ABSTRACT

Title of Thesis:	NATIVE PLANTING IN TIDAL WETLANDS FOR *PHRAGMITES AUSTRALIS* MANAGEMENT: FIELD AND MESOCOSM EXPERIMENTS
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Efforts have been made in U.S. wetlands to eradicate the invasive grass *Phragmites australis*. But eradication of *Phragmites* does not always lead to the return of native plants. This research investigated native vegetation recolonization across 12 tidal wetland study sites in the Chesapeake Bay watershed and tested the potential of planting perennial native wetland species to accelerate site recovery following *Phragmites* removal. Our study found that site salinity was a dominant driver of plant recolonization

rate: low salinity sites (0.5-3 ppt) had, on average, 4.3x greater aboveground biomass and 2.5x higher vegetation cover than brackish sites (5-9 ppt) two or more growing seasons after *Phragmites* removal. The composition of returning plant species also differed by salinity, with a higher abundance of annuals and fewer graminoids at low-salinity sites. Site hydrology also influenced native plant recolonization—more frequently flooded sites had lower aboveground biomass of native vegetation two or more years following *Phragmites* removal. Experimental planting had variable results, with high die-off at several sites, but showed potential to accelerate vegetation recovery at brackish sites in the first years after *Phragmites* removal—plots with transplants at brackish sites had 17.5x, 2.4x, and 1.5x higher plant cover than unplanted plots in years one, two, and three, respectively, after planting. All sites had some amount of native vegetation recovery within three to four years following *Phragmites* removal, suggesting that native planting may not be necessary for many tidal wetland sites. Sites with especially high salinities and flooding frequencies may benefit the most from plantings, as larger plants may be able to survive in conditions that are not favorable for seedling emergence. In a mesocosm experiment, we planted six different clonal wetland species in a sand-vermiculite mixture at three different elevations in a tidal creek on the Rhode River in Maryland, USA. We found that peak plant biomass in the sandy substrate occurred at lower elevations and higher flooding frequencies than is typical in marsh environments and than was observed in other mesocosm experiments with organic soils. In well-drained, sandy substrates, wetland plants may benefit from more frequent tidal pulses, likely due to increased water supply and nutrient flux. This has implications for wetland-restoration practitioners using dredged sand to create or elevate tidal wetlands, as wetland species may grow at different elevations and flooding frequencies in these conditions than in a typical tidal marsh with organic soils.

NATIVE PLANTING IN TIDAL WETLANDS FOR *PHRAGMITES AUSTRALIS* MANAGEMENT: FIELD AND MESOCOSM EXPERIMENTS

By

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Chapter 1: Introduction

Wetlands are especially vulnerable to plant invasions due to their position in the landscape, where they accumulate water, sediment, nutrients, contaminants, and debris, which can disperse seeds and create disturbances, allowing opportunistic species to become established (Zedler and Kercher 2004). To protect these ecosystems from the biodiversity loss associated with invasive species, land managers across the world pour resources into invasive species management, often with mixed success (Reid et al. 2009). Successful invasive plant management involves not only eliminating the invader but also restoring a site to its full ecosystem functioning. In wetlands, restoring native vegetation can both prevent re-invasion (Byun et al. 2013) and restore the ecosystem services of a healthy wetland (e.g., animal habitat, water quality enhancement, and carbon storage). Restoration can involve creating the conditions for growth (e.g., restoring wetland hydrology or reducing nutrient runoff) and relying on the seedbank or seed dispersal to begin the revegetation process. Alternatively, if the seed bank is poor and seed dispersal is limited, seeding can be necessary to establish plant recolonization (Kettenring and Tarsa 2020). Another alternative is using native plantings, either grown in nurseries or transplanted sods from a native plant community, which often has higher success than seeding, but requires a higher upfront financial and time investment (Palma and Laurance 2015).

In tidal wetlands in the United States mid-Atlantic region, *Phragmites australis* ssp. *australis*, a grass species of Eurasian lineage, has spread widely (Saltonstall 2002), posing a threat to native plant and animal biodiversity (Silliman and Bertness 2004; Hunter et al. 2006; Robichaud and Rooney 2017). *Phragmites* is the tallest grass in the region, growing up to six meters and in dense monocultures that crowd out native plants. *Phragmites* grows deeper roots than most plants, which allow it to access

additional nutrients (Mozdzer et al. 2016). There is also evidence that *Phragmites* can outcompete native species through allelopathy, where root exudates and litter decomposition release phytotoxins into the soil (Uddin et al. 2017). Because of *Phragmites'* high aboveground and belowground productivity relative to other wetland plant species, it has been suggested that *Phragmites* may provide benefits in a changing climate, as tidal wetlands are submerging under rising seas and face increasing storm pressures. For instance, a modeling study found that *Phragmites* marshes provide better flood protection than native cattail marshes, reducing storm damage to inland areas (Sheng et al. 2021). In addition, it has been suggested that *Phragmites* has potential to elevate marshes that are submerging under sea level rise and can effectively sequester carbon through litter and root production (Rooth et al. 2003; Caplan et al. 2015). But it has also been shown that *Phragmites* can act as a barrier to native plants migrating upland as sea levels rise, leading to shrinking of native marshes (Kirwan and Gedan 2019; Jobe IV and Gedan 2021). The holistic effects of *Phragmites* on tidal marshes, particularly in response to global change, are still not fully understood.

Management of *Phragmites australis* is challenging, as one-time eradication efforts are rarely sufficient to eliminate it from a site; multi-year management is typically required (Hazelton et al. 2014). In fact, simply mowing *Phragmites* can stimulate its growth and increase stem density (Hazelton et al. 2014). Successful strategies typically include pesticide application or solarization (covering the soil surface with black plastic, which heats the soil to temperatures that are lethal to *Phragmites* rhizomes) in combination with a form of biomass removal, such as mowing, cutting, or burning (Hazelton et al. 2014; Rohal et al. 2019).

However, *Phragmites* eradication does not necessarily lead to native plant regrowth. Wetland recovery can be variable (Hazelton et al. 2014; Rohal et al. 2019). Planting native species following

Phragmites removal may have potential to accelerate site recovery and restore ecosystem functions—e.g., by protecting soils from erosion through the establishment of strong root systems, providing animal habitat, and continuing carbon sequestration. Planting is often part of wetland restoration, but the research on its benefits, successes, and failures is limited, particularly for tidal wetlands.

In this study, we tested native planting in both a field and mesocosm experiment to explore the potential of using plantings as part of post-*Phragmites* ecosystem restoration. In our field experiment, we removed *Phragmites* and planted five different perennial native wetland species across 12 tidal wetland sites in Maryland, USA. Our goal was to assess native vegetation recovery and site ecosystem functions following *Phragmites* eradication with and without native plantings. In a mesocosm experiment, we planted the same species, as well as *Phragmites,* at three different elevations in a tidal creek, to help inform the ideal tidal position for the planting of each species and to quantify carbon stored by the different species. We planted the mesocosms in a mixture of sand and vermiculite to facilitate analysis of root production and carbon storage, inadvertently creating well-drained, oxidized soil conditions that differ from those in reduced, organic tidal wetland soils. We later realized that the mesocosm soil conditions may reflect those used in restored wetlands that use dredged sand as a substrate—the growth patterns of species in our mesocosms may help inform how wetland plants respond to tidal inundation in sandy substrates at restored wetland sites.

Chapter 2: Restoration of Native Wetland Vegetation following *Phragmites australis* Management: A Field Experiment

Introduction

Phragmites australis ssp. *australis* is a grass species of Eurasian lineage that has expanded rapidly into wetlands throughout the continental United States and southern Canada in recent decades (Saltonstall 2002). *Phragmites*' rapid spread is facilitated in part by disturbances and nutrient enrichment in wetlands – conditions that allow *Phragmites* seedlings to become established and obtain a competitive advantage over native wetland species (McCormick et al. 2010; Kettenring et al. 2011; Kettenring et al. 2015). Its spread is of particular concern in the United States mid-Atlantic region, where our study is conducted and where *Phragmites* is a dominant species in tidal freshwater and brackish wetlands (Chambers 1999).

Phragmites australis is a threat to biodiversity, as it grows in dense, tall monocultures that crowd out native plants as well as certain estuarine animals that depend on native plant species (Meyerson et al. 2000; Silliman and Bertness 2004; Hunter et al. 2006; Robichaud and Rooney 2017). However, *Phragmites'* rapid growth can also provide certain beneficial ecosystem services, including nutrient and heavy-metal sequestration, carbon storage, and storm protection (Meyerson et al. 2000; Windham et al. 2003; Kiviat 2013; Caplan et al. 2015; Sheng et al. 2021). The effects of *Phragmites* on wetland ecosystems are complex and still not fully understood, particularly in a changing climate. It has been suggested that *Phragmites* may enhance coastal wetland resilience to sea level rise by elevating the marsh surface (Rooth et al. 2003), but *Phragmites* growing at the coastal wetland-upland boundary may

also block upland migration of native species under pressure from rising seas, leading to further shrinking of native marsh habitat (Kirwan and Gedan 2019; Jobe IV and Gedan 2021).

Phragmites eradication, especially for smaller patches, has been shown to be possible through multi-year control; effective methods include a combination of physical removal (e.g., through mowing, cutting, or burning) and pesticide application or solarization (covering cut stems with black plastic to heat and kill rhizomes) (Hazelton et al. 2014; Rohal et al. 2019). Removing small stands following an initial invasion may be critical for management, as small populations have lower genetic variation and don't produce as many viable seeds, but as a stand grows, genetic diversity and seed viability increases, leading to further spread of *Phragmites* (Kettenring et al. 2011). In addition, small patches may have the greatest potential for native plant recolonization (Rohal et al. 2019). Eradication of invasive species and restoration of native plant communities may also be more successful at sites with limited degradation, where there is still a thriving native plant community (Reid et al. 2009).

Even with extensive management efforts, *Phragmites* control doesn't always lead to native plant recovery – native plants can be slow to revegetate certain sites, allowing for *Phragmites* reinvasion and potentially impairing wetland ecosystem functions during a recovery period (Martin and Blossey 2013; Hazelton et al. 2014; Rohal et al. 2019; Rohal et al. 2021). *Phragmites* stands in tidal wetlands can contain robust seed banks with an array of diverse native species (Hallinger and Shisler 2009; Baldwin et al. 2010), but despite their presence in the seed bank, native species don't always germinate after *Phragmites* is removed. Further, the first species to emerge following a disturbance are typically annuals, which may not provide the same ecosystem services of a mature, perennial plant community; native graminoids were found to be underrepresented in emerging plant communities following *Phragmites* eradication (Rohal et al. 2021).

Differences in native vegetation recovery following *Phragmites* removal can be due to differences in hydrology and site degradation, among other factors (Carlson et al. 2009; Rohal et al. 2019; Rohal et al. 2021). Multi-site experiments are thus critical to understand the range of ecosystem responses to *Phragmites* removal. Further, limited or slow revegetation from the seed bank may suggest a need for active revegetation through native planting (Hazelton et al. 2014; Rohal et al. 2019; Rohal et al. 2021). Previous research has found that the presence of native plants can competitively exclude *Phragmites* and prevent reinvasion (Wang et al. 2006; Peter and Burdick 2010; Byun et al. 2013), although no previous field experiments, to our knowledge, have included native plantings as part of post-*Phragmites* restoration efforts.

Native plantings used as part of tidal wetland restoration can face a wide range of stresses, including anoxia in saturated or flooded soils (Gleason and Zieman 1981) and erosion stress generated by wind or currents (Callaghan et al. 2010). Recent research has shown that in these stressful tidal wetland conditions, clumped, closely spaced plantings can facilitate each other's growth, compared to more dispersed, evenly spaced planting designs often used in wetland restoration projects (Silliman et al. 2015; Renzi et al. 2019; Duggan-Edwards et al. 2020).

In this study, we planted native wetland species after removing *Phragmites* across 12 tidal wetland sites along three different tributaries of the Chesapeake Bay in Maryland, USA. We selected perennial, clonal species, which have potential to store carbon and stabilize the substrate, restoring key ecosystem services to the marsh, through the production of extensive root systems that persist year-round. As seedling germination in tidal wetlands can be inhibited by both flooding and salinity (Baldwin et al. 1996; Baldwin et al. 2001) and ecological restoration efforts with plantings typically have higher survival than those with seeding (Palma and Laurance 2015), we chose pre-grown plants over seeding

on the assumption that they would better withstand the stressful wetland conditions following *Phragmites* removal.

Our study objectives were to (1) assess native plant recovery following *Phragmites* eradication in low and brackish wetland sites across a range of tidal flooding frequencies and soil characteristics, (2) determine how planting influenced native vegetation recovery and which planted species were most effective, (3) test the effect of planting configuration (clumped versus dispersed arrangements) on planting survival and growth, and (4) characterize site ecosystem functioning during site recovery by examining root growth, carbon storage, and soil oxidation-reduction potential. To evaluate these objectives, we monitored vegetation recovery for three years post-*Phragmites* removal by quantifying plant cover, measuring above- and belowground biomass, as well as tracking site characteristics including flooding frequency, soil carbon content, and soil oxidation-reduction potential.

Methods

Study Area

The twelve study sites were located at tidal wetlands in three Chesapeake Bay, Maryland, USA tributaries: the Severn River, Rhode River, and Parkers Creek (Figure 2-1). The three sites in the Severn River and three sites in Parkers Creek were oligohaline (Cowardin 1995) with salinities ranging from 0.5-3 ppt, hereafter referred to as low salinity sites. Three sites in the Rhode River and three sites in Parkers Creek were mesohaline (Cowardin 1995), with salinities ranging from 5-9 ppt, hereafter referred to as brackish sites (Figure 2-2 and Table 2-1). The experiment was conducted in areas that were nearly monotypic stands of *Phragmites australis* but with native wetland vegetation nearby. At the low salinity sites, common native species were *Peltandra virginica*, *Typha latifolia*, and *Zizania aquatica*. At the

brackish sites, common native species were *Spartina alterniflora* and *Spartina cynosuroides* at Parkers Creek and *Schoenoplectus americanus* and *Schoenoplectus robustus* at the Rhode River. The top 25-50 cm of soil at all sites was organic with a mucky peat texture (Table S 2-1) and the estimated carbon content of the top 25 cm of soil at all sites ranged from 10-25% (Figure S 2-1 and Figure S 2-4). The study sites have semi-diurnal tidal cycles with a tidal amplitude of 30-40 cm.

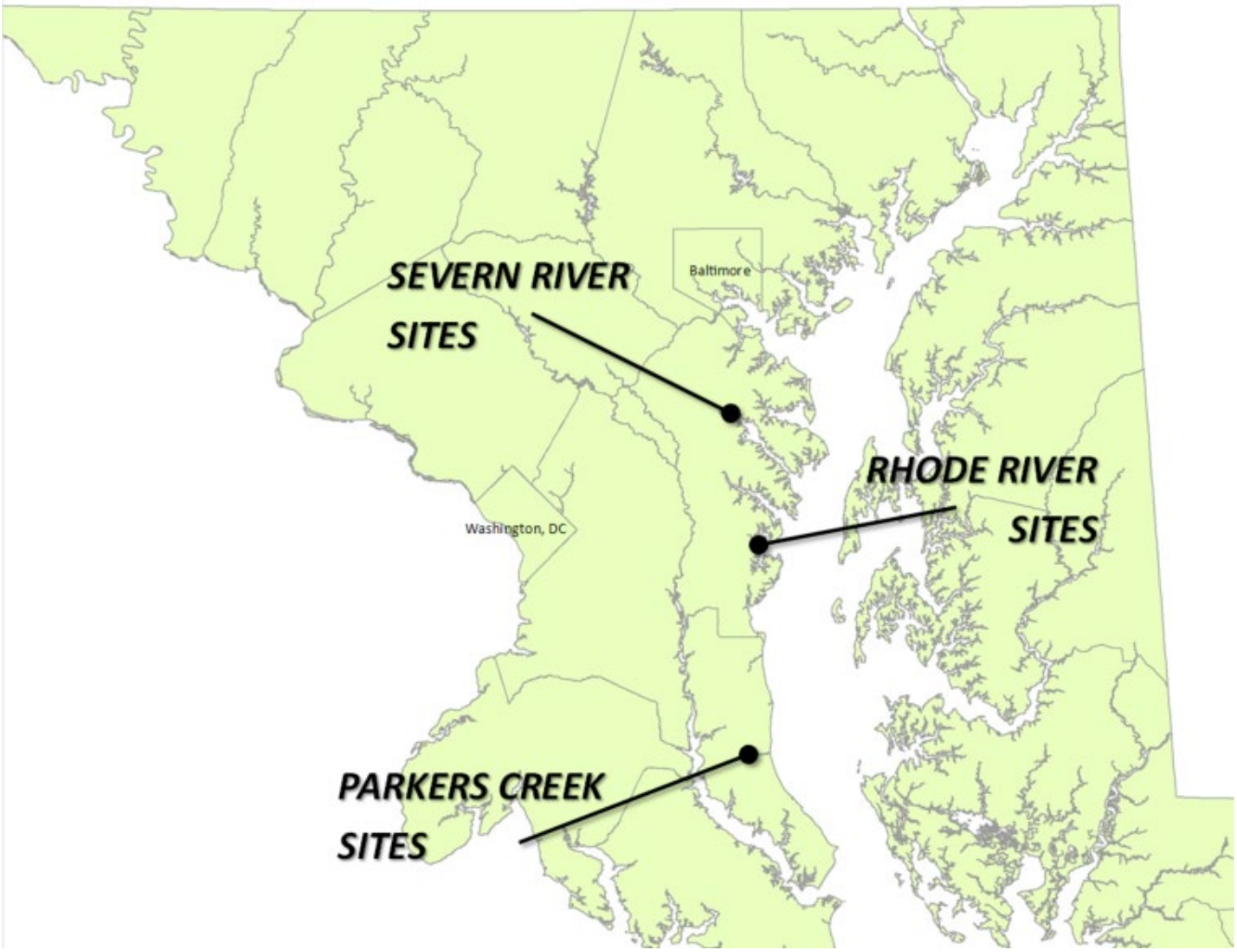


Figure 2-1. Locations of tidal wetland study sites along Maryland section of Chesapeake Bay.

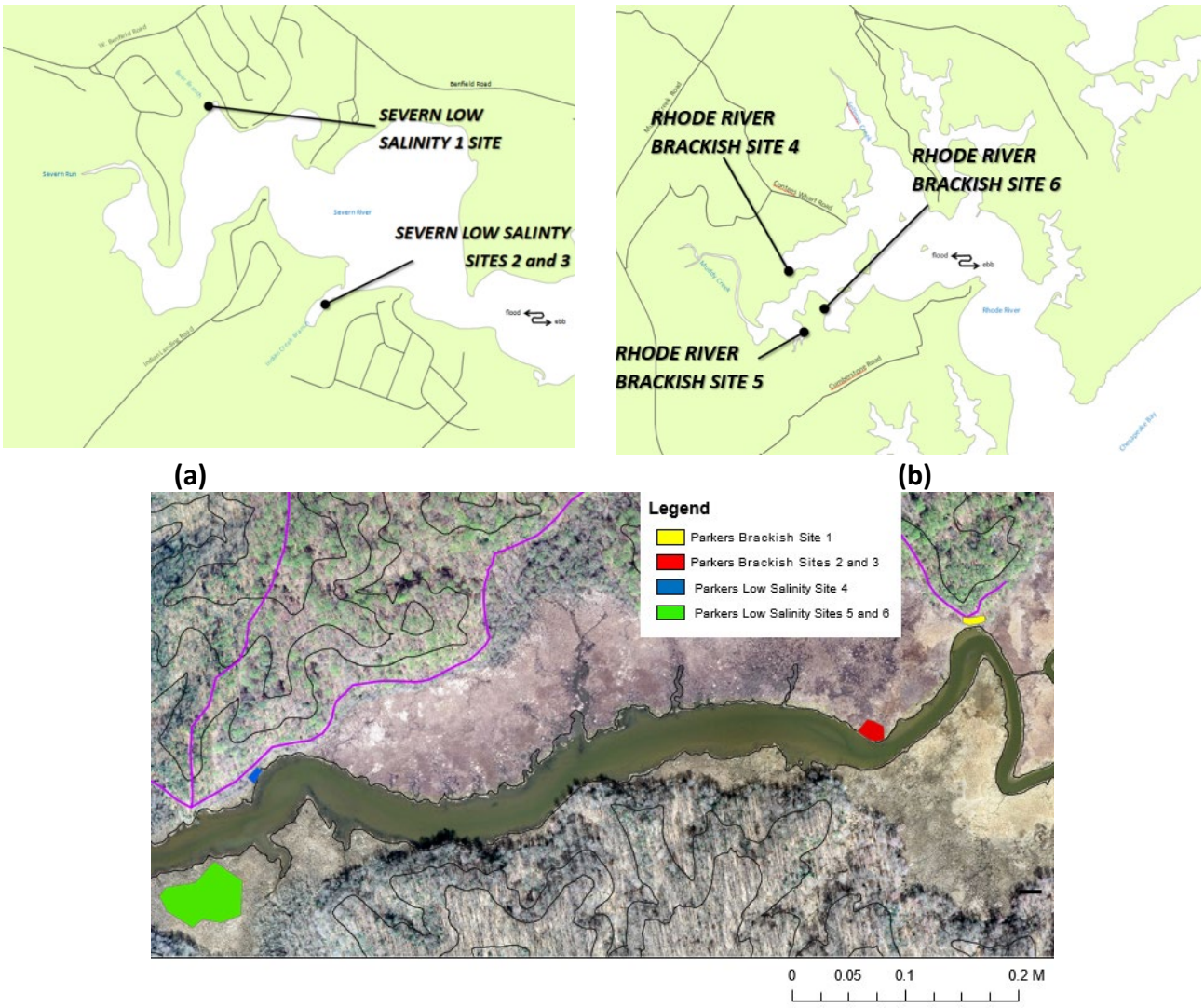


Figure 2-2. Maps of tidal wetland study sites at Severn River (a), Rhode River (b), and Parker's Creek (c). Adapted from figures by Eric Buehl.

Table 2-1. GPS Coordinates of twelve low salinity and brackish study sites.

