Recent interactions between an invasive (*Phragmites australis*) and a native plant species (*Spartina alterniflora*) in the upper reaches of Great Sippewissett marsh, Cape Cod

by

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Abstract

Salt marshes are critical coastal ecosystems characterized by tidal flow, halophytic vegetation, and muddy sediment, serving as nurseries for marine species, erosion buffers, and carbon sinks. However, the invasion of the salt-tolerant haplotype of common reed, *Phragmites australis*, in Eastern North America poses a threat to salt marsh ecosystems historically dominated by *Spartina alterniflora*. While a range of management strategies, including chemical, biological, and physical control methods, are utilized to address invasive species, the emphasis tends to be primarily on their removal rather than on the long-term impact of restoration efforts.

This study investigates the competitive interactions between *P. australis* and *S. alterniflora* in Great Sippewissett Marsh on Cape Cod. I conducted a one-season experiment manipulating *P. australis* by cutting its stems at ground level in three treatment plots. I then measured the resulting changes in *S. alterniflora* percent cover and compared them to values in three control plots. The results revealed that the invasion of *P. australis* impedes the upland migration of *S. alterniflora*, potentially through shading effects. Clipping stems of *P. australis* led to a rapid increase in *S. alterniflora* % cover, nearly doubling that of unclipped areas by the end of the growing season. This result suggests cover of *P. australis* might be managed to encourage cover of native marsh vegetation and prevent habitat loss. On a broader scale, this project gives insight into not only into invasive species removal but also into ecosystem restoration, crucial for reinstating native plant communities and ensuring long-term ecological resilience.

Introduction

Salt marshes and their ecological functions

Salt marshes are found in intertidal zones, where land meets the sea, creating a transition area between terrestrial and aquatic environments (Townend et al. 2011). They are characterized by a unique combination of tidal flow, halophytic vegetation, and muddy sediment (Townend et al. 2011; Vernberg 1993). Salt marshes are formed in sheltered coastal areas, such as estuaries, bays, and lagoons, where tidal fluctuations and the accumulation of sediment facilitate their development (Friedrichs and Perry 2001). The ebb and flow of tides help distribute nutrients and filter pollutants throughout coastal ecosystems. Tidal cycles influence the exchange of water and nutrients between salt marshes and adjacent coastal waters (Christiansen, Wiberg, and Milligan 2000; Friedrichs and Perry 2001). During high tides, water flows into the marsh, carrying nutrients and organic matter, which support the diverse array of organisms inhabiting the marsh (Friedrichs and Perry 2001). Conversely, during low tides, water recedes, allowing for the flushing out of excess nutrients and facilitating the exchange of gases between the marsh and the atmosphere (Friedrichs and Perry 2001). Moreover, the dynamics of tides help to dissipate the energy of waves, reducing the impact on coastal areas and preventing or slowing down shoreline erosion (Barbier et al. 2011; zu Ermgassen et al. 2021).

Tides also contribute to the activities of microorganisms in the marsh. High tides create anaerobic conditions that support specific microorganisms by enabling anaerobic metabolism, breaking down organic matter into compounds like methane and hydrogen sulfide (Kostka, Roychoudhury, and Van Cappellen 2002). This process releases vital nutrients for other organisms (Kostka, Roychoudhury, and Van Cappellen 2002). Low tides, on the other hand, form aerobic conditions sustaining plants and microorganisms that require oxygen for respiration (Vernberg 1993). Moreover, the coexistence of anaerobic and aerobic conditions facilitates nitrogen cycling (Bowen et al. 2023). Nitrogen gas is converted into ammonia by bacteria under anaerobic conditions, later oxidized to nitrate under aerobic conditions, providing crucial nutrients for plant growth (Bowen et al. 2023). In short, the dynamic nature in salt marshes provides a rich source of energy and nutrients for the ecosystem, facilitating material cycling and maintaining ecological balance.

The halophytes, as another key feature of salt marshes, are divided into two categories: high marsh plants that grow in higher elevations that remain dry for longer periods, and low marsh plants that spread in areas regularly submerged by high tides (Bertness and Miller 1984; Pennings and Callaway 1992). In New England salt marshes, common low marsh vegetation includes salt-tolerant grasses, such as *Spartina* species, while common high marsh vegetation includes shrubs and herbs uniquely adapted to saline conditions, such as *Iva frutescens* and *Solidago sempervirens* (Bertness and Miller 1984). However, the dominant vegetation species can vary at different latitudes and in different countries.

Muddy sediment also plays a crucial role in the formation and function of salt marsh ecosystems. Muddy sediment in the salt marsh refers to sediment containing a high proportion of fine-grained particles, such as clay and silt, which settle at the bottom of the marsh or remain suspended in the water. This sediment typically has a soft texture and may appear murky, often forming due to slow water flow within the salt marsh environment. Within salt marshes, muddy sediment acts as a substrate for plant growth, providing stability for vegetation to take root (Friedrichs and Perry 2001). This sediment is often rich in organic matter, which is deposited through the interaction of tidal currents and the decay of plant material (Portnoy and Giblin 1997;

Valiela, Teal, and Persson 1976). As a result, salt marsh sediment serves as a nutrient source for the diverse array of plants and microorganisms that inhabit these environments.

Moreover, muddy sediment in salt marshes serves as a habitat and food source for various fauna. Burrowing organisms, such as worms and mollusks, thrive in the nutrient-rich sediment, contributing to the bioturbation process that enhances sediment mixing and nutrient cycling (Gutiérrez et al. 2006; J. Q. Wang et al. 2010). These organisms play a vital role in shaping the physical structure of the sediment and influencing nutrient availability, which in turn impacts the overall productivity of the salt marsh ecosystem (Gutiérrez et al. 2006; J. Q. Wang et al. 2010).

