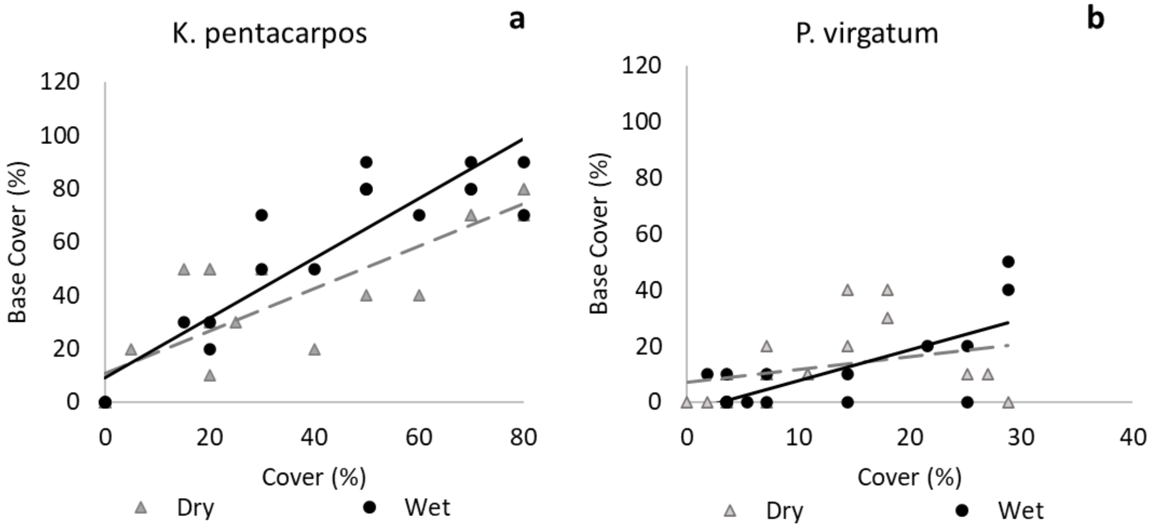


Figure C 2. Initial percent cover of the experimental plots measured on July 24, 2019, for salt marsh mallow (%MM), switchgrass (% SWG), bare ground (% Bare), and other species (% Other). The small size and young age of the seedlings may have resulted in an overestimation of the percent cover of switchgrass.