Site	GPS Coordinates (Lat, Long)
Severn Low Sal 1	39.0840299°, -76.6125312°
Severn Low Sal 2	39.0751166°, -76.6071418°
Severn Low Sal 3	39.0751943°, -76.6070571°
Parkers Low Sal 4	38.5347641°, -76.5372799°
Parkers Low Sal 5	38.5330351°, -76.5386098°
Parkers Low Sal 6	38.5330163°, -76.5385022°
Parkers Int Sal 1	38.5363982°, -76.527088°
Parkers Int Sal 2	38.5349834°, -76.5285302°
Parkers Int Sal 3	38.5350414°, -76.5284452°
Rhode Int Sal 4	38.882286°, -76.5486346°
Rhode Int Sal 5	38.87516782°, -76.54525616°
Rhode Int Sal 6	38.87828916°, -76.54332771°

Native Planting Experimental Design

Phragmites was removed from the study sites by a combination of cutting with weed whackers and "solarization," where black plastic was spread across the soil after *Phragmites* was cut, heating the soil to temperatures that are lethal to *Phragmites* rhizomes. The research team cut *Phragmites* and covered with black plastic in May 2020 at Severn River and Rhode River study sites, while the American Chestnut Land Trust cut and covered *Phragmites* at Parkers Creek study sites in 2017-2018 and removed black plastic covering in 2019, with the exception of Parker's low salinity sites 5 and 6, which were cut by the study team (Table S 2-2).

Four study plots were established at each *Phragmites* study site. Three plots were each planted with a different native wetland species and a control plot was unplanted (Figure 2-3). Four study sites also include a *Phragmites* reference area where a nearby undisturbed stand of *Phragmites* was also monitored for comparison. At most study sites, the entire *Phragmites* patch was removed for management purposes.

All species planted were native, perennial, clonal, wetland plants: *Peltandra virginica*, *Panicum virgatum*, and *Spartina cynosuroides* at low salinity sites and *Distichlis spicata*, *Spartina patens*, and *Spartina cynosuroides* at brackish sites. (Table 2-2). The species selected were all species observed at tidal wetlands surrounding the study sites.

The plantings were grown at Providence Center nursery in Maryland in the winter and spring of 2020 in planting trays; each cell in a tray was a 2.5'' square. Prior to planting, plants were acclimated for two weeks in salinities measured at the study sites. Planting was done at the beginning of July 2020 (planting date was delayed due to COVID-19 restrictions) in both a clumped and dispersed arrangement in two 2x1 m subplots, each planted with 18 plants. In the clumped design, plants were spaced 10 cm apart, while in the dispersed design plants were spaced 33 cm apart (Figure 2-3). We added boardwalks to all sites to reduce disturbance to the marsh vegetation and soils during site monitoring visits.

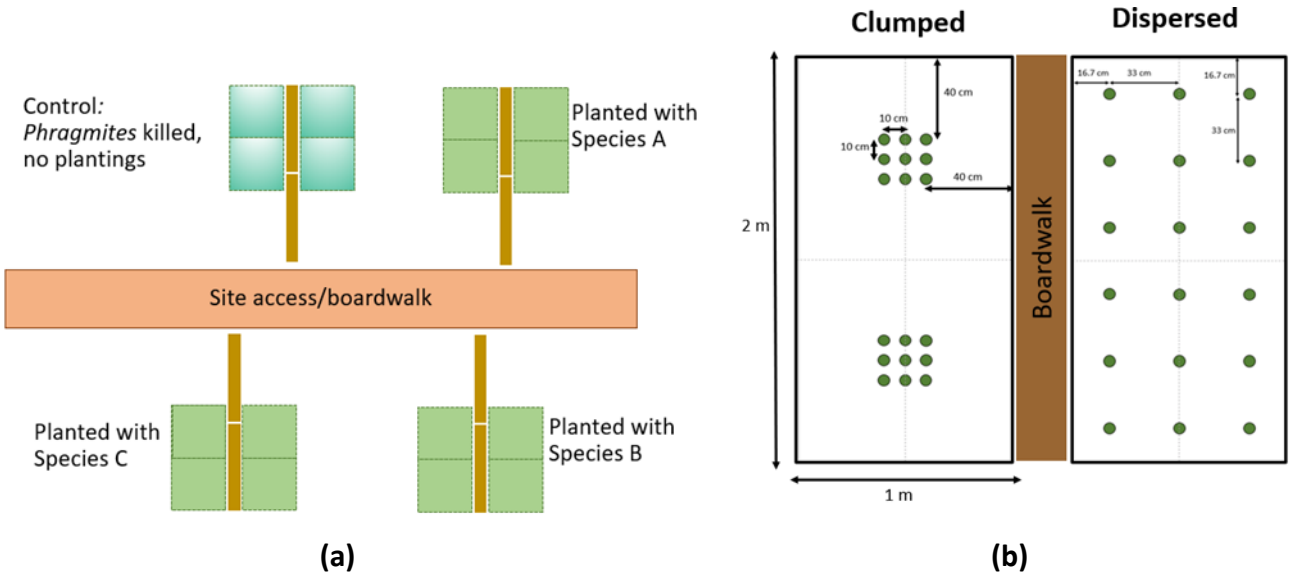


Figure 2-3. Site experimental layout: (a) Four pairs of 2x1 m plots, three planted with different native wetland species and one control plot without plantings for the purpose of monitoring natural site recovery (b) Clumped and dispersed planting designs: in the clumped arrangement, species were planted 10 cm apart; species in the dispersed arrangement were planted 33 cm apart.

Table 2-2. Planted species

Latin Name	Common Name
Planted at low salinity sites	
Peltandra virginica	Arrow Arum
Panicum virgatum	Switchgrass
Spartina cynosuroides	Big Cordgrass
Planted at brackish sites	
Distichlis spicata	Saltgrass
Spartina patens	Saltmeadow Cordgrass
Spartina cynosuroides	Big Cordgrass

Table 2-3. Mean salinity, elevation, flooding frequency, and water depth above ground surface for study sites. Flooding frequency is defined as the % of time the water level was higher than 15 cm above ground surface.

Site	Mean Salinity (ppt)	Mean Elevation (m NAVD88)	Flooding Frequency > 15 cm (% Time)		Average Water Depth (cm above ground surface)	
			Year 1	Year 2	Year 1	Year 2
Severn Low Sal 1	1.7	0.32	6	3	-0.61	-4.7
Severn Low Sal 2	2.4	0.28	9	8	2.6	3.3
Severn Low Sal 3	2.8	0.26	18	12	5.5	3.9
Parkers Low Sal 4	1.8	0.22	26	11	12	6.4
Parkers Low Sal 5	0.4	0.15	44	34	16	13
Parkers Low Sal 6	0.4	0.17	26	27	8.6	10
Parkers Brackish 1	5.8	0.27	13	8	2.6	0.89
Parkers Brackish 2	5.8	0.19	28	17	9.3	5.6
Parkers Brackish 3	5.7	0.21	32	16	11	4.9
Rhode Brackish 4	7.3	0.33	5	2	2.9	-1.6
Rhode Brackish 5	8.5	0.11	9	7	1.6	-0.57
Rhode Brackish 6	8.5	0.23	5	3	2.1	-2.9

Vegetation Cover

To assess survival and spread of planted species and to characterize vegetation recovery, we monitored plant cover (percent of plot shaded by vegetation) in all plots at the end of summer/early fall of 2020, 2021, and 2022. The percent cover of aboveground vegetation for planted and non-planted

species was visually estimated in 1x1 m subplots according to the ten-point scale method from Peet et al. (1998): 1 = trace, 2 = 0-1%, 3 = 1-2%, 4 = 2-5%, 5 = 5-10%, 6 = 10-25%, 7 = 25-50%, 8 = 50-75%, 9 = 75-95%, and 10 = >95%. The mid-point of each cover class was used for data analysis.

Above and Belowground Biomass Harvesting

Aboveground biomass growth was harvested in a 0.5m^2 (70x70 cm) area in the center of each study plot in the fall of 2021 and 2022 (only 2021 biomass data is included in this thesis). Clipped biomass was sorted by species and then dried in the lab to determine total aboveground dry weight. For large or dominant plants, we dried a representative subsample and determined the wet-dry ratio to calculate total dry weight.

Root biomass was measured for each study plot by collecting and compositing two 50-cm soil cores. Prior to compositing, each core subdivided into 0-15, 15-30, and 30-50 cm depth intervals. Live roots and rhizomes were separated from each depth interval, washed, dried, and weighed. We used the 0-15 cm root sample data for analysis, as below that depth there were mainly *Phragmites*' roots that were not reflective of native plant growth. We did not use the rhizome data for analysis, as it was mainly *Phragmites'* rhizomes that persisted in the soil following eradication, and the presence or absence of a rhizome led to high variability across samples. Total live belowground biomass from 0-15 cm per m^2 was estimated from the ratio of the soil core cross-sectional area to a 1-m^2 area.

Hydrology and Salinity

At each site, water levels were monitored by collecting data at 15-minute intervals through the 2020 and 2021 growing seasons using a HOBO pressure logger hung in a slotted PVC monitoring well. One additional HOBO logger was mounted above the water surface at one site per tributary for

determining atmospheric pressure. The water pressure was calculated by subtracting the ambient air pressure (measured with the atmospheric pressure monitoring logger) from each site's pressure readings. Water levels were then calculated from the pressure data using the hydrostatic equation:

$$P = \rho g h$$

Where P is the pressure of water, ρ is the density of water (effects of salinity on density were deemed negligible for the purposes of these calculations), g is the standard acceleration due to gravity, and h is the height of the water column above the data logger pressure sensor. Water depths were then adjusted to reflect a depth relative to the ground surface by matching a manually measured water depth at a given time.

Site flooding frequency was characterized as the % of time a site was flooded greater than 15 cm above the soil surface to distinguish sites that experienced frequent shallow surface ponding from those that had much higher depths of inundation – we found that tracking flooding frequency 15 cm above the soil surface was more reflective of the differences between site hydroperiods than flooding frequency as calculated as the % of time water is above the soil surface. We also calculated average water depth relative to the soil surface during the growing season. Hydrology metrics for growing season one in 2020 are calculated from July (time of planting) to early October (plant monitoring date), while for growing season two in 2021, hydrology metrics are calculated from April (beginning of growing season) through mid-September (date of biomass harvest). Individual study plots were surveyed with Real-Time Kinematic (RTK) GPS instrumentation to measure their elevation relative to the monitoring well's elevation to characterize differences in microtopography that may affect inundation levels and plant growth across a site. Soil porewater salinity was measured in each site's monitoring well during the growing season using a YSI 610 conductivity meter.

Soil Sampling

To assess how native plantings affected soil carbon storage and how differing soil properties affected vegetation recovery, we characterized soil bulk density and carbon content of each study plot. One soil core per site was described to characterize unique soil horizons up to 50 cm by color (Munsell Color 2010) and texture (USDA NRCS 2018). For each plot, we sampled two soil cores to 50 cm, recorded depths of distinct horizons for each core, and sampled representative 5-cm subsections for each unique horizon.

Samples of the known auger volume were dried to a constant mass at 60° C and weighed to the nearest 0.1 g to determine soil bulk density. Soil subsamples were then ground and sieved for organic content analysis using loss-on-ignition method, heating soil subsamples to 550° C for 2 hours to burn off soil organic matter (Keshta et al. 2021). Carbon content was estimated with the Craft et al. (1991) empirical relationship:

$$\% \text{ Corg} = 0.40 * \% \text{ LOI} + 0.0025 (\% \text{ LOI})^2$$

where % Corg is the percent of organic carbon and % LOI is the percent of mass lost through heating (loss-on-ignition).

For the purposes of comparing soil surface characteristics between sites, weighted averages of soil density and carbon fraction were also calculated for 0-25 cm. For example, if a core had distinct horizons from 0-10 cm and 10-50 cm with density1 and density2, respectively, the 0-25 cm weighted average for density was calculated using density1 for the first 10 cm and density2 for 10-25 cm: (10- 0)/25*density1 + (25-10)/25*density2.

Soil Oxidation-Reduction Potential

Soil oxidation-reduction (redox) potential was measured at all field sites in summer and fall of 2020. Five platinum-tipped redox electrodes (Megonigal and Rabenhorst 2013) were placed at haphazard locations in the center of each plot at 7-cm soil depth. A calomel reference electrode was placed into the soil surface of each plot (offset -244 mV). A multimeter with a high impedance circuit attachment (to prevent current flow from disturbing measurement) was used to measure the potential difference in the soil between the location of each probe and the reference electrode (Rabenhorst 2009). The pH of the soil was also measured with either a Hanna probe or YSI 1030 pH/conductivity meter.

Statistical Analysis

Many of our statistical analyses were conducted using each of our 12 study sites as independent replicates, with average plant cover, biomass, soil properties, salinity, and hydrology compared between sites. Although spatial locations cannot be truly independent, and some sites in our experiment are more clustered than others, they still represent a range of conditions at Chesapeake Bay tidal wetlands across three unique tributaries and were selected independently of the variable of interest, i.e., native plant recovery. Mixed model analyses were not always possible, given that certain key variables of interest like salinity and flooding frequency mainly varied between sites and not within sites. All statistical analyses were performed using R version 4.0.5.

We compared native plant recovery across three growing seasons between low salinity and brackish sites by comparing average total cover in site control plots with a repeated measures Analysis of Variance (ANOVA). One-way ANOVAs were used to compare control plot plant cover between low salinity and brackish sites for each year. Repeated measures ANOVA was also used to compare mean

plant cover in experimental planting plots compared to control plots across years for both low salinity and brackish sites. A two-sided t-test was used for comparisons of total control plot aboveground biomass between low salinity and brackish sites and a two-way ANOVA was used to test the effects of planting species and planting configuration (clumped vs. dispersed) on total plant cover and aboveground biomass. A two-sided, paired t-test was used to compare mean root density between planted and control plots in sites with planting survival. Assumptions were checked for ANOVA by visually inspecting model residuals to ensure homogeneity of variance and normality; the Shapiro-Wilk test was also used to check the normality of model residuals. For t-tests, response variables were checked for normality and homogeneity of variance with Shapiro-Wilk test and F-test. Root mass data was log-transformed to meet homogeneity of variance assumptions.

Multiple linear regression was used to assess correlations between control plot plant biomass across sites and environmental variables of interest – salinity, hydrology, soil organic content, soil density, and possible interactions between these variables. The model with the lowest Akaike Information Criterion (AIC) was selected to explain the greatest amount of variation in plant biomass using the fewest independent variables. Model assumptions of normality and homogeneity of variance were checked through visual inspection of residuals. We also checked that the absolute value of Pearson's correlation between model independent variables was less than 0.6. A linear mixed model (R package lme4, function lmer) was used to assess aboveground biomass on a plot level as a function of flooding frequency (adjusted using plot elevations relative to monitoring well elevation) using site as a random variable to check within site variability.

Non-metric multi-dimensional scaling (NMDS) using Bray-Curtis dissimilarity matrices were fit (using R package vegan, function metaMDS) to visualize plant cover species composition in two

dimensions for 2021 and 2022 data. (There was not sufficient 2020 plant growth to conduct NMDS analysis.) Plant cover was generally evaluated on a species level, but a few species were grouped by the genus level (*Typha* spp. and *Cyperus* spp.) when it wasn't possible to distinguish at the species level for all plots. Unknown species (all with cover less than 5%) were not included. NMDS stress values were below 0.2. A three-way PERMANOVA was used to assess the effects of salinity, flooding frequency, and year on species composition. Salinity and flooding frequency were included as categorical variables—low salinity and brackish and less than or greater than 13% of the time flooded above 15 cm, to split sites into two equal groups for each variable.

Results

Native Vegetation Recovery

Total plant cover developed more rapidly in low salinity sites than in brackish sites (Figure 2-4). In September and October 2020, after the first growing season, plant cover was low across all control (non-planted) study plots. Two low salinity sites (Severn low salinity site 1 and Parker's low salinity site 6) had over 20% plant cover in control plots by fall 2020, but all other study plots had below 6% plant cover in non-planted control plots. Toward the end of the second growing season (August 2021), average total plant cover in control plots across study sites was over 10x higher than the previous year. In 2021 overall, low salinity sites had a higher mean plant cover compared to brackish sites – low salinity site control plot plant cover values ranged from 60-130% cover, while brackish site control plot plant cover ranged from 0-90%. By August 2022, after the third growing season, average plant cover across site control plots was 1.8x higher than the previous year and was also higher in low salinity sites

than in brackish sites – low salinity site control plot plant cover ranged from 90-170%, while brackish site control plot plant cover ranged from 9-110%.

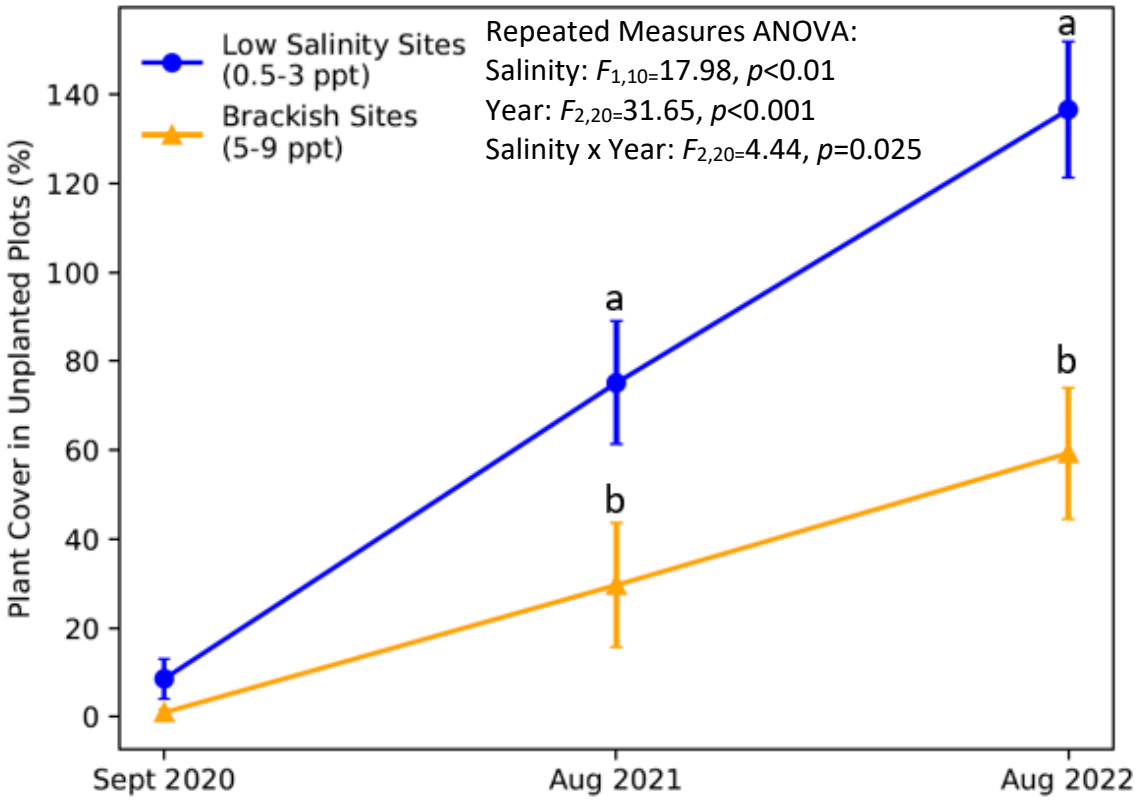


Figure 2-4. Mean and SE of total plant cover (area of plot shaded by aboveground plant growth) for native plant recovery in site control plots across 12 study sites. Cover above 100% can indicate overlapping vegetation cover of different species. One-way ANOVA found differences in total plant cover between low salinity and brackish sites in years 2 and 3 (2021 salinity: $F_{1, 10}$=5.31, p = 0.04; 2022 salinity: $F_{1, 10}$=13.17, p<0.01).

Total aboveground biomass in control plots after two years was also higher in low salinity sites in Severn River and Parkers Creek compared to brackish sites in the Rhode River and Parkers Creek (Figure 2-5). Almost half of the variation in biomass (46%) could be explained by salinity and flooding frequency (Figure 2-6). There was no effect of within-site microtopography on aboveground biomass, a result that was not surprising given that the study sites were relatively flat and the differences of

elevation, typically 5 cm or less between plots, were within the error range of the survey instrument. One site (Parker's brackish 1) had plots with elevations that differed by 10 cm or more, and there were also large differences in aboveground biomass, over 1000 g/m^2, between the highest and lowest elevation plots.

Species composition of control plot plant cover in both 2021 and 2022 differed between sites based on salinity and flooding frequency but not between years (Figure 2-7). Low salinity sites generally had higher species diversity and a higher abundance of annual species (Figure 2-8). Some species at the low salinity sites that had the highest cover by the third growing season (or fourth growing season for some Parkers Creek sites) included *Eleocharis parvula*, *Polygonum punctatum*, *Peltandra virgnica*, *Schoenoplectus tabernaemontani*, *Echinochloa walterii*, and *Pluchea odorata*. *Eleocharis parvula*, a short, 2-7 cm tall sedge, had high cover at several sites but low biomass, so the mean cover estimates may overrepresent the dominance of this species. At brackish sites, most species were perennial graminoids with *Spartina alterniflora* having the highest mean cover across sites; other species like *Schoenoplectus americanus*, *Spartina cynosuroides*, and *Schoneoplectus robustus* had high cover at one site but were rare or absent at other sites. Across all sites, the plant communities were composed of almost exclusively native vegetation, except for *Murdannia keisak*, an introduced species of Asian origin that occurred in low abundances at a few sites, as well as a few returning *Phragmites* shoots.

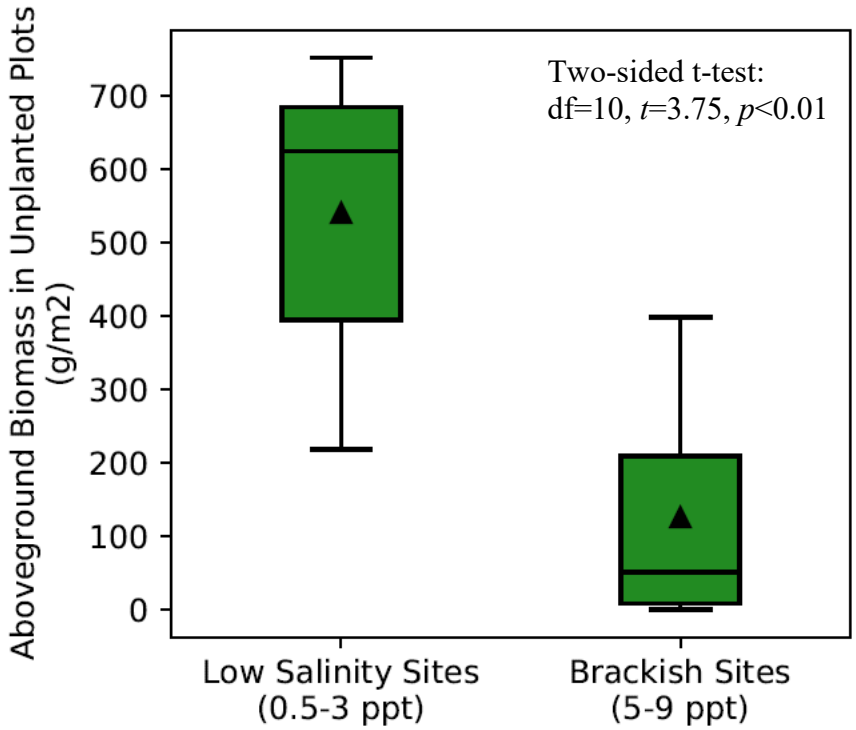


Figure 2-5. Control plot biomass in low salinity and brackish sites. The data are normalized per m^2 area. Boxes show interquartile range with a black line for median and a black triangle for mean; whiskers show data minimum and maximum.