Salt marshes are of significant interest to researchers, conservationists, and policymakers for several reasons. Firstly, they play a crucial role in coastal protection by acting as natural barriers against erosion, storm surges, and flooding (Barbier et al. 2011; zu Ermgassen et al. 2021). The dense vegetation and intricate root systems of salt marsh plants help stabilize the shoreline and dissipate the energy of incoming waves, thereby reducing the impact of coastal hazards on human settlements and infrastructure (Feagin et al. 2009; Kidson 1959).

Salt marshes are also recognized for their ability to sequester and store large amounts of carbon, making them valuable in the fight against climate change (Chmura et al. 2003; Drake et al. 2015). The organic matter accumulated in the waterlogged soils of salt marshes can remain trapped for centuries, effectively removing carbon dioxide from the atmosphere and mitigating the impacts of greenhouse gas emissions (Beaumont et al. 2014; Burden et al. 2013). According to other studies, the carbon burial per unit area in salt marshes ranks among the highest measured in numerous environments (Chmura et al. 2003; Duarte, Middelburg, and

Caraco 2005).

The exports from salt marshes serve as an important food and nutrient source to support coastal food webs. Tidal water movements flowing in and out of salt marshes lead to a notable export of energy-rich particulate organic matter, bolstering coastal food webs extending beyond the marsh fringe (Valiela, Lloret, and Chenoweth 2023). Furthermore, salt marshes release dissolved organic carbon compounds that support microbial activity in adjacent waters, along with nitrogen-containing materials, which serve as crucial nutrient sources for coastal primary producers (Valiela, Lloret, and Chenoweth 2023).

Salt marshes also play a significant role in improving water quality by filtering pollutants and trapping sediments. The vegetation and soils in these wetlands act as natural filters, removing excess nutrients, heavy metals, and other contaminants from the water (Almeida, Mucha, and Teresa Vasconcelos 2011; Nelson and Zavaleta 2012; Reboreda and Caçador 2007; Webb et al. 2012; Weis et al. 2002). This filtration process helps to maintain the delicate balance of coastal and estuarine environments, benefiting both aquatic and terrestrial species.

As a highly productive ecosystem, salt marshes provide valuable habitats for a diverse community of plant and animal species. These coastal wetlands serve as nursery grounds for many commercially and recreationally important fish species, as well as feeding and nesting areas for migratory birds, shorebirds, and waterfowl (Barbier et al. 2011; zu Ermgassen et al. 2021). The biodiversity supported by salt marshes contributes to the overall health and resilience of coastal ecosystems (Barbier et al. 2011; zu Ermgassen et al. 2021).

The natural richness and biodiversity of salt marshes have attracted various human activities over time, including early damaging practices such as peat mining, diking, filling, and draining for agriculture (Valiela, Lloret, and Chenoweth 2023). Additionally, there has been historical selective harvest of marsh grasses for hay and livestock grazing (Valiela, Lloret, and Chenoweth 2023). In recent times, salt marshes have become popular destinations for visitors interested in observing natural settings and wildlife, such as birds (Valiela, Lloret, and Chenoweth 2023). Salt marshes and related habitats have long served as areas for fishing and shellfish collection, although, in recent decades, there has been an increasing use of salt marsh estuaries for mariculture of macroalgae, holothurians, crustaceans, bivalves, and fish (Ferrón, Ortega, and Forja 2009).

Salt marsh invasive species

Invasive species are non-native organisms that have been introduced by humans, either intentionally or unintentionally, into an ecosystem where they did not evolve naturally and cause negative effects on native species or ecosystems (Keller et al. 2011; Sakai et al. 2001; Yan et al. 2001). These species can be plants, animals, or microorganisms, and they possess characteristics that allow them to outcompete and displace native species, often leading to significant ecological, economic, and/or social consequences (Keller et al. 2011; Yan et al. 2001).

Invasive species have garnered substantial interest from scientists, policymakers, and the general public due to their potential to cause severe environmental and economic impacts. These impacts can manifest in various ways, such as the disruption of ecosystem functions, the alteration of food webs, the loss of biodiversity, and the degradation of natural habitats (Gallardo et al. 2016; Pejchar and Mooney 2009; Riley, Dybdahl, and Hall 2008). By exploiting available resources more efficiently or lacking natural predators or control mechanisms, invasive species can rapidly proliferate and dominate an ecosystem, leading to the decline or even extinction of native species (Keller et al. 2011; Yan et al. 2001). This process can have cascading effects on the entire ecological community, potentially altering the structure and functioning of the ecosystem (Keller et al. 2011; Yan et al. 2001).

In recent decades, a salt-tolerant haplotype of the common reed, *Phragmites australis,* has proliferated across Eastern North America and expanded into wet areas, including salt marshes whose vegetation has historically been dominated by *Spartina alterniflora* (Chambers, Meyerson, and Saltonstall 1999; Guo et al. 2014; Kirk et al. 2011; Saltonstall 2002; Vasquez et al. 2005). A study in the Great Salt Lake revealed expansion rates of *P. australis* patches, ranging from 9-35% per year (Kettenring et al. 2016). The rapid pace of expansion and detrimental effects have garnered significant attention from scientists.