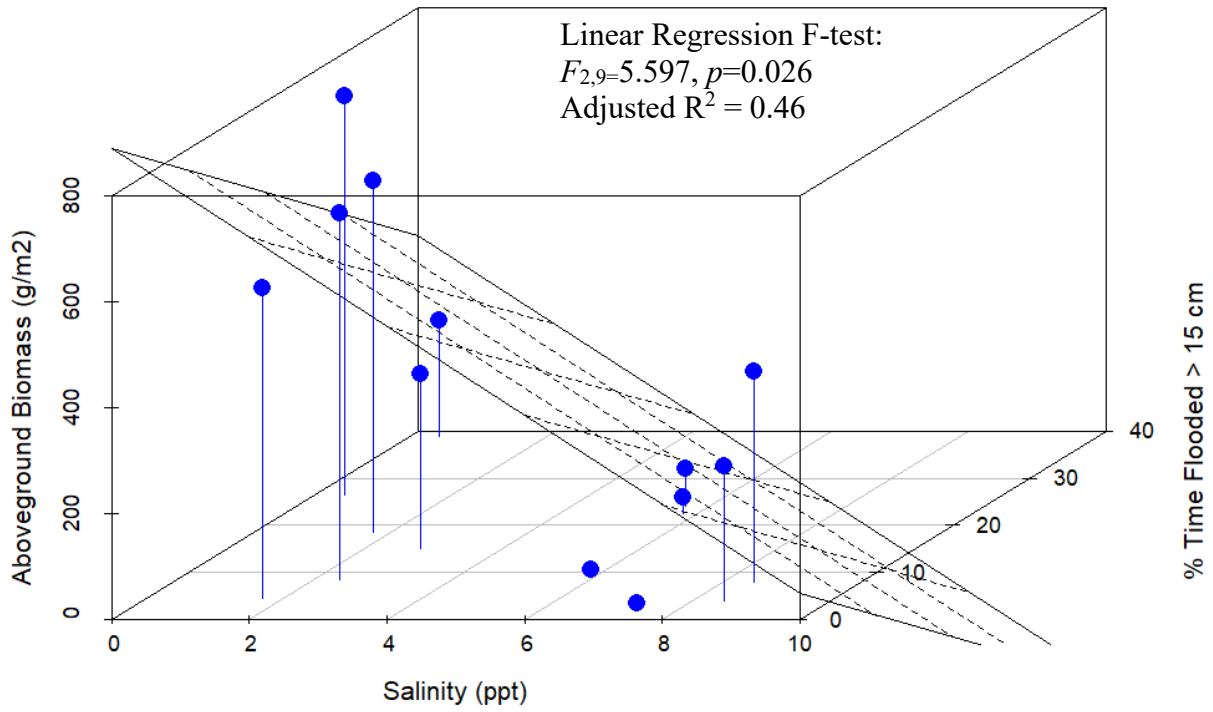


Figure 2-6. Mean site aboveground biomass in unplanted plots normalized per m^2 as a function of site salinity (ppt) and site flooding frequency (% of time a site was flooded over 15 cm during the growing season) with plane of best fit: Aboveground biomass = α(salinity) + b(flooding frequency) + c, α = -84 ±25, b = -13 ± 7, c = 889 ± 196. Aboveground biomass increased as salinity and flooding frequency decreased. The model that was selected to show the relationships had the lowest Akaike Information Criterion (AIC) compared to models that only included one environmental variable, an interaction term, or that included other site environmental characteristics such as surface soil density or soil organic matter content.

Figure 2-7. Non-metric multidimensional scaling (NMDS) of plant cover species composition for control plots in August 2021 and 2022. NMDS was conducted in two dimensions using Bray-Curtis dissimilarity matrices. Red and blue markers denote brackish and low salinity sites, respectively, while circles and triangles represent sites with higher and lower flooding frequency, respectively (splits sites into two groups of 6 based on whether site is flooded above 15 cm over 13% of time). Centroid of each species marked with 4-letter species codes. Brackish control plots shown in red and low salinity control plots are in blue, control plots at sites flooded above 15 cm over 13% of the time (6/12 sites) shown with circles and sites flooded <13% of the time NMDS stress was less than 0.2 and 0.1 for 2021 and 2022 ordinations, respectively. The influence of environmental variables on species composition was also tested with a three-way PERMANOVA: salinity: R^2= 0.20, $F_{1,15}$=5.70, p=0.001; flooding frequency: R^2=0.087, $F_{1,15}$=2.48, p<0.01; salinity x flooding frequency: R^2=0.072, $F_{1,15}$=2.05, p=0.023; year: R^2= 0.045, $F_{1,15}$=1.27, p=0.25.

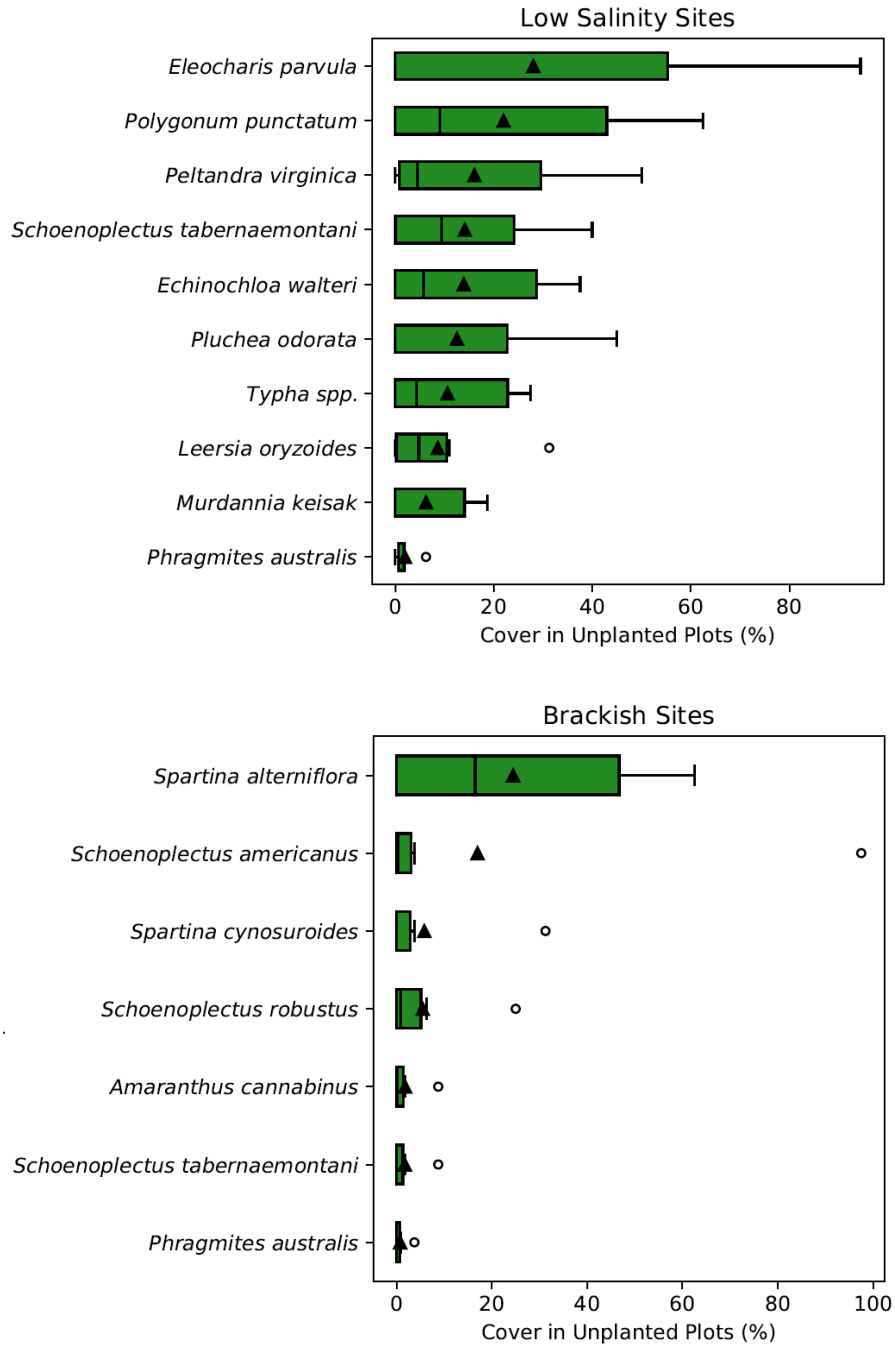


Figure 2-8. Species with highest mean percent cover in unplanted plots after the third (or fourth for some Parkers Creek sites) growing season following *Phragmites* removal. All species with a mean cover greater than 0.7% shown. Triangles show means across all 6 low salinity or brackish sites, boxes show interquartile range with a black line for the median, whiskers show minimum and maximum, outliers are shown as circles.

Planting Experiment

At most sites, experimental planting survival was low and most of the mortality occurred shortly after the initial transplanting. It was noted in the Methods that the plants were not available until early July. The plant seedlings were small (grown in 2.5" cells) and it was noted that they did not seem very vigorous, especially *Panicum virgatum* (D. Whigham personal observation). By August 2021, only five sites had planting survival with at least 20% cover of the plots: Rhode River brackish sites 4-6, Parkers low salinity site 4 and Parkers brackish site 1. At the other seven sites, nearly all plantings died over the first summer or during the winter. For the four brackish sites where native plantings survived, aboveground biomass and cover was higher in the plots that had been planted than in unplanted plots (Figure S 2-11). For the brackish sites, plant cover was higher in planted plots than in unplanted plots across all years (Figure 2-9; repeated measures ANOVA: plot type – planted or control: $F_{1,5} = 8.18$, $p = 0.035$: year: $F_{2,10} = 31.9$, $p < 0.001$; plot type x year: $F_{2,10} = 1.097$, $p = 0.37$). For low salinity sites, there were no differences in plant cover between planted and unplanted plots (Figure 2-9).

Of the five sites where the experimental plantings survived, (4 brackish sites and 1 low salinity site) no species had consistently higher biomass or plant cover (Figure S 2-9). There was also no consistent trend in differences of plant cover or biomass between clumped planting spaced 10 cm apart and dispersed plantings spaced 33 cm apart (Figure S 2-10).

Planting die-off mostly occurred during the first winter of the experiment. By September/October 2020, most plantings had survived at low salinity sites. Between 60-100% of *Peltandra virginica* and *Spartina cynosuroides* transplants survived and between 20-100% of *Panicum virgatum* plantings survived at the low salinity sites (Figure S 2-12). Transplant survival was more variable across brackish sites. Survival of all species was high at the Rhode River sites, with 95-100%

survival of *Distichlis spicata*, 65-100% survival of *Spartina patens* and 35-95% survival of *Spartina cynosuroides*. No plantings survived the first summer at Parkers brackish sites 2 and 3 but at Parker's brackish site 1, 60% survival of the *Distichlis spicata*, 50% of the *Spartina cynosuroides*, and 15% of the *Spartina patens* transplants survived in year 1.

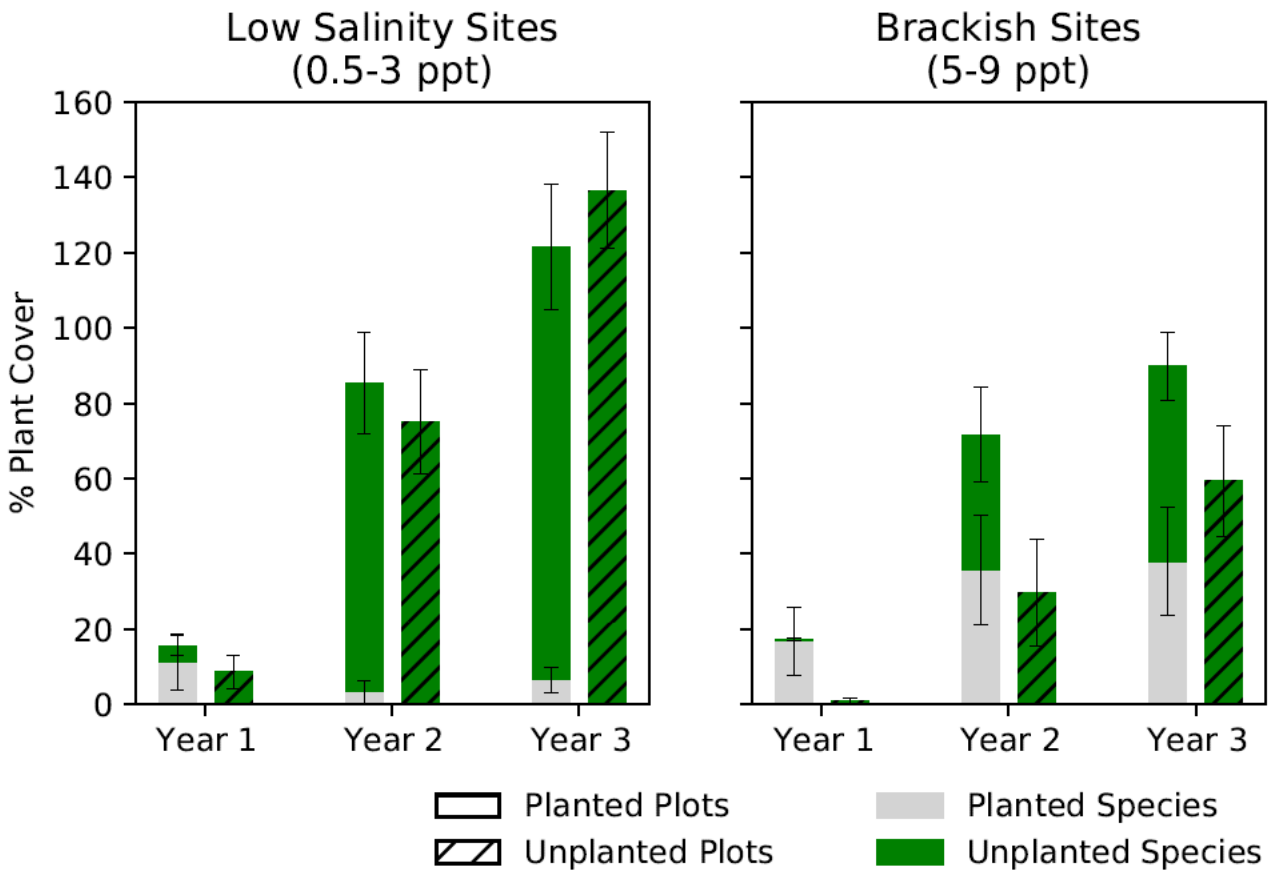


Figure 2-9. Mean and SE of total plant cover (% of plot shaded by vegetation – can be above 100% when plant species overlap) by study year comparing planted plots (solid fill) and unplanted plots (hatched fill). For planted plots, the gray fill is the portion of the total plant cover from the experimental plantings and the green shows plant cover for unplanted "volunteer" species.

Belowground Biomass

There was a trend of higher root biomass at sites with higher aboveground biomass, but there was a stronger correlation between perennial aboveground biomass and root biomass (Figure 2-10). At the Rhode River sites, there was higher root biomass in the 0-15 cm layer in planted plots compared to control plots, but across all sites with the highest planting survival (Rhode River brackish salinity sites 4-6, Parkers' low salinity site 4 and Parker's brackish salinity site 1) there were no statistically notable differences in root biomass between planted and control plots (two-sided paired t-test: df=3, t = 1.69, p = 0.19)

Soil Carbon

The surface substrate (0-25 cm) had a soil organic matter content ranging from 26-64% with an estimated carbon fraction ranging from 10-26% (Figure S 2-4). Soil densities ranged from 0.09 to 0.19 g/cm3 (Figure S 2-5). The Severn brackish site 1 had notably lower soil organic matter content (26%) and higher soil density (0.19 g/cm^3), than oher sites, including other Severn sites (surface soil OM content was 2x higher and soil density was less than half at Severn low salinity sites 2 and 3). There was no correlation between surface soil density or estimated soil carbon fraction in control plots and aboveground biomass across sites (linear regression with biomass as a function of site soil density $F_{1,10}$=0.50, p =0.49 and site soil carbon fraction $F_{1,10}$=0.004, p =0.95). At sites where transplant survival was the highest (Rhode River brackish sites 4-6, Parkers' low salinity site 4 and Parker's brackish site 1), there was no observed effect of planting treatment on soil organic matter content (Figure S 2-7 and Figure S 2-8).

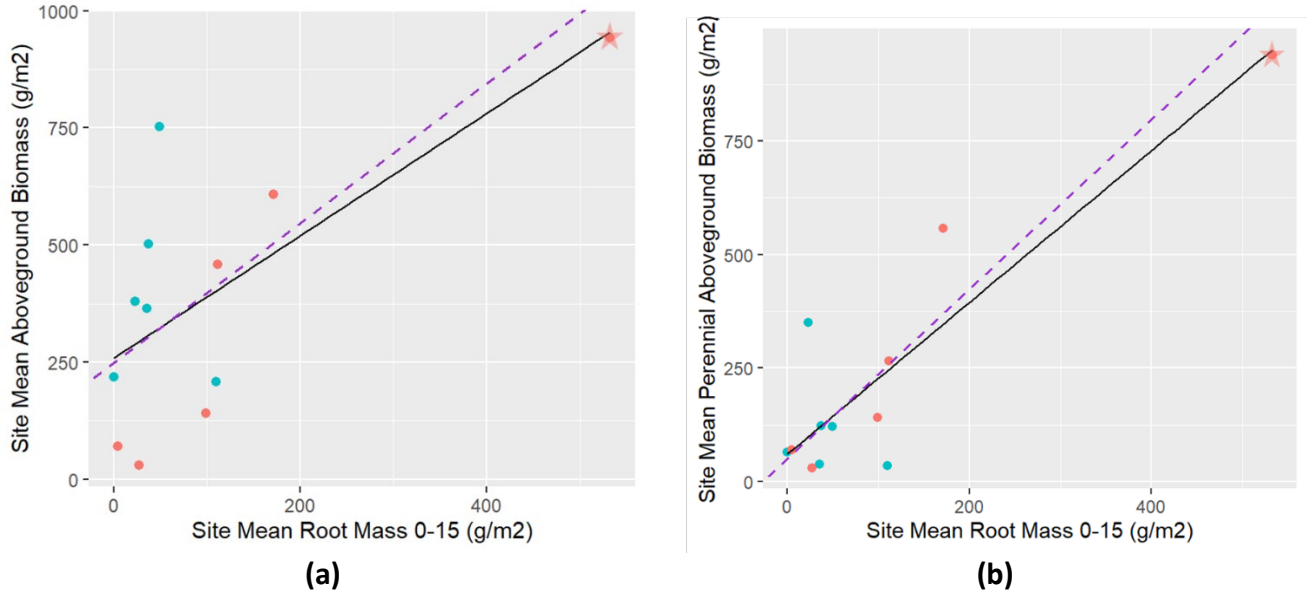


Figure 2-10. Linear regression of aboveground biomass (a) and perennial aboveground biomass (b) as a function of root biomass in the 0-15 cm soil layer. Biomass values are site averages across all study plots. The black line shows a linear regression with all data, while the dashed purple line is the regression line excluding the outlier (for Rhode River brackish site 6, which had much higher root biomass than other sites – red star). Total aboveground biomass regression with all data points: slope = 1.3, adjusted R^2 = 0.41, $F_{1,9}$ = 8.67, and p = 0.01; total aboveground biomass regression excluding outlier: slope = 1.5; adjusted R^2 = 0.03, $F_{1,9}$ = 1.29, p = 0.29; perennial aboveground biomass regression with all data points: slope = 1.7, Adjusted R^2 = 0.77, $F_{1,9}$ = 37.98, p <0.001; perennial aboveground biomass regression excluding outlier: slope = 1.9, Adjusted R^2 = 0.31, $F_{1,9}$ = 5.44, p =0.04.

Soil Oxidation-Reduction Potential

Soil oxidation-reduction (redox) potential readings were highly variable within sites and plots without a consistent trend across the different planting treatments. Readings were consistent across sites, with most measurements ranging from -200 – 200 mV in the August/September and October sampling events (Figure S 2-13). Soil porewater pH ranged from 5.5-6.5, an indication that the substrates were sufficiently reducing to favor the reduction of ferrihydrite to ferrous iron (Figure S 2-14).

Discussion

Vegetation Recovery in Unplanted Plots

The study control plots, which were left unplanted, enabled us to assess natural vegetation recovery following *Phragmites* eradication across a range of salinity and flooding conditions. Our study confirmed that native plant recovery is site dependent (Carlson et al. 2009; Rohal et al. 2019) and can vary widely even between spatially close wetland sites. Total plant cover and total aboveground biomass by the end of the study was higher at low salinity sites than at brackish sites. Site flooding frequency also influenced vegetation recovery, as less frequently flooded and better drained sites had higher total plant biomass. Slower vegetation recovery at more saline and more frequently flooded sites is likely due to the inhibition of seedling emergence at higher salinities (above 2-4 ppt) and flooding levels (Baldwin et al. 1996; Baldwin et al. 2001). Our results are also consistent with a mesocosm experiment that found that salinity and flooding had a greater suppressing effect on biomass following a disturbance (Baldwin and Mendelssohn 1998). Emerging plant communities following *Phragmites* removal may be more vulnerable to the stresses of salinity and flooding than mature, less disturbed wetland vegetation. However, over time, even brackish sites had recovered with control plots averaging 60% cover of native vegetation by year 3. But none of our study sites had mean salinities greater than 8.5 ppt; we speculate that vegetation recovery would be even slower at more saline salt marshes.

Species composition of recolonizing vegetation varied across sites that differed in salinity and flooding frequency. Many of the dominant species at low salinity sites were annuals, such as *Polygonum punctatum*, *Echinochloa walterii*, and *Pluchea odorata*, that were present but less abundant in adjacent, wetland areas where there was no *Phragmites* (S. Jacobson, personal observation), but may thrive in an

open marsh following a biomass removal disturbance. Vegetation at brackish sites, although slower to return, more closely resembled the species composition of adjacent marsh areas (S. Jacobson, personal observation). Brackish sites were dominated by perennial species such as *Spartina alterniflora*, *Spartina cynosuroides*, and *Schoenoplectus robustus* (Parker's brackish sites*)* and *Schoenoplectus americanus* and *Schoenoplectus robustus* (Rhode River sites). Some annuals—e.g., *Amaranthus cannabinus* and *Symphyotrichum subulatum*—were present at brackish sites, but they were not as dominant (i.e., lower cover and biomass) as annuals in low salinity study sites (Figure 2-8). As seedling germination of many tidal wetland species is inhibited by salinity (Baldwin et al. 1996), annual species that must regenerate from seed each year could emerge more rapidly at our low salinity wetland sites.

Differences in species composition across a gradient of flooding frequency may be due to higher biodiversity with lower flooding stress (Baldwin and Mendelssohn 1998). For example, the Severn River sites varied in the frequency of flooding and the site that flooded less frequently had a higher species diversity. Differences in cover, aboveground biomass, and species composition at the Severn sites that are located close to each other in the same part of the estuary may have also been related to differences in soil characteristics. Severn low salinity site 1 had a higher soil density (19 g/cm^3 in the top 25 cm) and lower soil carbon content (10% carbon in the top 25 cm), which likely resulted in more aerobic soil conditions that may have been more favorable for plant growth. But across most of our sites, surface soil textures, density, and organic matter fraction were more consistent, so it was difficult to assess the impact of soil characteristics on native plant recovery in this study.

Annual climatic differences may also have contributed to the between-year differences. Periods of reduced inundation during years with lower rainfall, particularly early in the growing season, can result in higher rates of seed germination under less flooded conditions (Baldwin et al. 1996; Baldwin et

al. 2001). Flooding frequencies were lower across all sites in the second growing season of the study (Table 2-3). March-May 2021 had lower reported mean sea levels (at Annapolis, MD NOAA station) compared to the period following planting the previous year (https://tidesandcurrents.noaa.gov/sltrends/sltrends_station.shtml?id=8575512). This may have resulted in higher levels of seed germination and seedling success, resulting in increased plant cover in 2021, especially in unplanted control plots.

Another interesting finding of this study is that almost all the species that colonized the plots were native. This contrasts with some previous studies that have reported secondary invasions of other non-native species following *Phragmites* removal (Judd and Francoeur 2019; Robichaud and Rooney 2021). The patterns of colonization at our study sites may have been, in part, due to the presence of sites that were not dominated by *Phragmites* and were sources of seeds. Reid et al. (2009) and Rohal et al. (in press) found that proximity to native plant communities increases the recovery of native vegetation in area where *Phragmites* and other invasive plant species had been removed or reduced in abundance.

Experimental Planting Effects

Transplant survival was low, with only 5 of the 12 study sites averaging over 20% cover of transplanted species by year two of the experiment. As noted earlier, the transplants used in 2020 were small and were planted in July – both variables that lowered the probability of transplant success. Transplants of one species in particular, *Panicum virgatum*, were chlorotic and small and did not survive for long at any site. Interestingly, there was a lot of variation between sites in survival. At some sites, all plantings had died by year three. At all three brackish Rhode River study sites, survival was high and the clonal transplants spread rapidly to form patches that expanded beyond the 1 x 2 m plots by years two

and three. At the same sites, the biomass of planted areas compared to unplanted control plots was much higher. Therefore, if native plantings survive the first year, there may be restoration benefits at brackish sites where revegetation from the seed bank is slower.

Low transplant survival is a common, and perhaps underreported, challenge in ecosystem restoration (Cunha et al. 2012; Rodrigo et al. 2018; "Mangrove Restoration: To Plant or Not to Plant"). Planting in tidal wetland ecosystems may be particularly challenging due to anoxia in flooded soils (Gleason and Zieman 1981) and erosion stress from wind and currents (Callaghan et al. 2010). In our experiment, poor survival of plantings may have been due to a combination of factors, including exposure to waves and winds, high flooding frequencies, soil biogeochemical factors, the timing of planting, and the quality of the plants. The Rhode River brackish sites with the highest planting survival were relatively sheltered from the nearby tidal streams and plantings thus may have been more likely to remain rooted during the first winter; these sites were also among the least frequently flooded. Severn low salinity site 1 had very high survival and growth during the first growing season, but most experimental native plantings died during the winter, possibly due to the exposure of the site to the tidal creek, where wave exposure and ice may have uprooted plantings. Parkers brackish sites 5 and 6 had very poor plant survival during the first growing season, which may have been due to tidal creek wave exposure, high flooding frequency—especially the effects from a tropical storm that passed through the area shortly after the plants were transplanted to the sites, and the presence of toxic soil sulfides that form under anaerobic conditions in brackish wetlands. Evidence of sulfide—a potent phytotoxin—in soil porewater was observed when iron-coated IRIS films inserted into the soil turned black after 30 minutes (method similar to that in Rabenhorst et al. 2010, which used IRIS tubes).

Planting native species in early July may also have been too late in the growing season, with increased hypoxia, heat, and salt stress that could have led to plant mortality or decreased their ability to establish strong root systems that could withstand winds, waves, and winter ice. A subsequent planting experiment with planting in early June with larger plants (4-inch pots instead of 2-inch plugs) at the same study sites had higher planting survival across study sites (unpublished data not included in this thesis).

At the brackish sites where survival was highest (Rhode River brackish sites 4-6 and Parker's brackish site 1), there was no relationship between the species planted and either percent cover, above- or belowground biomass, or soil carbon. *Distichlis spicata*, *Spartina patens*, and *Spartina cynosuroides* transplants survived at the three Rhode River brackish sites, suggesting that any of these species could be appropriate choices if native planting is included as part of *Phragmites* eradication efforts. Site characteristics appeared to have a stronger effect on planting survival than species choice as noted by the fact that almost all transplants survived and grew well at some sites while at other sites survival and growth were low. As only one low salinity site (Parkers low salinity 4) had above 20% cover in planting plots by year 2 of the experiment, it is difficult to determine if the species chosen for the study (*Peltandra virginica*, *Panicum virgatum*, or *Spartina cynosuroides)* were good choices. Given more rapid natural recovery, native planting is likely not necessary at low salinity tidal wetlands if there is a robust seed bank or sources of seed dispersal.

Clumped planting configurations did not increase survival or cover of native plantings, contrary to our expectations; site characteristics seemed to have had more effect on planting survival and growth than planting configuration – typically either both clumped and dispersed plantings survived and spread or neither did. Previous research found benefits of clumped planting configurations from plant

facilitation in stressful wetlands environments with high salinities, erosion stress from waves and wind, and highly anoxic soils (Silliman et al. 2015; Fischman et al. 2019; Renzi, He, and Silliman 2019; Duggan-Edwards et al. 2020). However, there are thresholds of stress which cannot be overcome through plant facilitation (Fischman et al. 2019), which may have been the case at certain sites with highly flooded, bare soils following *Phragmites* removal.

Previous studies have reported transplant success by using sods harvested from natural marsh sites (Sparks et al. 2013) and older plantings (Palma and Laurance 2015). Nursery treatment to harden species for field conditions is also critical (Palma and Laurance 2015). In a second planting experiment at the same sites, we had higher planting survival overall (but still had low survival rates at a few tidal wetland sites) using larger plants, planting earlier in the growing season, and anchoring native plantings to the marsh with stakes (unpublished data). However, it is hard to assess the influence of each of these strategies as differing hydrology between years can also be a driver of planting survival – e.g., reduced tidal flooding early in the growing season and the timing of major storms.

Implications for Ecosystem Services following *Phragmites* Eradication in Tidal Wetlands

Given the correlation between high perennial aboveground biomass and root density across sites – which was stronger than the relationship between total aboveground biomass and root density— planting perennial species could help stabilize soils and add carbon to the substrate following the removal of *Phragmites*, which has high belowground productivity (Caplan et al. 2015). At brackish sites, this may be an appropriate strategy given that natural vegetation recovery remained low for the first years following *Phragmites* removal but may still be unnecessary as some native vegetation

returned within a few years independently of planting efforts. It is possible that at sites with higher salinities than those we tested in this study, natural vegetation recovery could be even slower and planting might make even more of a difference. At low salinity sites, there was a high abundance of annual plants, which are known for lower belowground biomass than perennial plants (Whigham and Simpson 1978). However, the early successional stage of vegetation at these sites can still provide animal habitat and potentially prevent re-invasion with *Phragmites australis*. An outdoor pot experiment, where seeds of wetland plants of different functional groups were germinated with seeds of *Phragmites,* found that early- and fast-growing annual species were most competitive with and resistant to invasion from *Phragmites australis* (Byun et al. 2013).

From our soil carbon sampling in year two of the experiment (two growing seasons following native planting), we did not see an effect of plant biomass production on soil carbon content – carbon storage processes may occur on a slower timescale. We also did not see an increase in soil oxidation-reduction differences between plots with and without plantings, suggesting that radial oxygen loss from newly established plant roots did not have a large effect on overall soil oxygenation.

Conclusions

Managing small stands of non-native *Phragmites australis* can help protect native vegetation by preventing *Phragmites* from spreading and replacing native species. However, killing *Phragmites* involves removing large amounts of biomass from the wetland in the short-term, so ensuring timely native plant recovery is critical to preserving marsh ecosystem functions like providing animal habitat, and promoting soil accretion and carbon storage. In this study, low salinity tidal wetland sites had rapid native plant revegetation after *Phragmites* removal, which can help prevent *Phragmites* reinvasion,

although it is not clear to what extent these transitional, annual-dominated plant communities provide the same ecosystem services as an undisturbed, native low salinity marsh. Vegetation at sites with higher salinity levels and flooding frequencies recovered more slowly. Our study found potential to increase native plant cover and biomass at brackish sites using perennial native plantings of *Distichlis spicata*, *Spartina patens*, and *Spartina cynosuroides.* More frequently flooded sites, however, may also have lower success with planting survival. Previous research and our observations suggest that hardening plants to wetland conditions in the nursery, using older/larger plants, planting earlier in the growing season, and anchoring native plantings to the marsh with stakes or another mechanism may help increase survival, but still cannot guarantee planting success. With the high risk of planting mortality in tidal wetland environments, the potential benefits of planting in higher salinity and more frequently flooded environments need to be weighed against the financial and time investment for restoration practitioners.

Supplemental Information - Chapter 2

Soils

Table S 2-1. Characteristics of the top 50 cm of soils at the twelve study sites. Color was determined by comparing samples in the field with Munsell Color charts and texture was based on USDA texture classes (USDA NRCS 2018)

Site	Horizon	Depths	Texture	Color
Severn Low Sal 1	1	0-8	Mucky peat	2.5Y 3/2
	2	8-35	Mucky peat	10YR 3/2
	3	35-50+	Silt loam	10YR 4/1
Severn Low Sal 2	1	0-5	Mucky peat	10YR 2/1
	2	5-28	Mucky peat	10YR 3/1.5
	3	28-33	Silt loam	10YR 4/2
	4	33-50+	Mucky peat	10YR 2.5/2
Severn Low Sal 3	1	0-9	Mucky peat	2.5Y 2.5/1
	2	9-35	Mucky peat	10YR 3/3
	3	35-50+	Mucky peat	10YR 3/2
Parkers Low Sal 4	1	0-25	Mucky peat	2.5Y 2.5/1
	2	25-50+	Mucky silt loam	2.5Y 3.5/1
Parkers Low Sal 5	1	0-10	Mucky peat	2.5/N
	2	10-38	Mucky peat	2.5Y 3/2
	3	38-50+	Mucky silt loam	5Y 3.5/1
Parkers Low Sal 6	1	0-15	Mucky peat	10YR 2.5/1
	2	15-39	Muck	10YR 3/2
	3	39-50+	Mucky silt loam	10YR 4/1
Parkers Brackish 1	1	0-33	Mucky peat	10YR 2/1.5
	2	33-50+	Silty clay loam	2.5Y 3/1.5
Parkers Brackish 2	1	0-32	Mucky peat	10 YR 2/1
	2	32-50+	Mucky silt loam	2.5Y 3/2
Parkers Brackish 3	1	0-9	Muck	2.5/N
	2	9-36	Mucky peat	10YR 2/1
	3	36-50+	Mucky silt loam	2.5Y 3/2
Rhode Brackish 4	1	0-18	Mucky peat	5Y 2.5/2
	2	17-25	Mucky peat	5Y 2.5/2
	3	25-50+	Silty clay loam	5Y 3.5/1
Rhode Brackish 5	1	0-28	Mucky peat	10YR 2/2
	2	28-50+	Peat	10YR 4/4
Rhode Brackish 6	1	0-35	Mucky peat	10YR 2/1.5
	2	35-50+	Silty clay loam	10YR 3/1

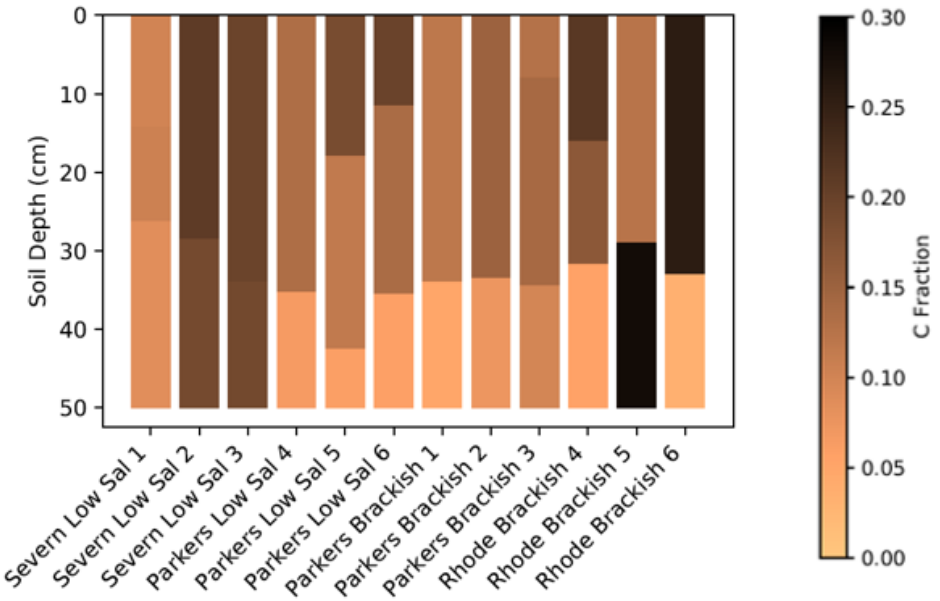


Figure S 2-1. Soil carbon content by depth for study sites. Soil samples from all study plots (n=8/site) averaged within each horizon to find mean C fraction and mean horizon depth zonation across site. Carbon fraction estimated from loss-on-ignition and Craft et al. (1991) equation: %C = 0.4*%LOI * 0.0025*(%LOI)^2

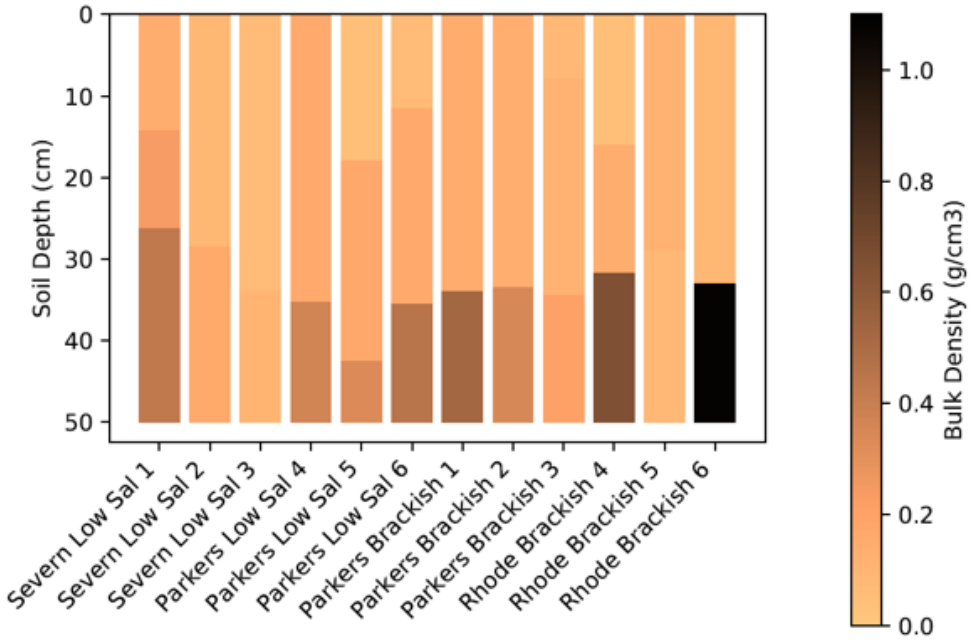


Figure S 2-2. Soil bulk density by depth for study sites. Soil samples from all study plots (n=8/site) averaged within each horizon to find mean density and mean horizon depth zonation across site.

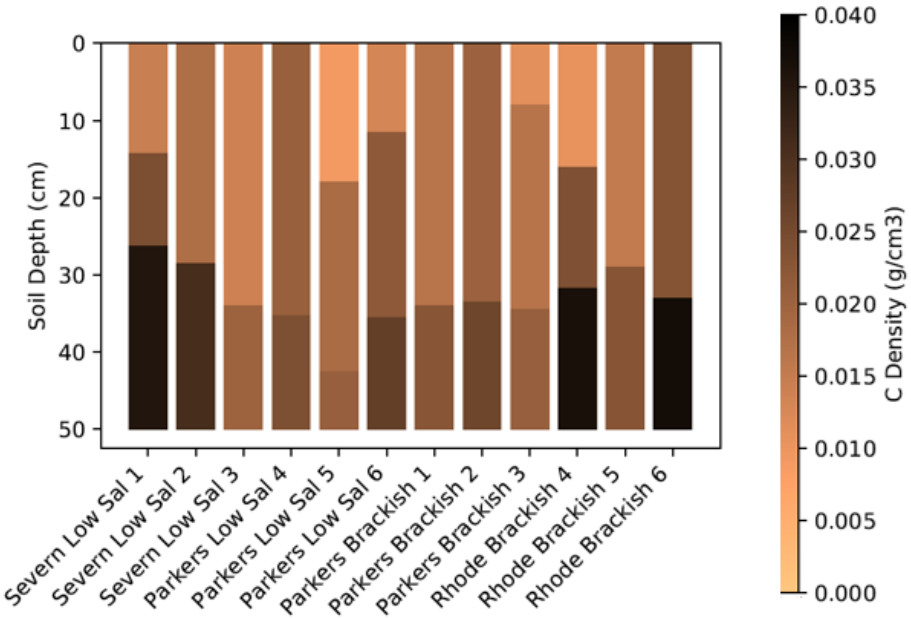


Figure S 2-3. Soil carbon density by depth for study sites – calculated as carbon fraction * soil bulk density as an estimate of total carbon storage per volume soil. Soil samples from all study plots (n=8/site) averaged within each horizon to find mean C density and mean horizon depth zonation across site.

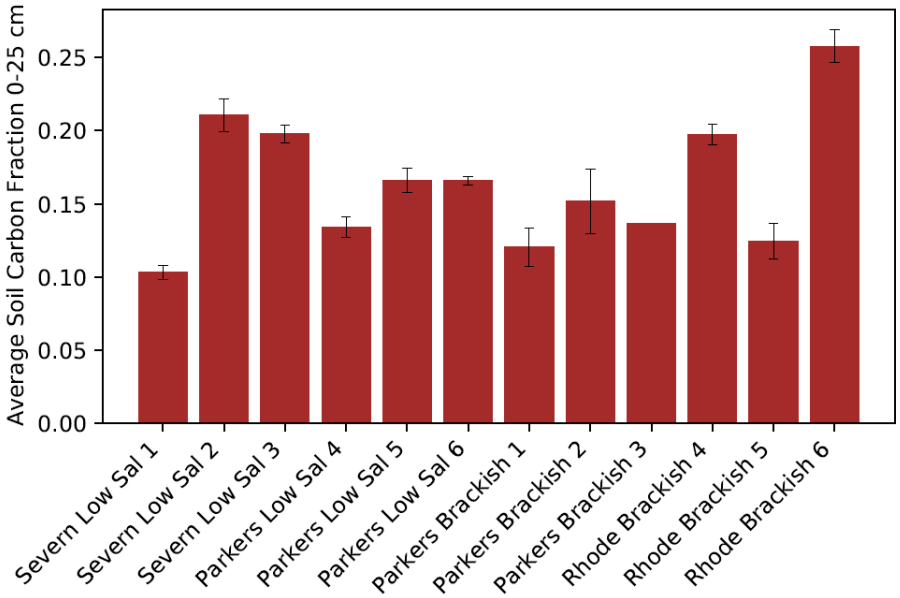


Figure S 2-4. Mean and SE soil carbon content for 0-25 cm. Soil samples from all study plots (n=8/site) averaged within each horizon to find mean C fraction and mean horizon depth zonation across site; average soil carbon from 0-25 cm is then calculated using a weighted average from horizons in that depth range. Carbon fraction estimated from loss-on-ignition and Craft et al. (1991) equation:%C = 0.4*%LOI * 0.0025*(%LOI)^2

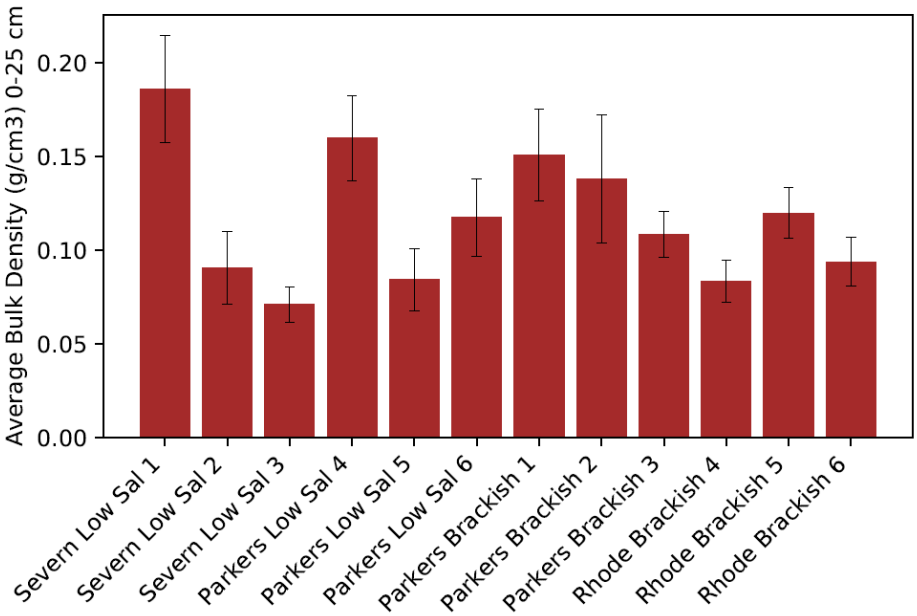


Figure S 2-5. Mean and SE soil bulk density for 0-25 cm. Soil samples from all study plots (n=8/site) averaged within each horizon to find mean C fraction and mean horizon depth zonation across site; average soil carbon from 0-25 cm is then calculated using a weighted average from horizons in that depth range.