Phragmites australis

P. australis, commonly known as common reed or reed grass, is a perennial grass species that has garnered significant interest due to its widespread distribution, ecological impacts, and potential applications (Engloner 2009). As a fresh water plant, it was originally from East Asia and Europe (Hazelton et al. 2014). However, in recent decades, it has arrived on the east coast of North America as an invasive salt-tolerant haplotype that poses a threat to many native salt marsh species (McCormick et al. 2010; Meyerson, Viola, and Brown 2010). This invasive haplotype can tolerate high levels of salinity, fluctuating water levels, and nutrient-rich or polluted waters, making it a successful colonizer of disturbed and degraded wetlands (Meyerson et al. 2000; Uddin and Robinson 2017).

One of the primary concerns regarding the invasiveness of *P. australis* is its ability to form dense, monospecific stands that outcompete and displace native vegetation (Windham and Lathrop 1999). This tall grass can cause deep shade and effectively exclude other plant species from establishing themselves (Windham and Lathrop 1999). Its extensive rhizome system and high seed production further contribute to its rapid spread and dominance in wetland habitats (Moore et al. 2012).

The proliferation of *P. australis* can lead to a significant reduction in native plant biodiversity, as native species are outcompeted for light, nutrients, and space (Back and Holomuzki 2008; Rice, Rooth, and Stevenson 2000). This loss of plant diversity can have cascading effects on the entire ecosystem, affecting the abundance and diversity of wildlife species that depend on these habitats for food, shelter, and breeding grounds (Chambers, Meyerson, and Saltonstall 1999). For example, in North America, the spread of *P. australis* has been implicated in the decline of various bird species, such as the Saltmarsh Sparrow and the Black Rail, which rely on coastal marshes for nesting and foraging (Valiela et al. 2018).

Spartina alterniflora

S. alterniflora, commonly known as smooth cordgrass or saltwater cordgrass, is a perennial grass species that is native to the coastal salt marshes of the Atlantic and Gulf coasts of North America (Blum et al. 2007). Characterized by its tall, slender stems and long, narrow leaves, this hardy plant has garnered significant interest due to its ecological importance and its potential applications in coastal management and restoration efforts (Wan et al. 2009; G. Wang et al. 2008).

S. alterniflora is a keystone species in eastern North America salt marsh ecosystems, playing a crucial role in maintaining the structure and function of these valuable coastal wetlands (Pennings and Bertness 2001). Its dense root system and extensive above-ground biomass help stabilize the marsh sediments, preventing erosion and providing a buffer against storm surges and rising sea levels (Wails et al. 2021; Wang et al. 2008). Additionally, the tall, sturdy stems of *S. alterniflora* provide habitat and shelter for a wide range of wildlife, including migratory birds, fish, and invertebrates (Bertness 1984; Okoye, Li, and Gong 2020). Its ability to stabilize sediments and withstand harsh conditions makes it a valuable tool for shoreline protection, erosion control, and habitat restoration efforts (Carrion 2016; Davis et al. 2015).There characteristics have increased interests in *S. alterniflora* for its potential applications in coastal management and restoration projects. Ongoing research is exploring the use of *S. alterniflora* in living shoreline projects, where it is planted in combination with other natural materials to create a resilient and sustainable approach to coastal protection (Carrion 2016; Davis et al. 2015).

One of the key reasons for the interest in *S. alterniflora* is its remarkable ability to tolerate and thrive in the harsh conditions of salt marshes. This plant has evolved a range of adaptations that allow it to withstand high salinity, periodic flooding, and the physical stress of wave action (Maricle, Cobos, and Campbell 2007). These adaptations include specialized anatomical features, such as salt glands that excrete excess salt, and physiological mechanisms that regulate water and nutrient uptake (Maricle, Cobos, and Campbell 2007).

The ecological significance of *S. alterniflora* extends beyond its role in salt marsh habitat. This plant is also recognized for its contribution to carbon sequestration and climate change mitigation (Howes, Dacey, and Teal 1985; Xia et al. 2021; Zhang et al. 2021). The extensive root systems of *S. alterniflora* play a crucial role in capturing and storing carbon in the marsh sediments, effectively removing it from the atmosphere (Wan et al. 2009).

Study Site

The Great Sippewissett Marsh is a coastal salt marsh located in Falmouth, Massachusetts, on the southern coast of Cape Cod. It is renowned for its extensive wetland habitat, rich biodiversity, and ecological importance (Valiela 2015). The marsh encompasses a diverse array of habitats, including tidal creeks, mudflats, salt marshes, and upland areas, providing critical habitat for numerous plant and animal species.

I chose to study *S. alterniflora* and *P. australis* in the Great Sippewissett Marsh for several compelling reasons. Firstly, the marsh represents a prime example of a coastal salt marsh ecosystem, offering a natural laboratory for studying the dynamics of wetland plant communities and ecological processes. Secondly, the marsh is home to extensive stands of both *S. alterniflora* and *P. australis*. The co-occurrence of these two important wetland plants within the same ecosystem provides an excellent opportunity to study their interactions, competitive dynamics, and ecological impacts. Thirdly, decades-long monitoring and research activities in the Great Sippewissett Marsh provide extensive historical data (Valiela 2015; Valiela et al. 2024). Ongoing monitoring efforts provide valuable baseline information and allow for the study of temporal changes and trends in the marsh ecosystem, including shifts in vegetation composition and distribution (Valiela 2015; Valiela et al. 2024). Additionally, the accessibility and relatively undisturbed nature of the Great Sippewissett Marsh make it an attractive study site for long-term ecological monitoring and experimental studies.