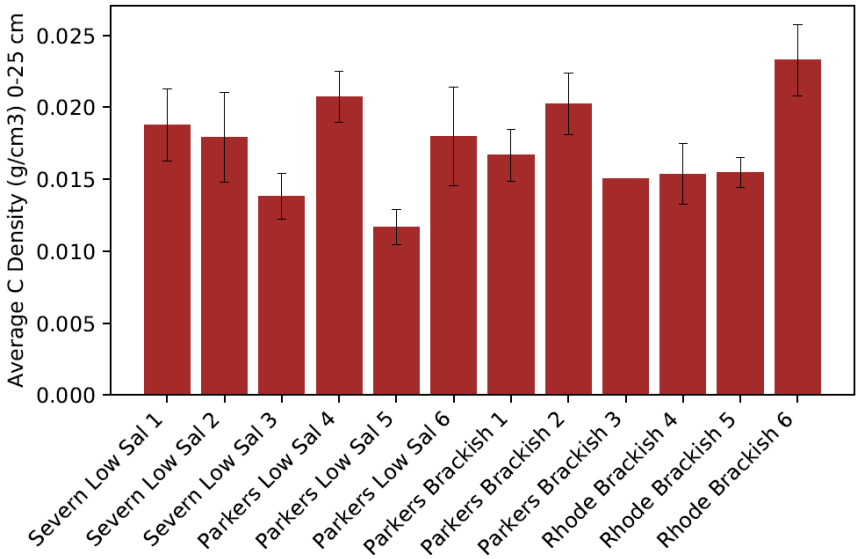


Figure S 2-6. Mean and SE soil carbon density for 0-25 cm. Carbon density is calculated as C fraction * bulk density to characterize carbon storage for a given soil volume. Soil samples from all study plots (n=8/site) averaged within each horizon to find mean C fraction/density and mean horizon depth zonation across site; average soil carbon density from 0-25 cm is then calculated using a weighted average from horizons in that depth range. Carbon fraction estimated from loss-on-ignition and Craft et al. (1991) equation: %C = 0.4*%LOI * 0.0025*(%LOI)^2

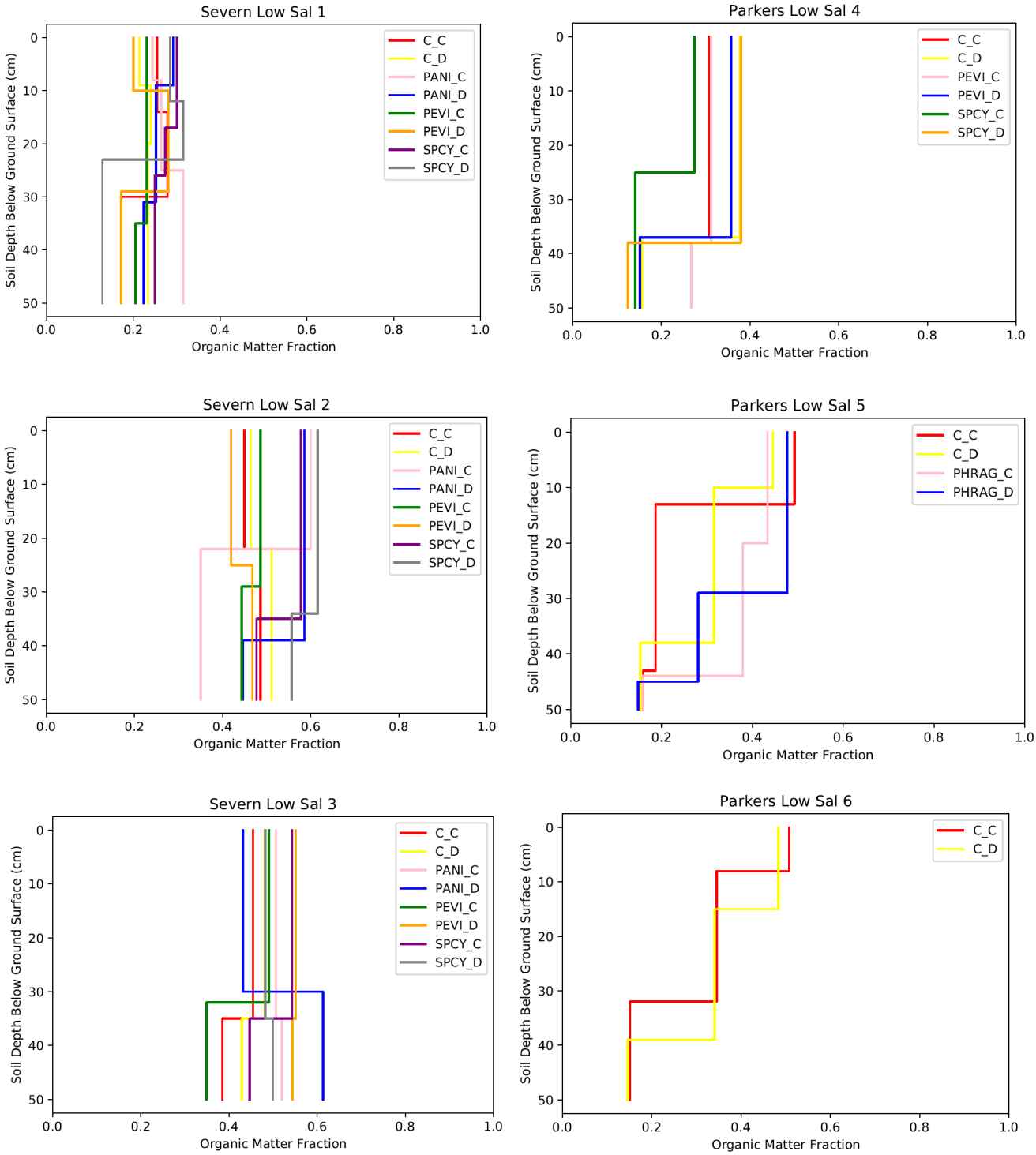


Figure S 2-7. Organic matter fraction by horizon depth for low salinity sites. In the legend, the first letter denotes study plot: C=Control, PANI=*Panicum virgatum*, PEVI=*Peltandra virginica*, SPCY=*Spartina cynosuroides*, SPPA=*Spartina patens*, DISP=*Distichlis spicata*, and PHRAG =*Phragmites australis* reference area. Second letter denotes subplots (C=clumped, D=dispersed, for control or reference plots this just indicates subplot replicate ID).

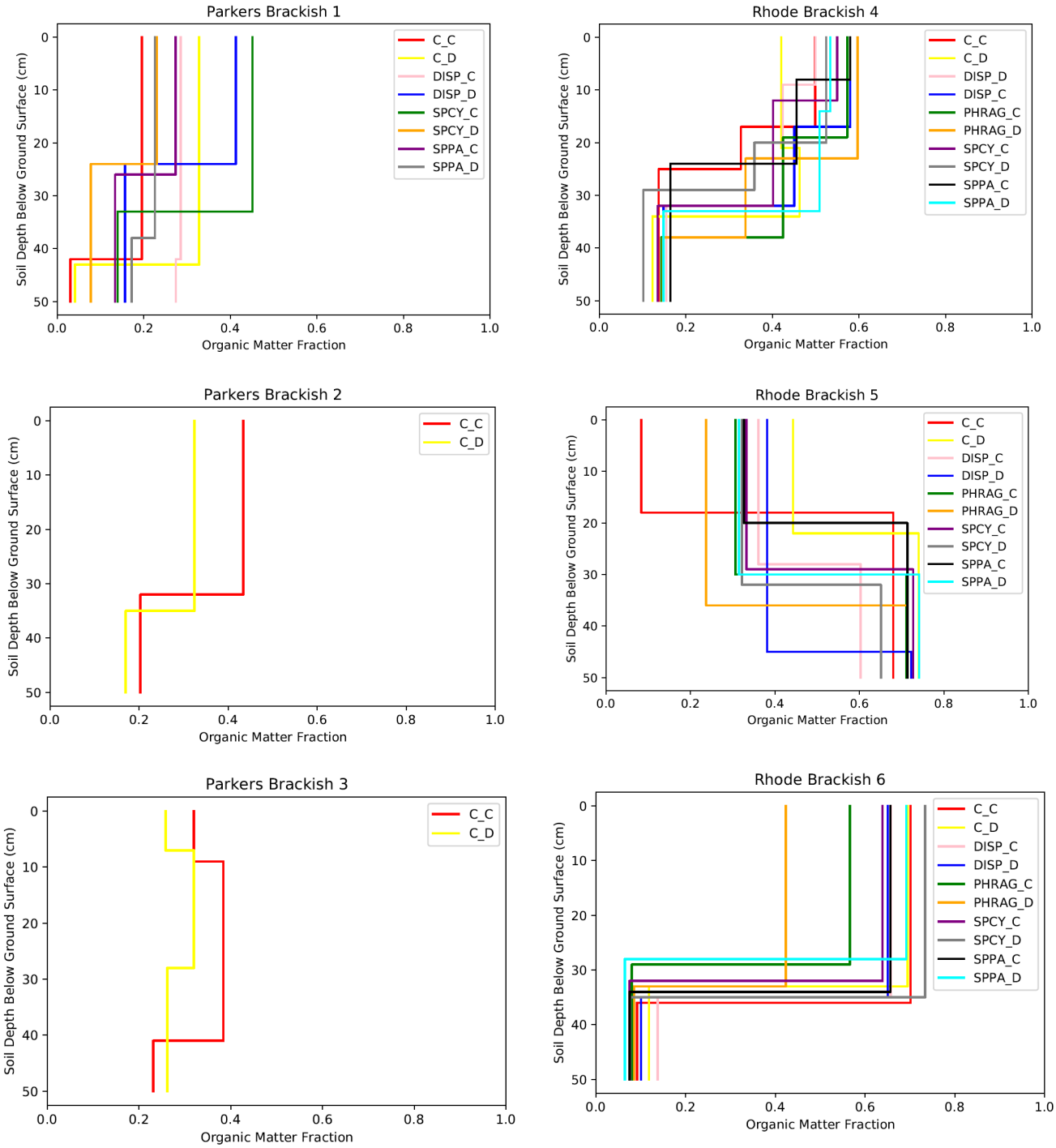


Figure S 2-8. Organic matter fraction by horizon depth for brackish sites. In the legend, the first letter denotes study plot, C=Control, PANI=*Panicum virgatum*, PEVI=*Peltandra virginica*, SPCY=*Spartina cynosuroides*, SPPA=*Spartina patens*, DISP=*Distichlis spicata*, and PHRAG =*Phragmites australis* reference area. Second letter denotes subplots (C=clumped, D=dispersed, for control or reference plots this just indicates subplot replicate ID).

Plant Growth

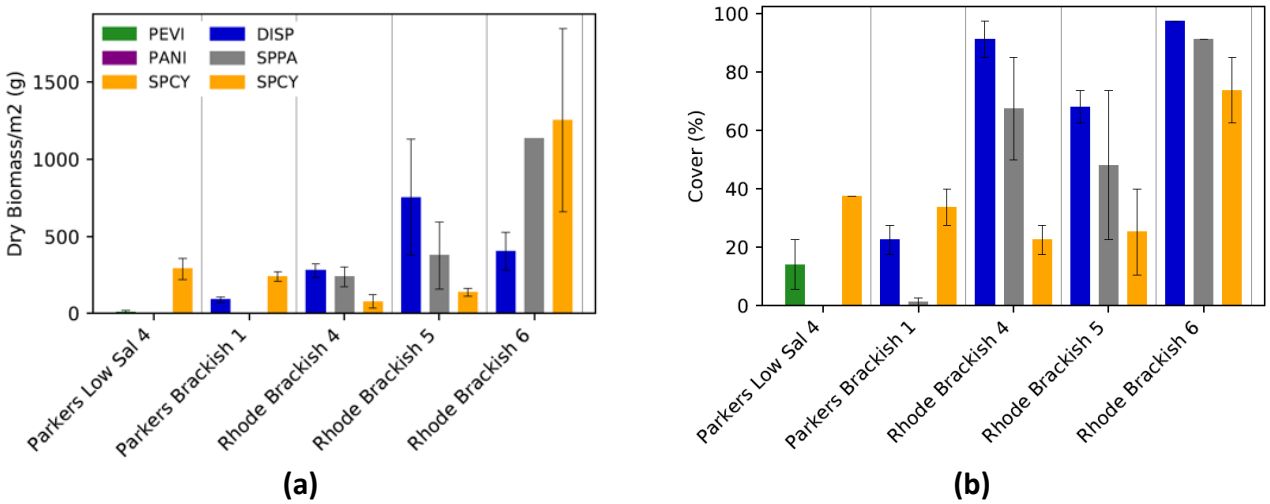


Figure S 2-9. Mean and SE for planted species of (a) dry biomass normalized per m2 area (September 2021) and (b) plant cover (August 2021). Only sites with highest survival of transplants shown (>20% cover of planted species by year 2). Planted species at low salinity sites (only Parkers Low Sal 4 had notable transplant survival): PEVI = *Petlandra virginica* (green), PANI = *Panicum virgatum* (purple – no plantings survived), SPCY = *Spartina cynosuroides* (orange); Planted species at brackish sites: DISP = *Distichlis spicata* (blue), SPPA = *Spartina patens* (gray), SPCY = *Spartina cynosuroides* (orange). Each species biomass/cover is averaged across both clumped and dispersed planting plots.

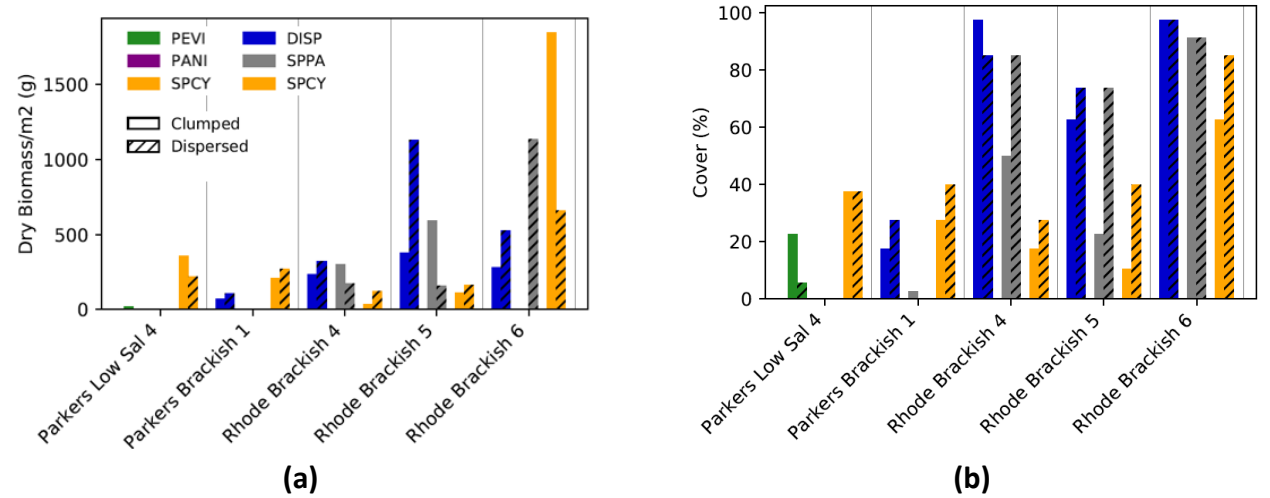


Figure S 2-10. Dry biomass (a) and plant cover (b) from summer/fall 2021 for clumped (solid fill bars) and dispersed (hatched bars) planting plots, which were planted 10 cm and 33 cm apart, respectively). Only sites with highest survival of transplants shown (>20% cover of planted species by year 2). Planted species at low salinity sites (only Parkers Low Sal 4 had notable transplant survival): PEVI = *Petlandra virginica* (green), PANI = *Panicum virgatum* (purple – no plantings survived), SPCY = *Spartina cynosuroides* (orange); Planted species at brackish sites: DISP = *Distichlis spicata* (blue), SPPA = *Spartina patens* (gray), SPCY = *Spartina cynosuroides* (orange). There were no significant differences in biomass or cover by brackish species or clumped/dispersed planting arrangement according to a two-way ANOVA for both biomass and plant cover data.

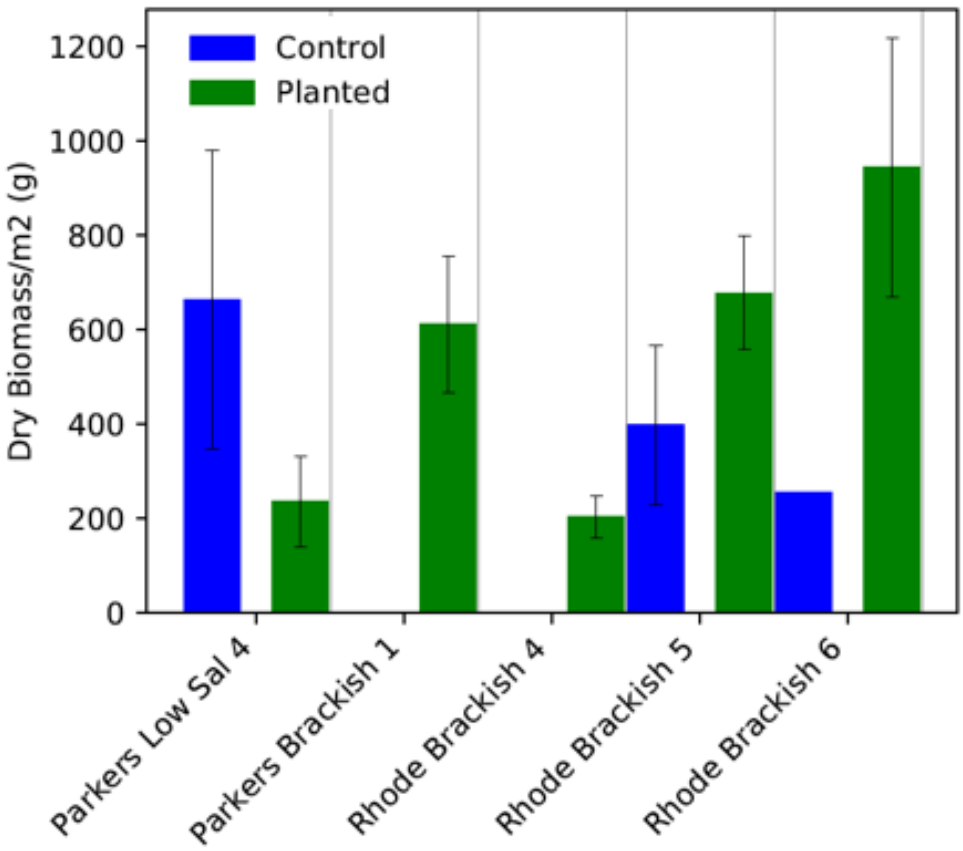


Figure S 2-11. Mean and SE of total dry biomass normalized per m^2 area for planting and control plots at the five study sites that had highest survival of native plantings. There were no plants in unplanted (control) plots at Parkers brackish 1 and 4 sites.

Figure S 2-12. Planting survival after growing season 1 by species across study sites. Survival after growing season 2 and 3 is captured with plant cover and biomass metrics.

Soil Oxidation-Reduction Potential

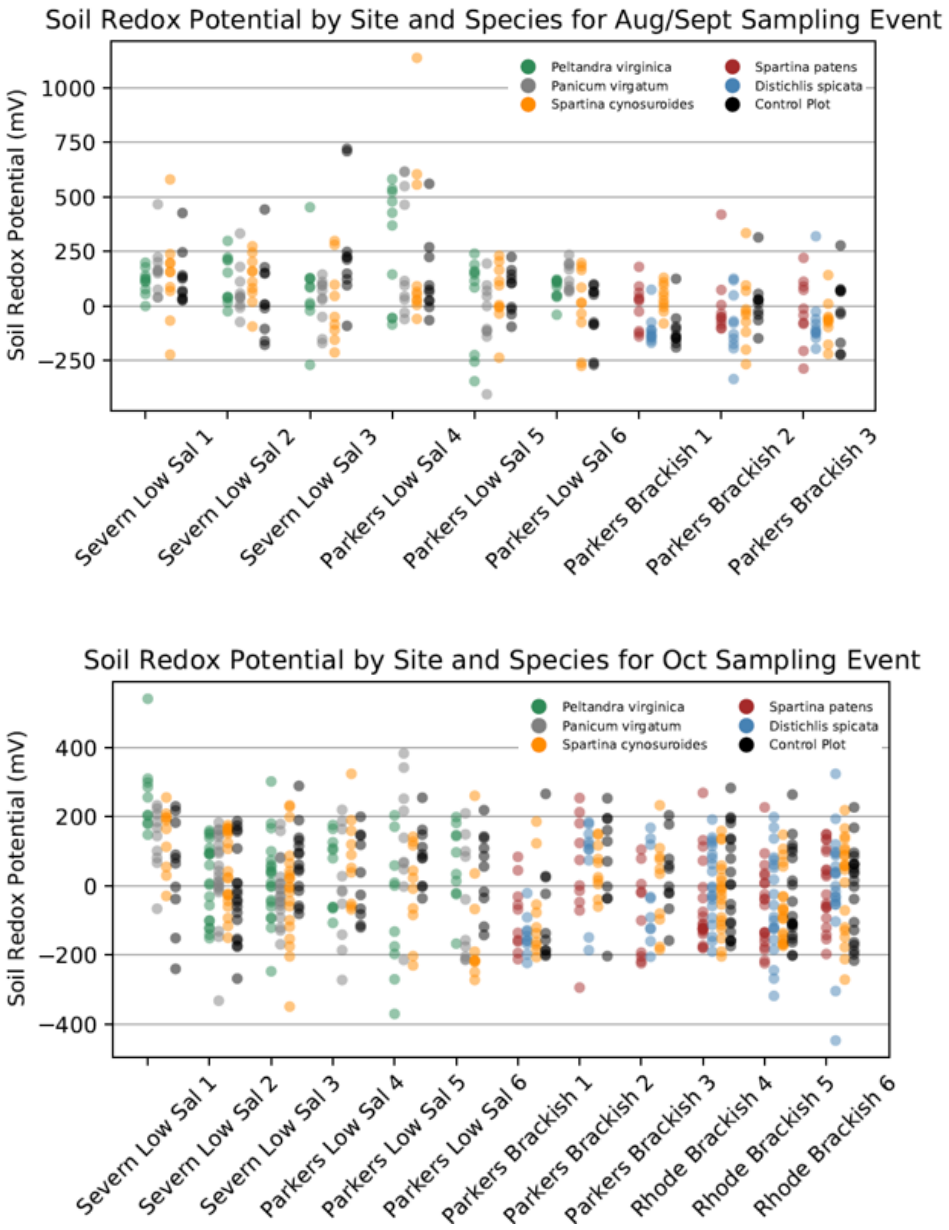


Figure S 2-13. Soil oxidation-reduction potential measured at field site study plots in 2020.