Recent studies of interaction between invasive P. australis and S. alterniflora

Recent studies on the interaction between *P. australis and S. alterniflora* have revealed that both of these plant species play crucial roles in salt marsh ecosystems, and these roles have led to different invasion patterns in different areas. In Eastern North America, the salt-tolerant haplotype of *P. australis* has proliferated and expanded into wet areas, including salt marshes whose vegetation is dominated by *S.*

alterniflora (Chambers, Meyerson, and Saltonstall 1999; Guo et al. 2014; Kirk et al. 2011; Saltonstall 2002; Vasquez et al. 2005). *P. australis* has extensively encroached upon the upper boundaries of salt marshes in numerous locations. The encroachment of the *P. australis* potentially threatens the capacity of *S. alterniflora* to sustain cover within its existing elevation range in salt marshes (Valiela et al. 2024). Additionally, *P. australis* is gradually dominating in low-lying areas that are adjacent to existing salt marshes, where native marsh species might find it possible to migrate landward in response to rising sea levels (Valiela et al. 2024).

However, in the coastal regions of eastern China, the interaction between *S. alterniflora* and *P. australis* was reversed. *S. alterniflora* was intentionally introduced to China in the 1970s for coastal protection and sand stabilization (Nie et al. 2023). However, this plant has exhibited strong invasive characteristics in China's coastal areas, rapidly spreading from the low marsh toward high marsh and displacing native coastal vegetation, including *P. australis* (Nie et al. 2023). Along the east coast of China, *S. alterniflora* grows rapidly, forming dense stands (Li, Wang, and Zhang 2014). A research study reveals that *S. alterniflora* exhibits a leaf litter decomposition rate 2.2 times faster than that of the indigenous *P. australis*, which aids *S. alterniflora* in outcompeting *P. australis* in the middle tidal zone (Cheng et al. 2024).

Various factors may explain the diverse invasion patterns observed across continents. Biogeographical contexts can influence the availability of open niches and the resistance of native communities to invasive species (Hierro, Maron, and Callaway 2005). Climatic conditions, resource availability, and environmental factors vary across continents and regions, favoring the establishment and spread of certain invasive species while hindering others (Zhao et al. 2010). Additionally, invasive species may possess distinct evolutionary histories and adaptations compared to native species in recipient regions, providing them with competitive advantages, such as more efficient resource exploitation or resistance to introduced predators and pathogens, not coevolved with native species (Hierro, Maron, and Callaway 2005).

Invasive species management

The management of invasive species like *P. australis* in coastal wetlands has been a subject of extensive research. A variety of management strategies have been proposed and evaluated, each with its own advantages and limitations (Hazelton et al. 2014). The choice of approach often hinges on site-specific factors such as the extent of invasion, environmental conditions, and available resources.

Chemical control methods rely on the application of herbicides to suppress or eliminate invasive plants. These methods are highly efficient and can achieve significant reductions in invasive plant populations within a relatively short timeframe (Martin and Blossey 2013). Chemical control also has the potential to completely eradicate invasive species (Hazelton et al. 2014). Nevertheless, the use of herbicides can have significant environmental impacts, including non-target effects on surrounding ecosystems and potential contamination of water bodies (Mozdzer et al. 2008). Careful consideration and proper application are essential to minimize these risks.

Prescribed burning can effectively remove aboveground biomass, but it requires specialized skills and resources for fire management and carries the risk of uncontrolled fires and unintended ecological consequences (Rohal et al. 2019). Furthermore, the nutrient-rich ash that remains can serve as an ideal fertilizer, fostering the growth of unburned below-ground shoots of the invasive species that have already outcompeted other vegetation (van Der Toorn and Mook 1982).

Biological control, through the introduction of host-specific herbivores, pathogens, or plant competitors, has the potential for long-term, self-sustaining control with minimal ecosystem disturbance (Hazelton et al. 2014). However, extensive research and testing are necessary to ensure the safety and efficacy of biological control agents, and their establishment and effectiveness can be unpredictable (Thomas and Reid 2007; Tu, Hurd, and Randall 2001).

Habitat management, such as manipulating water levels, salinity, or nutrient availability, can create unfavorable conditions for invasive species while promoting native vegetation growth (Hazelton et al. 2014). This approach requires a thorough understanding of the ecological requirements of both invasive and native species, and consistently achieving the desired habitat conditions can be challenging (Rohal et al. 2019).

Increasingly, researchers advocate for an integrated management approach that combines multiple strategies, such as mechanical removal followed by herbicide application or habitat manipulation (Carlson, Kowalski, and Wilcox 2009; Hellings and Gallagher 1992; Rolletschek et al. 2000; Teal and Peterson 2005). While offering potentially more effective and sustainable control, integrated management demands careful planning, coordination, and resource allocation, as well as ongoing monitoring and adaptation to account for complex interactions between different techniques.

Compared to the methods above, physical control methods involving direct manipulation of the invasive plants through techniques such as hand-cutting, mowing, or excavation can rapidly reduce the abundance and coverage of invasive plants. These techniques require less professional knowledge to implement and are cost-effective. Additionally, physical control methods generally have minimal environmental impact compared to chemical methods, as they do not involve the use of potentially harmful substances. However, they can be labor-intensive and time-consuming, particularly for large-scale infestations, and they may also change the structure of local ecosystems.

Furthermore, it is crucial to recognize that, while many management studies primarily concentrate on the removal of invasive species, few address the vital aspect of ecosystem restoration, particularly the regrowth of native plant species following management interventions (Hazelton et al. 2014). Restoration efforts are essential for reinstating the ecological balance and functionality of ecosystems impacted by invasive species (Lyons et al. 2008). Restoring native plant communities helps enhance biodiversity, stabilize soil, improve habitat quality for wildlife, and promote ecosystem resilience to future disturbances (Lyons et al. 2008).