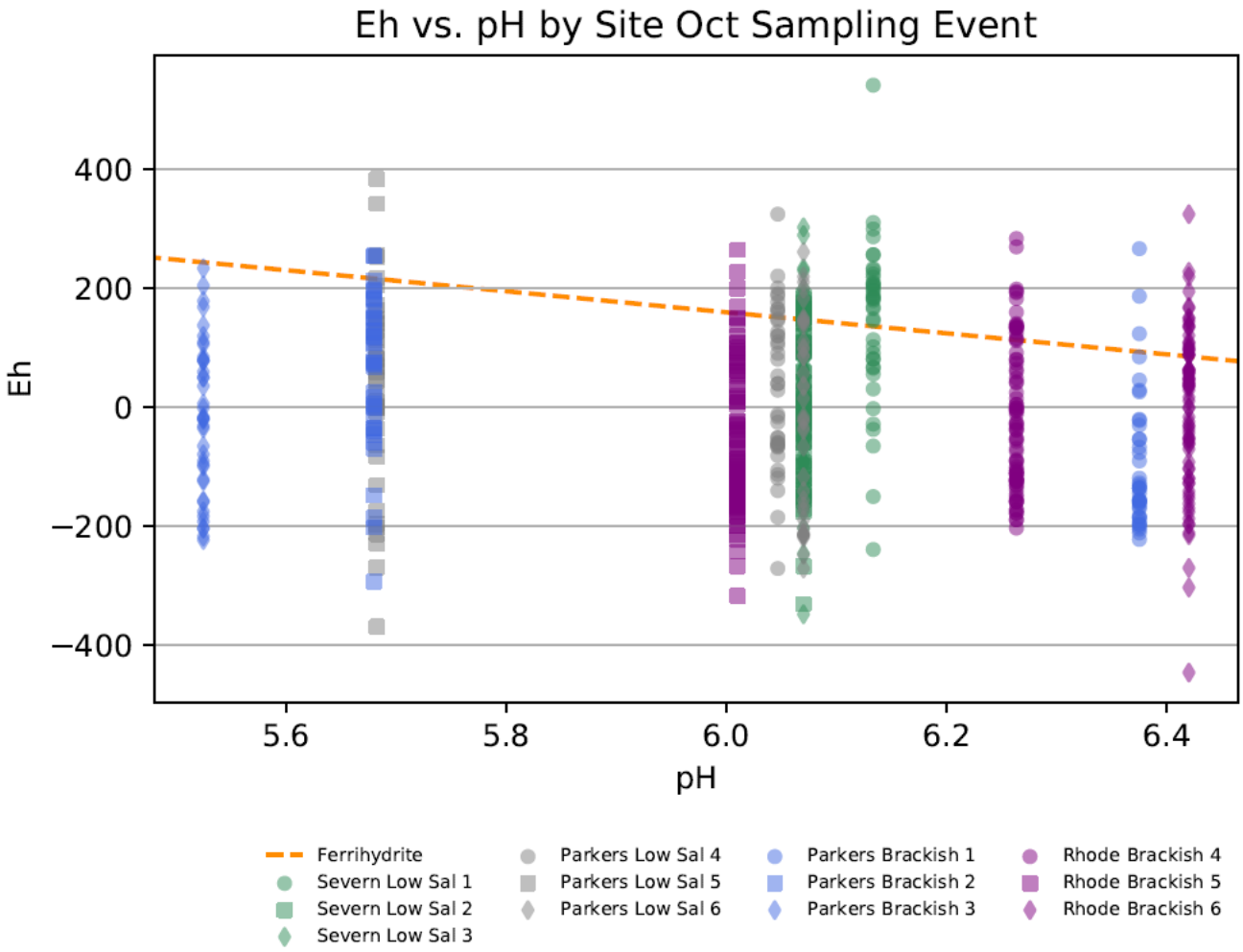


Figure S 2-14. Eh (soil redox) by site pH for all study sites (individual plot measurements pooled by site). Dashed orange line shows reduction threshold for ferrihydrite to ferrous iron.

Methods

Table S 2-2. Phragmites management methods and timing details.

Site	*Phragmites* Control Method and Timing
SERC and Severn Sites (6 sites total)	*Phragmites* cut and covered with black plastic in May/June 2020. Areas cut out of plastic for Year 1 planting in July. All plastic removed in May/June 2021 before Year 2 planting.
Parkers Brackish 1	American Chestnut Land Trust (ACLT) cut and covered in summer 2017, plastic removed in October 2019.
Parkers Brackish 2 and 3	ACLT cut but did not cover in October 2017. Cut for a second time and then covered in May-June 2018 with clear and black plastic sections. Clear plastic degraded and was removed in February 2019. Black plastic was removed in September 2019. ACLT did not observe any differences in *Phragmites* removal effectiveness between the two areas where plastic was removed at different times.
Parkers Low Salinity 4	ACLT cut but did not cover in April 2018. Cut a second time and covered June-August 2018 with clear and black plastic sections. Clear plastic section was removed in February 2019 and black plastic was removed August 2019. ACLT did not observe any differences in *Phragmites* removal effectiveness between the two areas where plastic was removed at different times.
Parkers Low Salinity 5 and 6	Sea Grant research team cut in May and June 2020. It was not feasible to cover with black plastic.

Chapter 3: High Flooding Frequencies Stimulate Wetland Plant Growth in a Sandy Substrate

Sea level rise alters wetland plants' growth dynamics and the allocation of resources to aboveground and belowground biomass production. Species-specific responses to sea level rise will determine the fate of different types of wetlands and their ability to store carbon and provide other ecosystem functions. Previous studies have noted that at higher elevations in coastal marshes, increases in inundation stimulates productivity, leading to marsh stabilization through increased organic matter production and sediment trapping (Morris et al. 2002; Kirwan and Guntenspergen 2012). In contrast, at lower elevations, where vegetation may already be experiencing flooding stress, increased inundation reduces productivity and leads to marsh collapse (Morris et al. 2002; Kirwan and Guntenspergen 2012). In particular, belowground productivity was found to decline with increasing inundation (Mudd et al. 2009; Langley et al. 2013; Mueller et al. 2016). As root production is critical for organic accretion and carbon storage (McKee et al. 2007; Neubauer 2008), lower belowground productivity in response to increased tidal inundation has substantial implications for coastal marsh resilience.

Biomass productivity in response to sea level rise is species-specific and can depend on environmental factors such as nutrient enrichment. Low marsh plants such as *Spartina alterniflora* and *Schoenoplectus americanus* increase biomass production with inundation (Morris 2006; Langley et al. 2013; Mueller et al. 2016) because they can tolerate higher levels of flooding than high marsh species such as *Spartina patens* (Langley et al. 2013).

Given coastal wetlands' critical ecological value and increasing vulnerability to sea level rise, there have been efforts to restore and protect existing coastal wetlands and even construct new coastal

wetlands using dredged material (e.g., in Cahoon et al. 2019; Staver et al. 2020). Dredged materials typically have a much higher sand content and are lower in nutrients compared to organic marsh soils, which can limit vegetation growth in restored wetlands (Langis et al. 1991; Zedler 2000). Wetland plant responses to differing levels of inundation under sea level rise may therefore differ in response to substrate characteristics.

In this study, we assessed growth of six wetland perennial plants under three different tidal flooding levels using *in situ* mesocosms. Our study objective was to determine how flooding frequency affected above and belowground biomass production, root-to-shoot ratios, shoot height, clonal growth as measured by ramet density, and carbon storage. The experiment included six perennial clonal wetland species: *Peltandra virginica*, *Panicum virgatum*, *Spartina cynosuroides*, *Phragmites australis*, *Distichlis spicata*, and *Spartina patens*. We hoped to simulate conditions in wetlands where native plantings would be planted in marshes (as done in this thesis chapter 2) following eradication of the non-native lineage of *Phragmites australis,* an invasive species in mid-Atlantic USA wetlands (Saltonstall 2002). To facilitate quantification of carbon storage and root production, we used a substrate of sand and vermiculite in the mesocosms, which inadvertently created a well-drained substrate that we later realized was more aerobic than those found in naturally occurring tidal wetlands but may be representative of soils at restored wetlands. As a result, this study provides an opportunity to track species-specific responses to differing levels of tidal inundation in a sandy, well-drained substrate such as occurs in many restoration sites.

Methods

Experimental Design

A field-based mesocosm experiment was conducted using "marsh organs," an experimental configuration where plants are grown in containers placed at differing tidal elevations (e.g., in Morris 2007; Langley et al. 2013; Mueller et al. 2016). The marsh organs are located at the Smithsonian Environmental Research Center in Edgewater, Maryland, USA at two sites in the Rhode River subestuary of the Chesapeake Bay. Salinity at one site (76.55827569°, 38.88385943°), hereafter called "low salinity," averaged 2.0 ppt with a range of 0.1 – 4.3 ppt during the experiment. Salinity at the other site (-76.54647137°, 38.8748484°), hereafter called "brackish," averaged 8.1 ppt with a range of 5.6 – 10.5 during the experiment. The experiment was conducted for two growing seasons. At each location plants were grown in pots that were positioned on platforms at three elevations within the tidal creek (Figure 3-1). The three elevations used in the experiment were approximately 5 cm below sea level, 5 cm above sea level, and 15 cm above sea level (measured elevations in Table 3-1). In 2021, to accommodate other research at the facility, the plants were moved to newly constructed platforms with the same 10 cm spacing between platforms, but the elevations shifted about 7 cm upward at the brackish marsh organ.

At each marsh organ, we had 36 pots (4 species x 3 elevations x 3 replicates per elevation). Species at the low salinity marsh organ site were *Peltandra virginica*, *Panicum virgatum*, *Spartina cynosuroides*, and *Phragmites australis*. Species at the brackish marsh organ were *Distichlis spicata*, *Spartina patens*, *Spartina cynosuroides*, and *Phragmites australis*. *Phragmites australis* plants were grown from rhizomes harvested from nearby marsh locations. The other species were grown at the

Providence Center nursery in MD and were acclimated to the site salinities before being planted in pots at the marsh organs. Two plants were placed into 1-gallon pots that were 28 cm deep with a 16.5 cm diameter. Prior to planting, the pots were filled with a mixture of 50% sand and 50% vermiculite by volume. Three filled pots without plants were placed on the intermediate elevation level as control for measuring soil carbon content (procedure described below). During the winter (December – March) when the plants had senesced, all pots were placed at the low marsh elevation to prevent freezing.

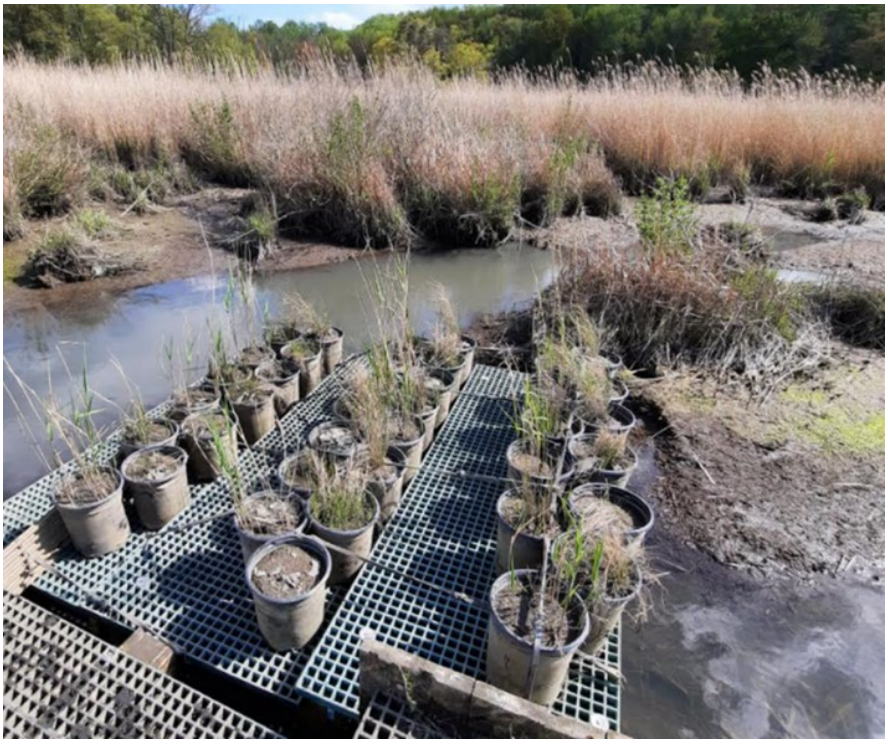


Figure 3-1. Marsh organ experimental configuration with three flooding levels at the brackish site.

Table 3-1. Elevations and flooding frequencies for marsh organ elevation levels by study year.

Low Salinity Marsh Organ								
	Elevation 2020 (m NAVD88)		**Elevation 2021 (m NAVD88)**		**Flooding Frequency 2020 (% Time)**		**Flooding Frequency 2021 (% Time)**	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
Low	-0.076	0.014	-0.0351	0.018	74	2.1	52	4.3
Med	0.030	0.013	0.048	0.0077	55	2.2	33	1.7
High	0.13	0.013	0.15	0.018	35	2.1	15	2.4
Brackish Marsh Organ								
	Elevation 2020 (m NAVD88)		**Elevation 2021 (m NAVD88)**		**Flooding Frequency 2020 (% Time)**		**Flooding Frequency 2021 (% Time)**	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
Low	-0.16	0.022	-0.066	0.0090	72	3.4	38	1.7
Med	-0.055	0.026	0.038	0.0032	54	6.5	19	0.58
High	0.073	0.020	0.14	0.0058	30	3.6	6.7	0.58

Plant Growth Monitoring

Plant growth was monitored in summer and fall of 2020 and 2021 by measuring the height of the tallest leaf or inflorescence of the plants in each pot. For *Peltandra virginica*, *Spartina cynosuroides*, and *Phragmites australis*, we also counted the number of aboveground shoots. For clonal species with many aboveground shoots (*Panicum virgatum*, *Distichlis spicata*, and *Spartina patens*) we estimated the spread of the plants by measuring diameter on the major and minor axes of the portion of the pot occupied by the plants. Area was calculated from the diameter measurement as: л (d1/2*d2/2), where d1 is the diameter along axis one and d2 is the diameter along axis 2.

Soil Oxidation-Reduction Potential

In July 2021, soil oxidation-reduction potential (Eh) was measured using platinum-tipped Eh probes (Megonigal and Rabenhorst 2013). Four probes were inserted in each pot at a 15-cm depth and a

calomel reference electrode was placed into the soil surface of each pot (offset -244 mV). A multimeter with a high impedance circuit attachment (to prevent current flow from disturbing measurement) was used to measure the potential difference in the soil between the location of each probe and the reference electrode (Rabenhorst 2009).

Biomass and Soil Organic Matter

In October 2021, after the second growing season, aboveground and belowground biomass was harvested and soil samples were collected from each pot. Aboveground biomass was clipped at the soil surface and the material in the pots was washed to collect live plant roots and rhizomes. Biomass was dried to a constant mass at 50°C and weighed. For the brackish site, belowground biomass was processed separately by two different teams, one of which unintentionally cut off the upper portion of plant rhizomes. To correct for this error, the ratio of belowground biomass between the two teams was calculated for each species by comparing plants of the same species and same inundation level. It was then possible to find a mean ratio of group 1-to-group 2 belowground biomass for each species and all values were converted to reflect the full belowground biomass (Table S 3-1 and Figure S 3-1).

After aboveground biomass had been harvested and before the substrate was washed for root collection, two soil cores were collected from each pot and combined to measure soil organic matter. The composited samples were dried at 60°C until they reached a constant mass and then at 550 °C for 2 hours to burn off organic matter and determine the samples' organic content based on loss-on-ignition (Keshta et al. 2021).

Hydrology and Salinity

The salinity of the tidal creek was measured 2-3 times in each growing season using a YSI 610 conductivity meter. Water levels were tracked continuously throughout the growing season in 15-minute intervals using HOBO pressure loggers hung in slotted PVC monitoring wells. Water pressure was calculated by subtracting the ambient air pressure (measured with a nearby atmospheric pressure monitoring logger) and was then converted to a water depth using the hydrostatic equation:

$$P = \rho g h$$

Where P is the pressure of water, ρ is the density of water (effects of salinity on density were deemed negligible for the purposes of these calculations), g is the standard acceleration due to gravity, and h is the height of the water column above the data logger pressure sensor. Water depths were then adjusted to reflect the water depth relative to the potted plant soil surface using the elevation difference between the well and the marsh organ pots and by matching a manually measured water depth for at a given time. Elevations were surveyed using Real-Time Kinematic (RTK) GPS instrumentation. Site flooding frequency was characterized as the % of time the soil surface of the potted plants at each elevation was inundated.

Statistical Analysis

One-way ANOVAs were used to compare aboveground biomass, belowground biomass, and root-to-shoot (R:S) ratios for each species as well as plant growth metrics (height, live stem count, and plant basal area) for the final set of growth measurements in October 2021. Tukey's HSD was used to assess pairwise differences between elevations. Normality and homogeneity of variance assumptions

were checked by visually inspecting residuals and the Shapiro-Wilk test was also used to check the normality of model residuals. Statistical analyses were performed using R version 4.0.5.

Results

Soil Oxidation-Reduction Potential

There was no trend in soil oxidation-reduction potential (Eh) by elevation or species (Figure S 3-3 and Figure S 3-4). Marsh organ sandy soils were oxidized to moderately reduced (Fiedler et al. 2007) – most Eh readings ranged from 400-700 mV and 200-700 mV at the low salinity and brackish marsh organ mesocosms, respectively (Figure 3-2). For comparison, the Eh of wetland soils near the marsh organs was measured in the field experiments (this thesis chapter 2), at a shallower depth of 7 cm. The marsh soils were highly to moderately reduced (Fiedler et al. 2007), with most Eh measurements ranging from -300-300 mV (Figure 3-2).

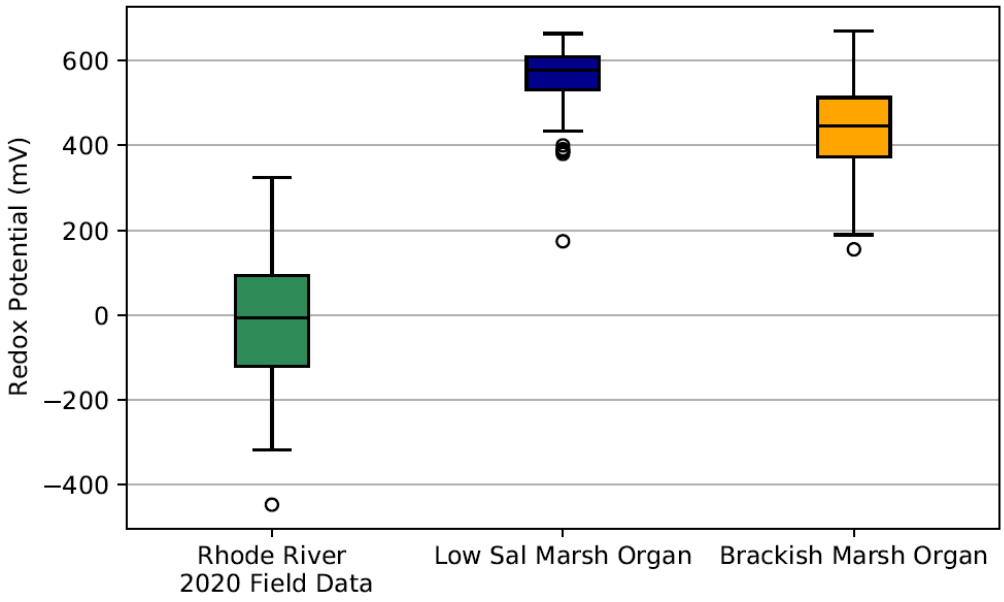


Figure 3-2. Soil redox measurements at low salinity and brackish marsh organs in 2021 at 15-cm depth and soil redox measurements from nearby Rhode River marsh at 7-cm depth as reference.

Above- and Belowground Biomass

Aboveground biomass for *Panicum virgatum*, *Spartina cynosuroides*, *Phragmites australis*, and *Spartina patens* increased with increasing flooding frequency (Table 3-2). For *Peltandra virginica* and *Distichlis spicata*, there was no clear relationship between aboveground biomass production and flooding. *Spartina cynosuroides* and *Phragmites australis*—at both low salinity and brackish marsh organs—also had higher belowground biomass at elevations that flooded more frequently, while *Spartina patens* had less belowground biomass at the lowest elevation; *Panicum virgatum*, *Distichlis spicata*, and *Peltandra virginica* showed no trend between belowground biomass production by flooding frequency (Table 3-3). With the exception of *Peltandra virginica,* which had low overall growth and survival, all species had lower root-to-shoot (R:S) ratio at higher flooding frequencies/lower elevations, but only *Spartina patens*, *Distichlis spicata*, and *Spartina cynosuroides* at the brackish marsh organ had a statistically significant decrease in R:S ratio with flooding frequency at $p<0.05$ (Table 3-4). *Peltandra virginica* had low survival and biomass production—only 5/9 pots had living plants by the end of the second growing season (two surviving plants at low elevation, two at intermediate elevation, and one at high elevation).

Table 3-2. Aboveground biomass (g) by mesocosm elevation level (Mean ± SE). Different letters indicate pairwise differences with $p<0.05$ (Tukey HSD).

Species	Elevation			
	Low	Medium	High	ANOVA Statistics
Low Salinity Marsh Organ				
P. virginica	0.8 ± 0.4	0.3 ± 0.3	0.1 ± 0.1	$F_{2,6}$=1.32, p=0.33
P. virgatum	82.7^{a} ± 4.8	58.5^{b} ± 6.3	44.7^{b} ± 7.6	$F_{2,6}$=9.99, p=0.01
S. cynosuroides	44.9^{a} ± 3.6	20.8^{b} ± 1.2	16.9^{b} ± 2.6	$F_{2,6}$=32.0, p<0.01
P. australis	121.2^{a} ± 24.9	62.1^{ab} ± 9.3	26.2^{b} ± 2.6	$F_{2,6}$=9.67, p=0.01
Brackish Marsh Organ				
S. patens	108.3^{a} ± 9.3	69.9^{b} ± 5.0	65.3^{b} ± 6.2	$F_{2,6}$=11.2, p=0.01
D. spicata	79.4 ± 27.6	37.0 ± 1.6	60.0 ± 7.2	$F_{2,6}$=1.65, p=0.27
S. cynosuroides	60.7^{a} ± 4.9	18.5^{b} ± 2.4	11.2^{b} ± 0.7	$F_{2,6}$=70.2, p<0.01
P. australis	63.3^{a} ± 6.5	49.7^{ab} ± 8.8	26.3^{b} ± 7.6	$F_{2,6}$=5.91, p=0.04

Table 3-3. Belowground biomass (g) by mesocosm elevation level (Mean ± SE). Different letters indicate pairwise differences with $p<0.05$ (Tukey HSD).

Species	Elevation			
	Low	Medium	High	ANOVA Statistics
Low Salinity Marsh Organ				
P. virginica	2.3 ± 2.3	3.1 ± 2.9	1.0 ± 1.0	$F_{2,6}$=0.23, p=0.80
P. virgatum	46.7 ± 1.5	50.3 ± 5.5	49.7 ± 12.2	$F_{2,6}$=0.063, p=0.94
S. cynosuroides	82.3^{a} ± 7.8	60.0^{a} ± 4.6	34.0^{b} ± 2.0	$F_{2,6}$=20.3, p<0.01
P. australis	144.0^{a} ± 25.4	89.0^{ab} ± 11.0	45.3^{b} ± 4.7	$F_{2,6}$=9.29, p=0.01
Brackish Marsh Organ				
S. patens	45.8^{a} ± 1.6	61.6^{a} ± 4.7	85.4^{b} ± 6.5	$F_{2,6}$=17.7, p<0.01
D. spicata	77.9 ± 4.9	86.0 ± 5.3	81.3 ± 5.1	$F_{2,6}$=0.64, p=0.56
S. cynosuroides	123.5^{a} ± 11.5	61.0^{b} ± 11.0	70.5^{ab} ± 5.5	$F_{2,6}$=12.0, p=0.04
P. australis	131.7^{a} ± 6.2	104.0^{b} ±1.2	79.0^{c} ± 0.7	$F_{2,6}$=52.2, p<0.001

Table 3-4. Root-to-shoot ratio by mesocosm elevation level (Mean ± SE). Different letters indicate pairwise differences with p<0.05 (Tukey HSD).

Species	Elevation			
	Low	Medium	High	ANOVA Statistics
Low Salinity Marsh Organ				
P. virginica	7.8*	45.2 ± 44.78	10.0*	$F_{2,6}$=0.16, p=0.87
P. virgatum	0.6 ± 0.03	1.0 ± 0.02	1.1 ± 0.27	$F_{2,6}$=3.46, p=0.10
S. cynosuroides	1.9 ± 0.25	2.9 ± 0.37	2.1 ± 0.14	$F_{2,6}$=3.68, p=0.10
P. australis	1.2 ± 0.08	1.5 ± 0.16	1.8 ± 0.31	$F_{2,6}$=1.90, p=0.23
Brackish Marsh Organ				
S. patens	0.4^{a} ± 0.03	0.9^{b} ± 0.09	1.3^{c} ± 0.09	$F_{2,6}$=32.2, p=<0.001
D. spicata	1.2^{a} ± 0.34	2.3^{b} ± 0.18	1.4^{ab} ± 0.15	$F_{2,6}$=6.55, p=0.03
S. cynosuroides	2.2^{a} ± 0.34	3.8^{ab} ± 1.02	6.1^{b} ± 0.03	$F_{2,6}$=9.91, p=0.05
P. australis	2.1 ± 0.20	2.2 ± 0.37	3.4 ± 0.77	$F_{2,6}$=2.09, p=0.20

*Only one *Peltandra virginica* plant at low and high marsh organ elevation levels had non-zero aboveground biomass so the R:S ratio is calculated for only one plant at these levels.

Plant Growth

After two growing seasons, the mean height of most species was greatest at the lowest elevation where flooding frequency was the highest (Figure 3-3). For most species, the differences in height by elevation became more pronounced after the second growing season. Some species (*Panicum virgatum* and *Spartina cynosuroides* at the low salinity marsh organ) initially grew shorter at the lowest elevation in the first growing season of summer 2020.

After two years, *Spartina cynosuroides* and *Phragmites australis* shoot numbers were higher at the lowest elevation at both sites (Figure 3-4). There were no clear trends in the area covered by shoots for the two clonal species (Figure 3-5), although by 2021 *Distichlis spicata* had a larger basal area at the lowest and highest elevation compared to the medium elevation.

Soil Organic Content

Organic content of the sandy substrate was low, ranging from 0.4%-1.1% across all species at both sites, and there were no statistical differences by species or elevation (Figure S 3-2).

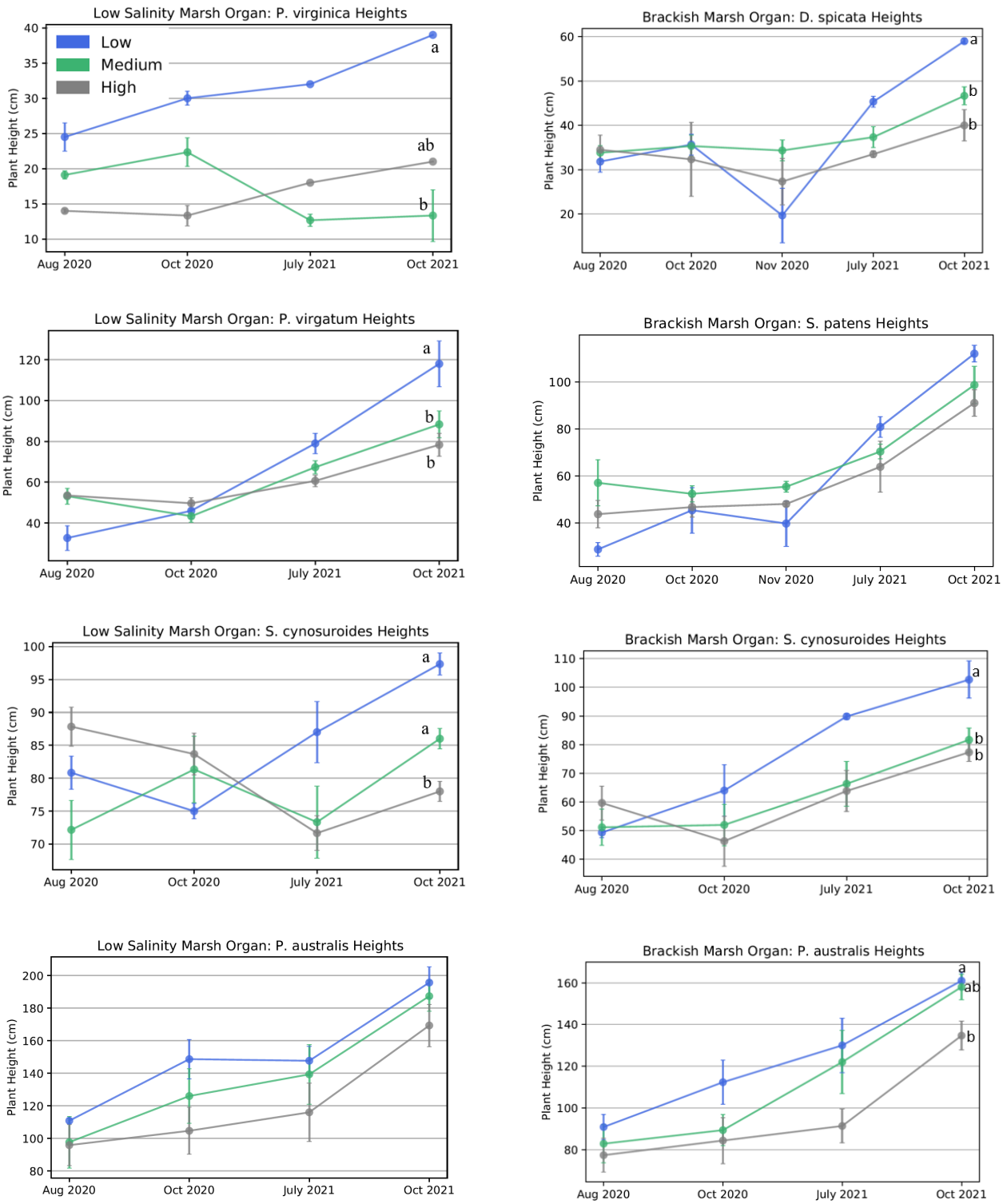


Figure 3-3. Height of tallest leaf or inflorescence by marsh organ elevation (blue=lowest elevation, green=medium, gray=high). Different letters indicate differences in growth between elevations for Oct 2021 with $p<0.05$.

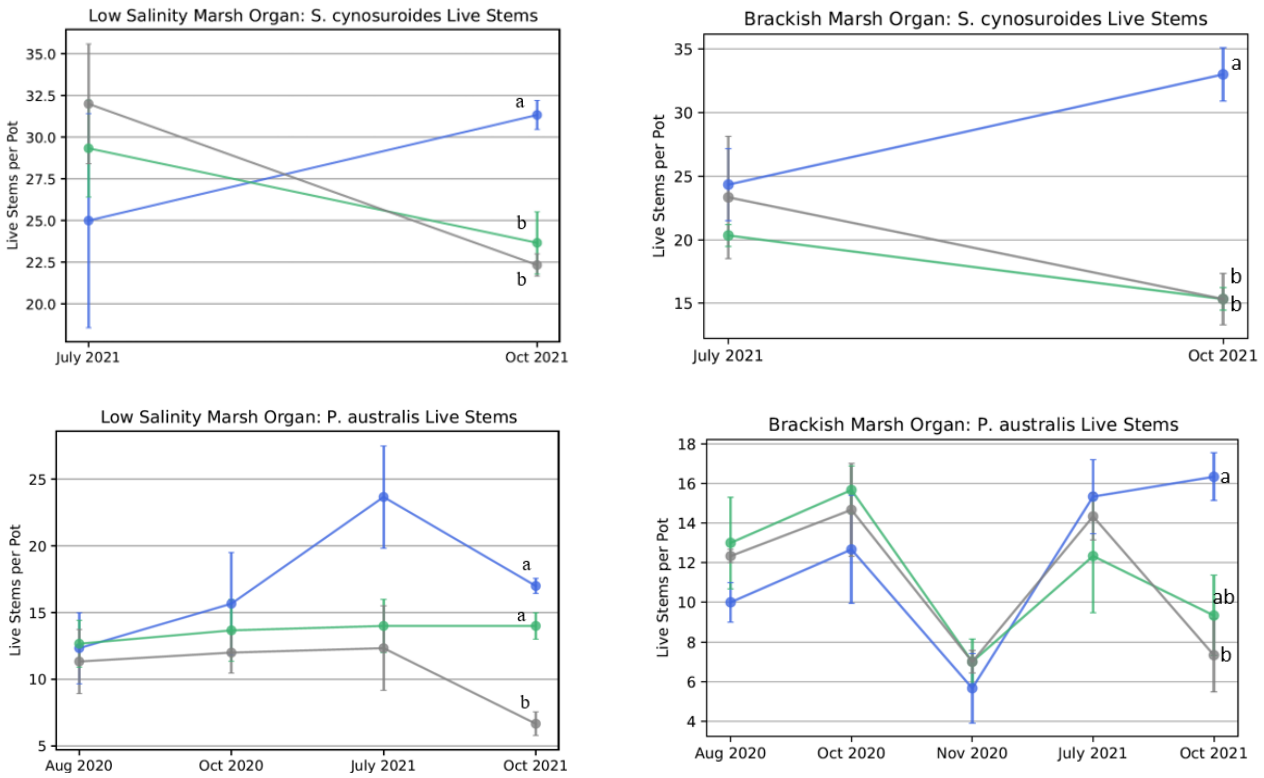


Figure 3-4. Number of living stems by marsh organ elevation (blue=lowest elevation, green=medium, gray=high). Different letters indicate differences in growth between elevations for Oct 2021 with $p<0.05$.

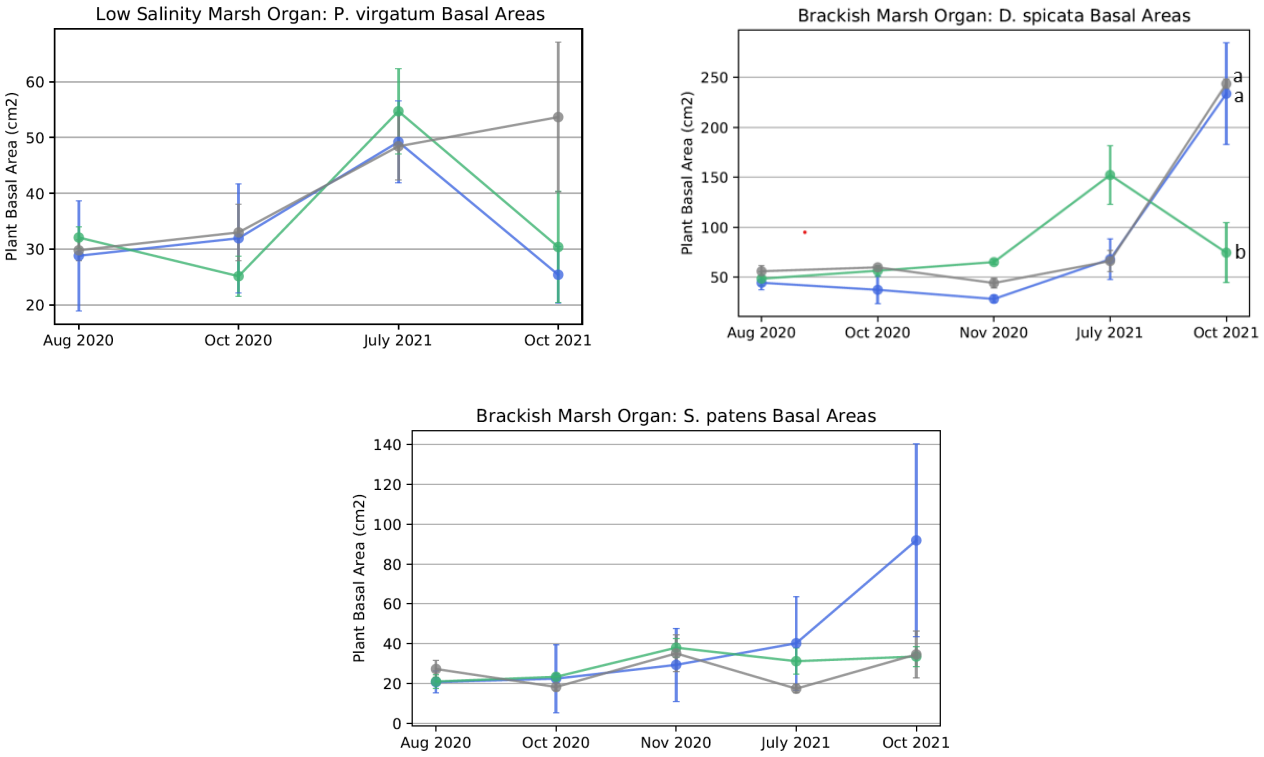


Figure 3-5. Basal area of plant growth by marsh organ elevation (blue=lowest elevation, green=medium, gray=high). Basal area is calculated as pi(d1/2*d2/2) where d1 and d2 are the major and minor axes of the elliptical plant base. Different letters indicate differences in growth between elevations for Oct 2021 with $p<0.05$.

Discussion

High Biomass Production with High Flooding Frequencies in Sandy Substrate

Previous research on the effects of inundation in tidal wetlands found that high levels of tidal inundation can promote growth and biomass production through nutrient enrichment (Steever et al. 1976; Odum et al. 1995) but can also depress plant growth when the physio-chemical environment in the substrate is stressful because of anaerobic, sulfide-rich conditions (Koch et al. 1990; Baldwin et al. 2001; Tobias and Nyman 2017; Hollis and Turner 2021). Our experiment demonstrated that increasing tidal flooding enhanced growth in the absence of the biogeochemical constraints present in highly organic soils.

The well-drained, sandy substrates in the pots created conditions where wetland plants thrived at higher flooding frequencies and lower elevations than in a typical tidal marsh as well as in previous mesocosm experiments with peaty soils. We speculate that the high soil redox potential (Eh) (ranging from 160-680mV) and low carbon pool (organic matter content of 0.4-1.1%) limited microbial reduction of oxygen and sulfate, preventing the highly anaerobic and toxic sulfidic soils that can lead to plant stress in tidal wetland organic soils (Koch et al. 1990; Tobias and Nyman 2017; Hollis and Turner 2021). Our Eh measurements were comparable to those at many upland sites (Eh> 400 mV) with some more reducing microsites (Eh<300mV) that could be typical for a moderately reduced wetland and might lead to some nitrate and iron reduction but likely not sulfate reduction (Peters and Conrad 1996; Pennington and Walters 2006; Brookins 2012). Eh also did not differ by inundation level or between planted and unplanted pots as was observed in previous marsh organ mesocosm experiments at the same

facility as used for our brackish marsh organ (Mueller et al. 2016; Mueller et al. 2020), suggesting that there was little microbially mediated reduction even at the most flooded elevations.

After two years, there were no differences in substrate carbon content between species or in response to flooding frequency. The lack of any differences in soil carbon may have been due to the rapid decomposition of any roots that died during the experiment. Or, because the plantings were recent, there may have been little root turnover in the pots.

Species-Specific Responses to Differing Sea Levels

Our study tracked the differing responses of six wetland plant species to variable sea levels in a low-nutrient, sandy substrate. Although most species had higher aboveground biomass production (and often higher total biomass production) and grew taller at the highest flooding frequency in our experiment, belowground growth responses were more variable between species. *Spartina cynosuroides* and *Phragmites australis* both had highest belowground biomass at the lowest elevations at both low salinity and brackish conditions, while *Panicum virgatum*, *Distichlis spicata*, and *Peltandra virginica* had similar belowground growth across flooding levels*; Spartina patens*' belowground production decreased with increased flooding frequency. The differing responses suggest differing thresholds of inundation tolerance across different species, as well as differing nutrient responses.

Spartina cynosuroides and *Phragmites australis* had highest productivity at low elevations and high levels of flooding that would be unusual for their typical growth in coastal marshes (with the pot soil surface flooded 74% and 52% of the time at the low salinity marsh organ in the 2020 and 2021 growing seasons, respectively, and 72% and 38% of the time at the brackish marsh organ in 2020 and 2021). The expansion of the invasive lineage of *Phragmites australis* is often associated with the upland

fringe of lower salinity wetlands where it thrives under lower flooding frequencies and lower depths of inundation (e.g., flooding frequencies < 10%) (R. M. Chambers et al. 2003b; Tulbure 2008; Randolph M. Chambers, Meyerson, and Dibble 2012). Once established in a less flooded zone, *Phragmites* can grow clonally into more inundated environments (including flooding frequencies up to 100%) (R. M. Chambers et al. 2003a). Partly, it is seedling emergence that is hindered by high flooding frequencies, which we did not test in our study, but shoot growth has also shown to be suppressed with high flooding levels (Hellings and Gallagher 1992). In our mesocosm, *Phragmites* had highest total biomass production with flooding frequencies over 70%, suggesting that *Phragmites* may not be as sensitive to high flooding frequencies and flooding depths in a sandier substrate. *Phragmites australis* is known for thriving under high-nutrient conditions (Silliman and Bertness 2004; Kettenring et al. 2011), so it may benefit from near-continuous nutrient inputs from frequent tidal pulses when it is not constrained by the highly anaerobic, sulfidic conditions in poorly-drained, high-carbon soils. *Phragmites* invasion could thus be a potential challenge in restored wetland sites with sandier substrates. A previous study in the Great Lakes region found that *Phragmites* invasion occurred predominantly on sandy substrates (Tulbure 2008), although another study did not find sandy sediment to increase *Phragmites'* dominance (Wang et al. 2006).

Spartina cynosuroides may also have benefited from the nutrient subsidies in more frequent tidal pulses – previous research found that both higher levels of salinity and increased duration of tidal inundation increased nutrient content in *Spartina cynosuroides* (McHugh and Dighton 2004), but salinities above 14 ppt may reduce *S. cynosuroides* growth (White and Alber 2009). *Spartina cynosuroides* produced 1.3x higher aboveground biomass and 1.5x higher belowground biomass at the brackish marsh organ's lowest elevation compared to the low salinity marsh organ's lowest elevation.

Since flooding levels were lower at the brackish marsh organ (at least in year 2), and *S. cynosuroides* increased biomass with flooding frequency in our experiment, we speculate that higher biomass at the brackish conditions may be due to higher nutrient levels in the brackish zone (~8.5 ppt) of the tidal creek.

For Spartina patens, aboveground biomass was highest at the lowest mesocosm elevation (-16 cm NAVD88 with 72% flooding frequency in 2020 and -6.6 cm in 2021 with flooding frequency of 38%). Although *Spartina patens'* belowground biomass decreased with elevation, total biomass for this species peaked at the medium elevation with an elevation of -5.5 cm (NAVD88) with 54% flooding frequency in 2020 and 3.8 cm (NAVD88) and 19% flooding frequency in 2021. These are lower elevations and higher flooding frequency thresholds than observed in a previous marsh organ mesocosm at the same location with a peat-sedge substrate, which found reductions in *Spartina patens*' aboveground biomass below 30 cm above mean sea level (flooding frequency less than 25%) and reduction in total biomass below 40 cm above mean sea level (flooding frequency less than 5%) (Langley et al. 2013). This species is associated with coastal wetland high-marsh zones, so it is not surprising that we saw some reductions in total growth at high flooding frequencies of 38-72%, but the threshold at which total growth declined was at a lower elevation in the sandy substrate.