Project goals and implications

The interactions between *P. australis* and *S. alterniflora* are occurring in numerous Cape Cod salt marshes, including the Great Sippewissett Marsh. Initially, this project aims to assess whether *P. australis* is limiting the cover of *S. alterniflora*. Furthermore, recognizing the significance and the dearth of research on the restoration process following the removal of invasive species, the project intends to assess the regrowth of native *S. alterniflora* after physical removal of aboveground biomass of the invasive species.

This project marks the inception of a comprehensive study on restoration efforts involving the clipping of invasive *P. australis* within the Great Sippewissett Marsh. By concentrating on this specific control method, the project aims to shed light on the effectiveness of clipping as a management strategy for controlling invasive species and assisting restoration in salt marsh ecosystems. Through systematic monitoring and analysis of the regrowth of native plant species, valuable insights can be gleaned into the restoration process. The implications of this study extend beyond the Great

Sippewissett Marsh, offering valuable lessons and implications for other salt marshes grappling with similar invasive species challenges. Ultimately, this study seeks to contribute to the development of more effective and sustainable approaches for restoring and conserving salt marsh ecosystems globally, thereby enhancing resilience and biodiversity in these crucial coastal habitats.

Methods

Site description

The plots for this project were established within a privately-owned section of Great Sippewissett Marsh. These plots include two distinct zones—high marsh and low marsh—spanning the tidal gradient of the marsh landscape. Historically dominated by *S. alterniflora* with a sparse presence of *Distichlis spicata* and *Salicornia europaea*, the native salt marsh now exhibits a shift in dominance within the recent half century, with *P. australis* prevailing in the high marsh, while *S. alterniflora* tall and short forms respectively dominate the creek banks and low marsh (Valiela et al. 2024). Adjacent to the high marsh, a bike trail frequented by cyclists poses a potential source of disturbance, possibly facilitating the intrusion of the invasive species *P. australis*. Otherwise, the research site is encircled by fencing, effectively barring access to cyclists and mitigating external disruptions.

Set-up of experimental and reference plots

In the research site, six 3x2 m plots were described along the upper edge of the marsh as experimental plots. Each plot faced westward, ensuring consistent exposure to sunlight throughout the research site. Three of the plots were assigned to the clipping treatment and were alternated with three control plots (Fig. 1). Stems of *P. australis* were cut at ground level in the treatment plots, beginning on 8 May 2023. Since new growth of stems of *P. australis* took place through the season, I cut them weekly throughout the growing season until 13 October 2023. The control plots were left untreated plots. Any accumulation of dead grass wrack brought in by tides within the treatment plots was also cleared every week.

To ensure that placement of the plots was not confounded by other site differences, I set up six 3x0.5 m plots respectively at the down-gradient of each experimental plot, referred to henceforth as reference plots. The reference plots were uninvaded and untreated.

Elevation measurements were taken in both the experimental and reference plots. Initially, relative elevation was determined using hand levels and stadia rods. Subsequently, the relative elevation was calibrated by comparing it to a nearby point where the orthometric elevation (North American Vertical Datum of 1988 [NAVD88]) had already been accurately measured using differential GPS.

S. alterniflora percent cover

Percent cover of *S. alterniflora* in the plots was visually estimated. There are two common human-involved vegetation coverage measurement methods, visual estimation and point estimate. To conduct a point estimate, first mark 25 equally spaced dots on a transparent plastic sheet measuring 25*25 cm. Place the sheet on the targeted area. Count the number of dots that have vegetation directly below them vertically. Calculate the percentage of dots covered by vegetation as the percentage vegetation cover in the selected area.

Visual estimates of cover for this research are more time-effective and as accurate as point estimates (Fox et al. 2012). I tested the visual estimates early in the study by direct comparisons with point estimates. These tests demonstrated the reliability of the visual method, because I found a strong relationship between my visual estimates and point estimates approach (slope=0.86, df=24, R^2=0.9064, *p*<0.0001). Therefore, I continued the visual estimates as a good approximation to the more accurate point estimate (Fig. 2). I used the visual estimation method to draw vegetation percent cover graphs for each plot. Each graph was done by first setting up a line parallel to the lower periphery of the plot. The line was marked at 0.2 m intervals. I then mapped the vegetation contour within 0.2 m intervals from the left to right margin of the plot. To describe the vegetation in the plots, I specified spatial extent location of patches of monocultures of *S. alterniflora* or mixes of different species. Within each patch, we distinguished cover categories in bins of 10% cover. Then, I digitized graphs into shapefiles using QGIS (Valiela et al. 2018) and calculated the total *S. alterniflora* percent cover for each plot.

I used Microsoft Excel (16.16.27) to generate both the linear and non-linear regression of *S. alterniflora* % cover in experimental and reference plots during the growing season. Both the non-linear regression (slope=148.30, *df*=8, R^2=0.9300, *p*=0.001) and the linear regression (slope=0.27, *df*=8, R^2=0.8562, *p*=0.001) were significant in the treatment plots. In the control plots, both the non-linear regression (slope=43.92, *df*=8, R^2=0.8530, *p*=0.0061) and the linear regression (slope=0.08, *df*=8, R^2=0.7910, *p*=0.0031) were significant. Similarly, in the reference plots that were associated to the treatment plots, both the non-linear regression (slope=22.14, *df*=7, R^2=0.9560, *p*=0.0009) and the linear regression (slope=0.27, *df*=7, R^2=0.9556, *p*=0.0001) were significant. In the reference plots that were associated to the control plots, both the non-linear regression (slope=370.61, *df*=7, R^2=0.9420, *p*=0.0013) and the linear regression (slope=0.24, *df*=7, R^2=0.7880, *p*=0.0076) were significant. I chose the non-linear regression model for both the experimental and reference plots based on their R^2 values (Table 1 & 2).