Distichlis spicata is known to follow similar patterns of biomass allocation as *Spartina patens* and occupies a similar niche in the high-marsh zone of brackish tidal wetlands (Brewer et al. 1998). In our study, unlike *Spartina patens*, *Distichlis spicata* did not show a clear trend of higher aboveground biomass production with increasing flooding level nor a decrease in belowground production, suggesting that there are differences in this species' response to flooding and nutrient inputs. *Distichlis spicata* is known to decrease growth under high levels of flooding (Howard and Rafferty 2006), but has also been

shown to increase production with nutrient enrichment (Traut 2005; Fox et al. 2012). The interactions between the benefits of increased nutrient supply and stress of higher levels of inundation could have led to the high variability in aboveground biomass production without a clear trend by flooding frequency. Overall, the consistent production of total biomass and belowground biomass across all flooding levels shows that *Distichlis spicata* was tolerant of a wide range of flooding frequencies in sandy substrate conditions.

Panicum virgatum is an important biofuel crop in the United States (McLaughlin and Kszos 2005), but is less studied in the context of wetland responses to sea level rise and wetland restoration. *Panicum virgatum* has a great deal of genetic and phenotypic variation and can be found in wetland and upland conditions — it is the lowland ecotype of this species that is typically found in wetlands (Porter Jr 1966; Milano, Lowry, and Juenger 2016), where it can be a dominant species in high-marsh zones (Gedan and Fernández-Pascual 2019). Our study found increases in aboveground biomass and little change in belowground biomass with increased flooding, suggesting that *Panicum virgatum* thrived under high flooding frequencies in a sandy substrate. Our results are consistent with a previous study which found that this species can grow in highly flooded conditions (Edwards 2007).

Petlandra virignica's low growth and biomass production in our study may have been due to insufficient inundation, as surviving plants grew tallest at the lowest mesocosm elevation, suggesting that even elevations of -0.076 m (NAVD88) with flooding frequencies up to 74% are insufficient for *Peltandra virginica*'s growth in a sandy, well-drained substrate. Previous research has shown that *Peltandra virginica* is sensitive to water deprivation (Touchette et al. 2008), so this species may not have flourished under the well-drained mesocosm conditions. Further, *Petlandra virginica* typically allocates most of its biomass to belowground rhizomes and roots (Whigham and Simpson 1978), which

may not have had sufficient time to develop in our two year experiment. The elevations in our study are already on the lower range of this species typical coastal wetland habitat – a previous study found that, on average, *Peltandra virginica* was found at an elevation of 0.32 M NAVD88 and could be found at elevations ranging from 0-0.52 m NAVD88 within a mid-Atlantic freshwater tidal marsh (Delgado et al. 2018).

Decreasing R:S Ratio with Higher Flooding Frequencies

For all species, with the exception of *Peltandra virginica*, there was a trend of decreasing root-to-shoot ratio (R:S) with increasing flooding frequency, which suggests that higher nutrient availability from tidal pulses allows for greater allocation of resources to aboveground growth. This is consistent with previous research demonstrating that when nitrogen is not limiting, wetland plants increase aboveground production relative to belowground production (Valiela et al. Persson 1976; Wigand et al. 2004; Deegan et al. 2012; Wong et al. 2015). However, most species, except for *Spartina patens*, had similar or higher *total* belowground production with higher flooding frequencies, demonstrating that the wetland plant species' total production generally benefited from increased tidal flooding in a sandy substrate.

The root-to-shoot (R:S) ratios that we found for the wetland plant species in our mesocosm experiment were generally comparable with wetland field-based measurements. For *Phragmites australis*, mean R:S ratios across flooding levels in our experiment were 1.2-3.4, similar to various field-based estimates ranging from 1.1-4.9 (Roman and Daiber 1984; Lisamarie Windham 2001; Tripathee and Schäfer 2015). For *Spartina cynosuroides*, mean R:S ratios ranged from 1.9-3.8 across most flooding frequencies, which is comparable with a field-study R:S ratio of 2.5 (Schubauer and Hopkinson

1984). At the highest elevation of the brackish marsh organ, we measured a mean R:S ratio of 6.1 for *Spartina cynosuroides*, suggesting that this species may allocate a greater portion of biomass toward root growth at low flooding frequencies and low nutrient conditions. For *Distichlis spicata*, mean R:S ratios in our experiment ranged from 1.2-2.3, where a field study reported 1.1, but the study speculated that this may have been an underestimate (Tripathee and Schäfer 2015). *Peltandra virginica* is known for high allocation of biomass to belowground growth with a reported mean R:S ratio of 8.4 (Whigham and Simpson 1978). Our low and high elevation R:S ratios were close to this value, although our medium elevation estimate was much higher at 45.2. Due to low survival and low biomass production of *Peltandra virginica*, our R:S ratios are likely not as reliable for this species. For *Panicum virgatum*, we found R:S ratios of 0.6-1.1, which are lower than an estimate of 2.5 from an agricultural study (Sainju et al. 2017). For *Spartina patens*, our measured R:S ratios were also lower than a field-based estimate of 4.9 (Tripathee and Schäfer 2015). Since this species decreased root production with flooding frequency in our experiment, low R:S ratios could be a result of high nutrient availability at higher flooding frequencies or partly due to stress under hypoxic conditions. Previous research found associations between hypoxia and decreased root production in *Spartina patens*: high levels of flooding led to increased alcohol dehydrogenase activity in *Spartina patens*, indicating a shift to anaerobic respiration, which yields less carbon available for root structures (Naidoo et al. 1992). In addition, root growth in our mesocosms was limited to two years and might have been constrained by the pot volume.

Overall, our results suggest that species allocate biomass similarly in sandy substrates compared to organic wetland conditions and have similar responses of decreasing R:S ratio with increased flooding, which may have also increased nutrient access. Lower R:S ratios for *Spartina patens*, the one species we observed that had lower belowground production in response to high flooding frequencies,

may be an indicator of flooding stress for this species in sandy substrates at flooding frequencies of 72% and 38% in 2020 and 2021, respectively.

Implications for Wetland Restoration

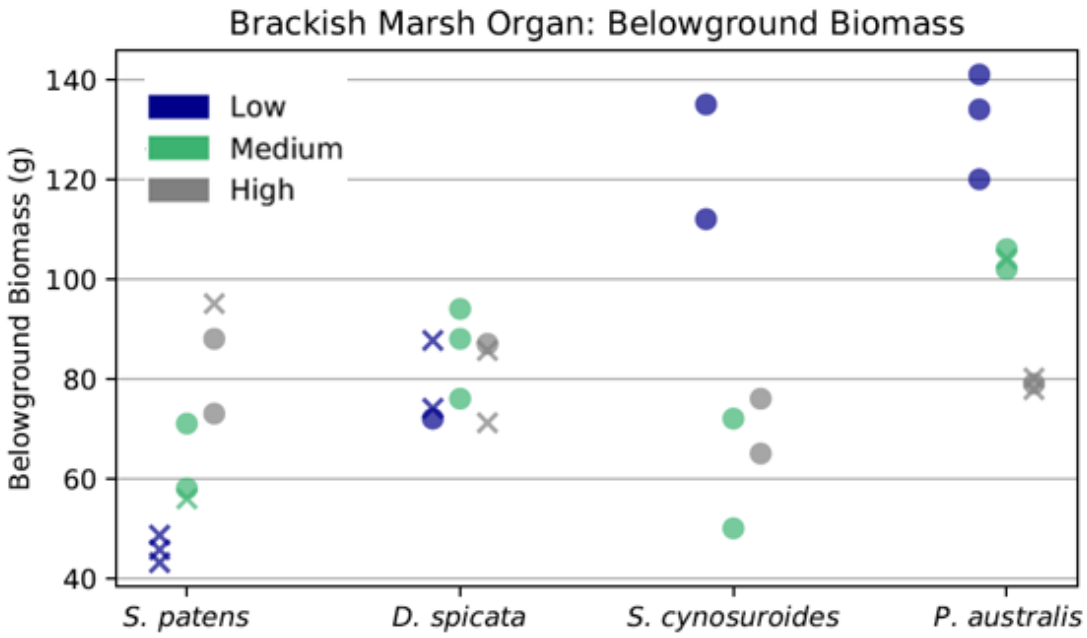
Dredged materials are increasingly being used to restore tidal wetlands or to elevate rapidly subsiding coastal marshes (e.g., in Ford et al. 1999; Ray 2007; Berkowitz et al. 2017; Cahoon et al. 2019; Staver et al. 2020). These materials are often coarse and sandy and can lead to reduced soil nutrient content, higher soil densities, and lower soil organic matter content (Ray 2007). For instance, a constructed marsh from Louisiana dredge material had eight times lower organic matter than a natural reference marsh (Cheng and White 2022). Coastal wetland plant communities may have differing responses to sea level rise and differing growth patterns in these sandy, low-carbon substrates compared to in organic wetland soils. Most research on wetland species responses to sea level rise focuses on natural marsh systems or mesocosm experiments with organic substrates. Our study suggests that for a sandy substrate, increased tidal exposure likely increases nutrient supply without creating highly reducing, anoxic conditions, stimulating biomass production for perennial wetland plants at low elevations and high flooding frequencies that would lead to plant stress in organic soils.

Supplemental Information - Chapter 3

Table S 3-1 Belowground biomass measurements for each group. Group 2 cut off top portion of rhizomes and missed a substantial portion of belowground biomass, so we converted group 2's values to reflect the full belowground biomass. A ratio of group1:group2 belowground biomass was found for each species and elevation where data from both groups was available. The average ratio for each species was used to convert group 2's measurements to match group 1's measurements and reflect the entirety of the belowground biomass. For *Spartina cynosuroides*, group 2 only measured one sample, so this data point was dropped from the analysis.

Species	Relative Elevation	Group 1 Average	Group 2 Average	Group 1 :Group 2 Ratio	Species Average Group 1 :Group 2 Ratio	Standard Deviation of Ratio
P. australis	High	79.0	41.3	1.9	1.9	0.0008
	Med	104.0	54.4	1.9		
	Low	131.7	None			
D. spicata	High	87.0	35.2	2.5	2.2	0.35
	Med	86.0	None			
	Low	72.0	36.3	2.0		
S. patens	High	80.5	26.0	3.1	3.7	0.79
	Med	64.5	15.3	4.2		
	Low	None	12.5			
S. cynosuroides	High	70.5	None		Not enough group 2 data to find reliable ratio so we just dropped group 2's roots data	
	Med	61.0	31.2	2.0		
	Low	123.5				

Figure S 3-1. Belowground biomass at brackish marsh organ by species and elevation. Circles are datapoints that were measured by group 1 and X's are root samples that were measured by group 2 and then converted using the species ratio to match group 1's procedure and reflect the entirety of the belowground biomass (conversion factors shown in Table 2-1).



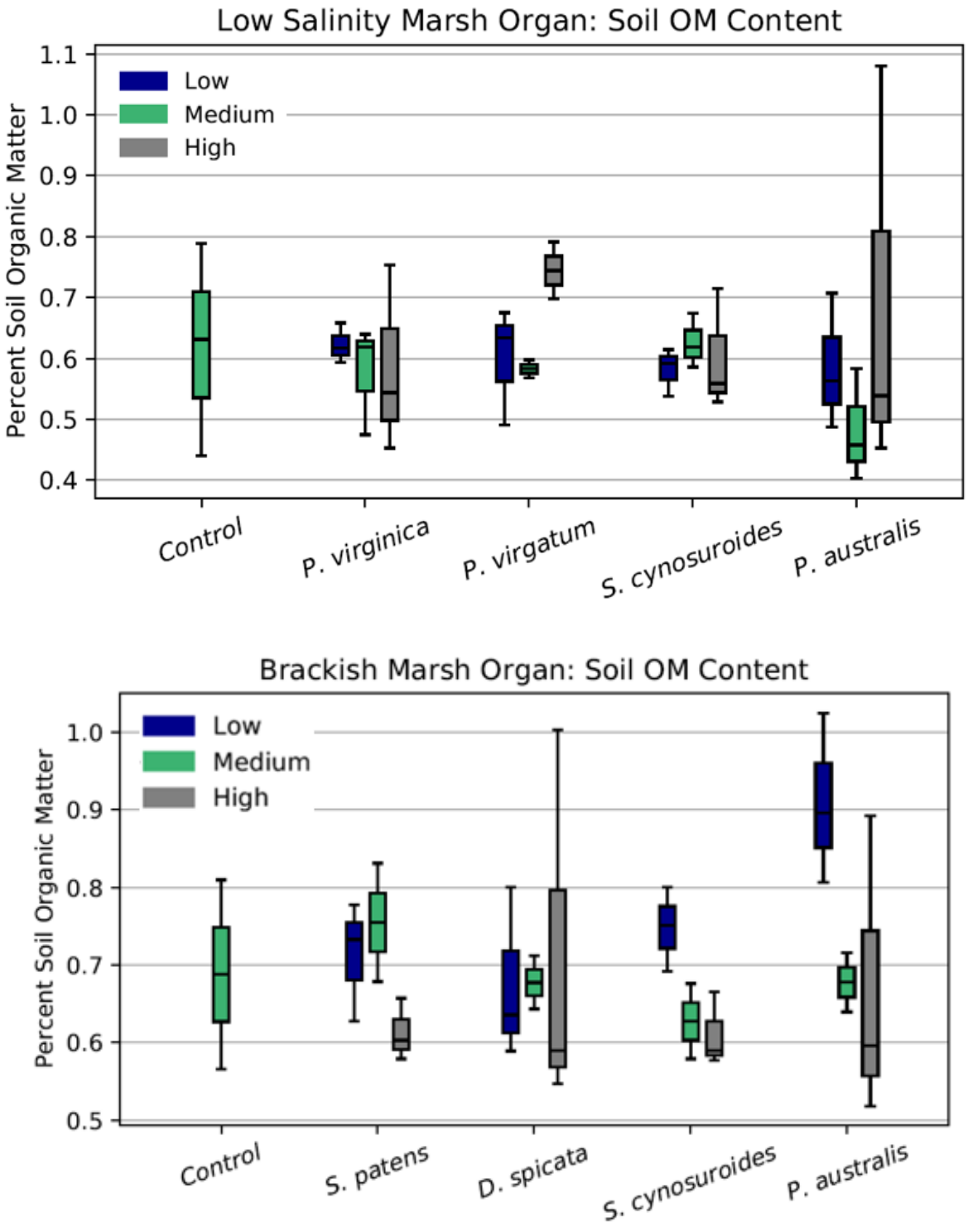


Figure S 3-2. Soil organic content (%) across species and elevations at low salinity and brackish marsh organs (blue=lowest elevation, green=medium, gray=high).

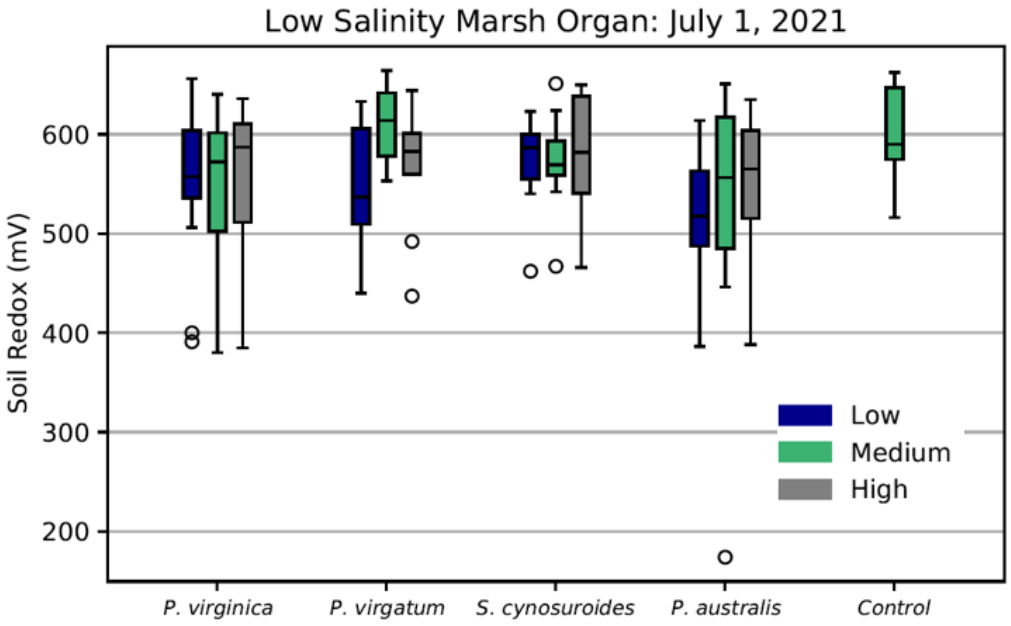


Figure S 3-3. Soil oxidation reduction potential (redox) measured in low salinity marsh organ pots at 15-cm depth at low, medium, and high elevations.

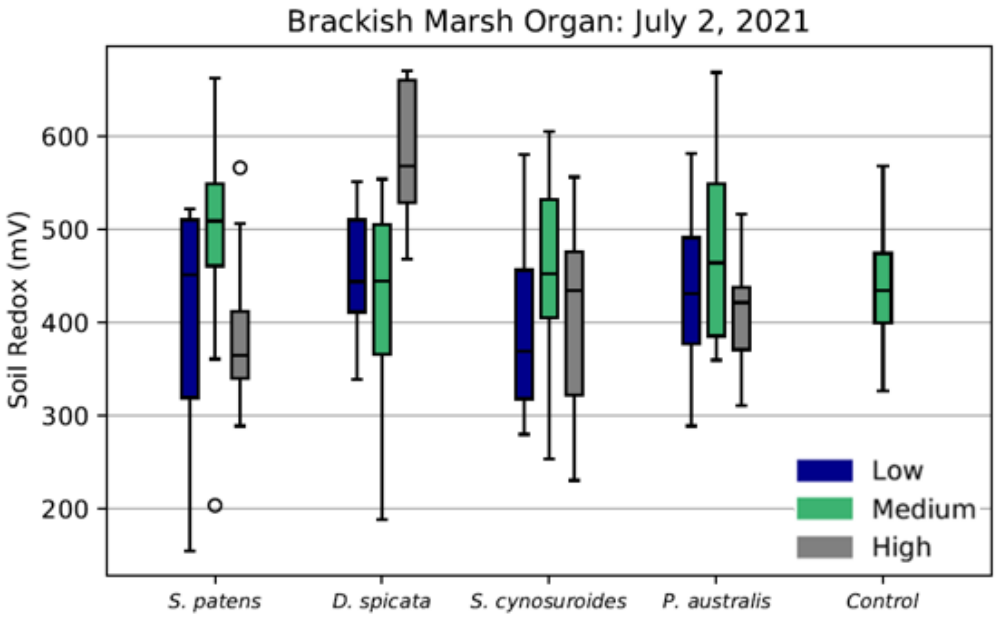


Figure S 3-4. Soil oxidation-reduction potential measured in brackish marsh organ pots at 15-cm depth at low, medium, and high elevations.

Chapter 4: Conclusions

Our field and mesocosm experiments demonstrate that salinity and hydrology are dominant drivers of restoration outcomes in tidal wetlands. In our field experiment, the rate and composition of vegetation recovery following *Phragmites* eradication was dependent on salinity and flooding frequency: native vegetation developed more rapidly at low salinity and less frequently inundated tidal wetland sites. At low salinity sites, many annual species and a few perennials were dominant following *Phragmites* removal. Annual plants may be especially resilient to *Phragmites* reinvasion due to their ability to grow rapidly early in the growing season (Byun et al. 2013), although they produce less belowground biomass (Whigham and Simpson 1978), and thus may not provide the same ecosystem services as a mature, perennial wetland plant community. Higher salinities and flooding levels are known to suppress seed germination and seedling growth (Baldwin et al. 1996; Baldwin et al. 2001), and the suppression of plant growth may be amplified following a large disturbance (Baldwin and Mendelssohn 1998), such as the clearing of *Phragmites*.

Native planting helped increase vegetation cover and aboveground biomass at brackish sites, which recovered more slowly without planting than low salinity sites. At a few brackish sites, planted perennial species (i.e., *Distichlis spicata*, *Spartina patens,* and *Spartina cynosuroides*) spread rapidly and formed dense mats of vegetation. We found a correlation between perennial aboveground biomass and belowground biomass, suggesting that re-establishing perennial vegetation through planting may help promote belowground growth following *Phragmites* removal. However, planting survival was low at many sites, illustrating the risk of investing resources in planting when outcomes can be variable. Further research could help test strategies for successful planting in tidal wetland environments, which

are dynamic ecosystems with fluctuating tides and wind exposure and can have anoxic and saline soil porewater that can inhibit plant growth. Past studies have found that planting success can be increased by planting in clusters to harness intra-species facilitation in stressful environments with saline conditions or high wave exposure (Silliman et al. 2015; Renzi et al. 2019; Fischman et al. 2019; Duggan-Edwards et al. 2020), but we did not see an effect of planting configuration on survival or growth of plantings in our study. It may be that the benefits of facilitation cannot overcome certain thresholds of environmental stress. Other recommended methods for planting success in restoration include using older plantings (Palma and Laurance 2015) or harvesting sods of native graminoids from nearby sites (Sparks et al. 2013). We also speculate that anchoring plantings to the marsh with a stake or another mechanism could help plantings withstand wind, waves, and ice. Both native planting efforts and natural vegetation emergence are at the mercy of sea level and weather fluctuations and likely vary between years – drier periods early in the growing season can promote seedling establishment (Baldwin et al. 2001) and may allow native plantings to become established so they can later withstand storms and the highly reducing soil conditions of the peak growing season.

Our mesocosm study may help inform planting efforts for wetland restorations that use sandy, dredged materials as substrate. We found that perennial wetland plants can tolerate—and may require—higher flooding frequencies for peak biomass production in a sandy substrate compared to what others have observed in organic soils. Increased tidal exposure in a low-carbon, well-drained substrate likely increases water and nutrient supply without creating anoxic, sulfide-rich conditions. In a sandy substrate, increased tidal inundation stimulates biomass production in a sandy substrate.

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