I also did a Repeated Measures ANOVA to test for differences in mean *S.*

alterniflora percent cover with clipping and control treatments as a two-level factor and time frame of the experiment as the repeated measure. To explore whether similar effects were present in my reference plots, I conducted a second Repeated Measures ANOVA to look for differences in *S. alterniflora* percent cover among reference plots during the growing season.

Irradiance

To determine if light supply made a meaningful difference for the *S. alterniflora* in the treatment and control plots, I measured photosynthetically active radiation (PAR, $\mu mol/m^2\ s^{-1}$) in all plots on July 20th. PAR was measured in nine regularly spaced points within each plot, using a Licor 2200 meter and averaging the nine points to get mean irradiance for each plot. In order to ensure uniform initial irradiance levels across all experimental plots, I measured PAR in each reference plot using identical methods and conducted on the same day. Then, I used JMP (17.2.0) to conduct two t-tests respectively for identifying the differences of PAR values between treatment and control plots and between reference plots associated with treatment and control plots.

Results

S. alterniflora percent cover

The Repeated Measures Analysis of Variance (ANOVA) for the experimental plots revealed a significant time effect, implying growth in *S. alterniflora* percent cover across experimental plots throughout the growing season (Table 3, $F_{7,32} = 3.98$, $p = 0.003$). There was also a significant treatment effect with higher mean percent cover of *S. alterniflora* between in treatment than control plots (Table 3, $F_{1,32} = 30.32$, $p = 0.000005$). However, no significant interaction effect was observed, suggesting that the relationship between time and clipping remained consistent (Table 3, $F_{7,32} = 1.13$, $p = 0.367$).

In contrast, the Repeated Measures ANOVA of the reference plots showed no statistically significant difference in *S. alterniflora* percent cover between reference plots associated with treatment versus control plots (Table 4, $F_{1,28} = 0.05$, $p = 0.825$). Interestingly, the time effect also was not significant (Table 4, $F_{6,28} = 2.38$, $p = 0.055$) because growth was not detectable across all reference plots. Again, the interaction effect between the type of reference plots and time was not significant (Table 4, $F_{6,28} = 0.17$, $p = 0.982$). Notably, the cover of *S. alterniflora* in these reference plots reached values of % cover considerably higher than those measured in the experimental plots, as would be expected given their slightly lower elevation (Fig. 5).

Irradiance

A t-test conducted on PAR values in the experimental plots revealed a significantly higher average PAR value in treatment plots compared to control plots (Fig. 6, $t = 18.5653$, $df = 2.1374$, $p = 0.0021$). Conversely, no significant difference in PAR values was found among the reference plots (Fig. 7, $t = 1.1732$, $df = 2.0264$, $p = 0.3602$).

Discussion

The findings of this study provide valuable insights into the competitive interactions between the invasive *P. australis* and the native *S. alterniflora* in Great Sippewissett Marsh, as well as the potential implications for invasive species management and ecosystem restoration efforts in salt marsh ecosystems.

Above-ground and below-ground competition factors

For the experimental plots, combining the significant time effect (Table 3) with the observed difference in percent cover (Fig. 3), it becomes evident that there was a significant increase in *S. alterniflora* percent cover during the growing season, consistent with expectations of seasonal growth. The significant treatment effect (Table 3) underscores the inhibitory impact of the invasive species on the establishment and growth of native *S. alterniflora*. This finding aligns with prior research indicating that *P. australis* can outcompete native species, forming dense monospecific stands that reduce plant diversity and alter ecosystem structure and function (Kirk et al. 2011; Saltonstall 2002). Furthermore, the lack of a significant interaction effect (Table 3) implies that the relationship between time and treatment effect remained consistent and unaffected by other variables, indicating a stable treatment application.

For the reference plots, the lack of a significant time effect in the reference plots may be attributed to relatively large standard errors (Fig. 4). However, the p-value close to the confidence level (0.055) and the increasing slope still suggest a growing trend (Fig. 4).The non-significant treatment effect indicates that the percent cover of *S. alterniflora* in reference plots associated with treatments was comparable to that in reference plots associated with control plots, suggesting no additional factors influencing *S. alterniflora* growth in the experimental plots during the growing season. Once again, the non-significant interaction effect reaffirms the in general consistently untreated and uninvaded condition of the reference plots.

The shading effect of *P. australis*, evidenced by the significant higher PAR values in the treatment plots compared to the control plots (Fig. 6), likely contributed to the observed increase in *S. alterniflora* cover. Despite generally high levels of PAR in the reference plots, there was a discrepancy between the average PAR in the reference plots under the control and treatment plots (Fig. 7). This discrepancy can be attributed to the presence of *P. australis* invading one of the reference plots for the control conditions, which shaded the shorter *S. alterniflora*. This lowered PAR in one of the control reference plots influenced the overall average PAR value for the control reference plots. Nevertheless, this does not detract from the overarching conclusions of this study, which are consistent with prior research demonstrating that reduced light availability due to the tall stature and dense canopy of *P. australis* can impede the growth and establishment of understory vegetation, including *S. alterniflora* (Hirtreiter and Potts 2012).

While the shading effect appears to play a significant role in the inhibition of *S. alterniflora* by tall *P. australis*, as evidenced by the higher light levels in the clipped plots, belowground factors may also contribute to the invasive species' ability to outcompete the native vegetation (Moore et al. 2012). Future research should explore the belowground dynamics and resource utilization strategies of these two species to gain a more comprehensive understanding of their competitive interactions. One potential area of investigation could be the examination of root system architecture and the capacity for resource acquisition. *P. australis* is known for its extensive rhizome system, which may allow it to access and monopolize nutrient resources, such as ammonium and nitrate, more efficiently than *S. alterniflora* (Moore et al.

2012). Furthermore, it is possible that the invasive species may interfere with the root growth or nutrient uptake of the native species through mechanisms such as root exudation or alterations in soil chemistry. For example, a study in Louisiana found that the invasive species can employ mechanisms to alter the soil environment, such as through the release of allelochemicals or the modification of microbial communities, conferring a competitive advantage over native species (Schroeder et al. 2020). By examining these belowground factors, combined with aboveground shading effects, researchers may gain a more holistic understanding of the competitive dynamics, leading to more targeted and successful conservation and restoration efforts in salt marsh ecosystems threatened by invasive species.

S. alterniflora growth pattern across elevation gradient

Comparing the *S. alterniflora* percent cover between the reference plots and the experimental plots, the values in the reference plots were consistently higher throughout the growing season (Fig. 5). This can be explained by the lower elevations where the reference plots were located. According to previous studies, *S. alterniflora* is typically confined to low marsh habitats in salt marsh ecosystems, primarily due to competitive displacement (Bertness 1991). The ability of *S. alterniflora* to thrive in anoxic low marsh habitats is attributed to its capacity to oxygenate its roots and rhizosphere (Bertness 1991). Therefore, naturally, without the invasive species, during the growing season, *S. alterniflora* begins to establish itself at the lower margins of the marsh where there is no competition (Bertness 1991). The low marsh *S. alterniflora* can monopolize resources in the low marsh and gradually spread up the topographic gradient until they encounter other species who can fully outcompete them (Bertness 1991).

Invasive species and sea level rise threats

As sea levels rise, existing salt marshes face increased inundation, potentially jeopardizing habitats for native plant species like *S. alterniflora* whose growth starts from lower margins of the marsh (Valiela et al. 2018). Counteracting salt marsh submergence relies on either increasing accretion within the wetland or landward migration (Valiela, Lloret, and Chenoweth 2023). However, both mechanisms face challenges. Human uses of coastal land and water limit mineral supply for accretion, and wetlands relying on plant-generated accretion are disadvantaged against sea level rise (Valiela, Lloret, and Chenoweth 2023). Therefore, salt marsh vegetation would migrate landward, colonizing higher elevations as lower areas become unsuitable. However, landward migration is hindered by high slopes and human reluctance to relinquish valuable land, and further compounded by the invasion of *P. australis* from upper marsh areas, occupying and dominating these potential migration zones (Valiela, Lloret, and Chenoweth 2023). Therefore, native marsh plants may find themselves trapped, unable to escape the encroaching waters.

The consequences could be devastating for salt marsh ecosystems. The loss of native vegetation could lead to a significant reduction in biodiversity, as these habitats support a wide range of specialized plant and animal species. For example, the loss of *S. alterniflora* can lead to cascading ecological effects, including habitat loss of fiddler crabs (*Uca pugnax*), bivalves, and seaside sparrows (*Ammodramus caudacutus*) (Bertness and Miller 1984; Evgenidou and Valiela 2002; Gjerdrum, Elphick, and Rubega 2005). Furthermore, due to the tendency of *P. australis* to create monospecific marshes, which exhibit minimal resilience and are susceptible to increasingly frequent severe weather events exacerbated by climate change (Silliman, Grosholz, and Bertness 2009), the ecosystem services offered by salt marshes, including coastal protection, nutrient cycling, and carbon sequestration, may face significant compromise. This could have far-reaching implications not only for the local environment but also for the communities and infrastructure that rely on the protective and stabilizing functions of these ecosystems.

Addressing this multifaceted threat requires a comprehensive and proactive approach. Effective management strategies should not only focus on controlling the spread of invasive species like *P. australis* but also incorporate measures to facilitate the landward migration of native salt marsh vegetation. This may involve identifying and preserving suitable migration corridors, implementing habitat restoration efforts, and potentially considering assisted migration or relocation of native species to higher elevations.

Invasive species management methods

These findings above have important implications for invasive species management and ecosystem restoration in salt marsh ecosystems. The success of physical control methods, such as clipping *P. australis* stems, in promoting the recovery of native vegetation underscores the potential effectiveness of targeted management interventions for controlling invasive species and restoring ecological balance. While chemical control methods may offer rapid and efficient eradication of invasive species, they can pose environmental risks and have long-term consequences for ecosystem health (Chambers et al., 1999). One example of how chemical herbicides can harm ecosystem health is through their impact on non-target species (Chambers et al., 1999). While herbicides are designed to target specific plant species, they can also affect other organisms in the ecosystem, including insects, birds, and aquatic life (Chamberset al., 1999). For instance, the widespread use of herbicides can lead to a decline in pollinator populations due to the loss of habitat and food sources (Chambers, Meyerson, and Saltonstall 1999). Additionally, herbicides may contaminate water sources, posing risks to aquatic organisms and disrupting the balance of aquatic ecosystems (Chambers et al., 1999). Repeated exposure to herbicides can also lead to the development of herbicide-resistant plant species, further complicating eradication efforts and potentially leading to ecological imbalances (Hazelton et al. 2014). Overall, the indiscriminate use of chemical herbicides can have cascading effects on ecosystem health, affecting biodiversity, food webs, and ecosystem functioning.

In contrast, physical control methods are relatively simple, cost-effective, and environmentally friendly, potentially making them a viable option for managing invasive species in salt marsh ecosystems. However, it is important to acknowledge the labor-intensive nature of physical clipping methods, which may limit their applicability at larger spatial scales or in areas with extensive invasive species infestations. Manual clipping of plants can be time-consuming and resource-intensive, especially in cases where frequent maintenance is required to prevent regrowth. For this project, it took about 10 minutes to clip the new growth of *P. australis* shoots and clear accumulated wrack for each 3*2m plot each week. Assuming *P. australis* is currently only present in the upper reaches of the marsh, we estimate the areas that were already invaded by *P. australis* only constitute 1/10 of the marsh. Therefore, managing *P. australis* in the Great Sippewissett Marsh (140 acres, approximately 566,560 square meters) would require approximately 157 hours per week, excluding the time required to walk across the hazardous muddy marsh.

To address this limitation, future research could explore methods to scale up and optimize physical control approaches for broader application in salt marsh ecosystems. One potential avenue is the development of mechanical or automated clipping techniques that can cover larger areas more efficiently while minimizing labor requirements. For example, research could be conducted to develop mechanical cutting devices or drone technology to achieve larger-scale physical control methods. Additionally, exploration could be done on the processing and reuse of the waste from common reed after cutting, aiming to reduce the environmental impact of the processing and enhance the sustainability of the cutting method. For instance, exploring whether the removed biomass can be refined into a source of forage or utilized in the production of construction materials could be beneficial.

Research could prioritize identifying optimal timing and frequencies for physical control interventions, along with evaluating the effectiveness of these methods when combined with other management strategies such as prescribed burning, habitat manipulation, or biological control. By integrating multiple approaches, it may be possible to achieve more comprehensive and long-lasting control of invasive species while promoting the recovery of native vegetation. During my work, I observed that *P. australis* growth peaked in early summer, typically from June to July, after which its growth rate appeared to slow down. Additionally, in one of the treatment plots, I noticed a few seedlings of other native species grew back after clipping. Interestingly, the number of new *P. australis* shoots in this plot seemed to be lower compared to other treatment plots where only *S. alterniflora* regrew. Although there is a lack of statistical data to support this observation, I believe it is worth considering introducing native plant species for future research. Intentionally introducing more native species in restored areas after clipping may help inhibit the regrowth of invasive *P. australis*. Regarding frequency, I would suggest a maximum of one week between control interventions. I once returned after two weeks in June and found that the new *P. australis* shoots were already taller than the *S. alterniflora*. This observation suggests that their underground root system might have become more extensive, supporting continuous regrowth throughout the rest of the growing season.

Furthermore, the development of decision support tools and predictive models could aid in prioritizing management efforts and identifying areas most suitable for physical control methods. These tools could incorporate factors such as the extent of invasive species infestation, accessibility, environmental conditions, and potential impacts on native species, ensuring that resources are allocated effectively and efficiently.

Short-term and long-term ecosystem restoration monitoring

As discussed above, the restoration of native vegetation following invasive species removal is essential for enhancing biodiversity, restoring ecosystem functions, and promoting resilience to future disturbances. The observed increase in *S. alterniflora* cover following the clipping of *P. australis* highlights the potential for targeted management actions to facilitate the recovery of native plant communities in degraded salt marsh habitats. While the short-term results of this study are promising, it is crucial to recognize that ecosystem restoration is a long-term process, and the successful re-establishment of native plant communities may depend on various factors beyond the initial removal of invasive species (Pennings and Callaway 1992). Future research should focus on long-term monitoring and assessment of overall ecosystem dynamics following invasive species management interventions.

One important aspect to investigate is the succession patterns and trajectories of native vegetation recovery over multiple growing seasons. It is essential to understand whether the initial increase in *S. alterniflora* cover translates into sustained dominance and resilience of the native plant community. Monitoring changes in species composition, diversity, and structural complexity over time can provide valuable insights into the long-term ecological consequences of invasive species removal.

Additionally, although not reported in the result, as I mentioned above, there were an individuals of few *Distichlis spicata*, another kind of native plant species, growing back along with *S. alterniflora* in one treatment plot and also crab burrows in another treatment plot. Therefore, research should examine the potential for the re-establishment of other native species beyond *S. alterniflora*, as well as the interactions among these species and their roles in shaping the overall community structure and ecosystem functions. Salt marsh ecosystems are complex and diverse, and the restoration of a diverse and balanced native plant community may be crucial for maintaining ecological resilience and ecosystem services.

Furthermore, it is important to investigate the potential feedbacks and interactions between the restored native vegetation and other components of the ecosystem, such as soil properties, nutrient cycling, hydrology, and wildlife populations. These interactions may influence the long-term sustainability and stability of the restored ecosystem, and understanding them can inform adaptive management strategies and facilitate the successful transition towards a self-sustaining, resilient salt marsh ecosystem (Hazelton et al. 2014).

Long-term monitoring and research should also explore the potential for reinvasion or colonization by other invasive species following the removal of *P. australis*. Understanding the factors that contribute to the vulnerability or resistance of the restored ecosystem to future invasions can guide preventative measures and inform ongoing management efforts.

Improving Experimental Design for Future Research

For future iterations of similar experiments, there are several adjustments that could enhance the potential for valuable insights. Firstly, ensuring that the experimental plots have horizontally similar elevations would minimize potential confounding factors and improve the accuracy of the results. While the alternately set treatment and control plots in this study helped to balance elevation variations to some extent, selecting plots with more consistent elevations from the outset would be beneficial. This would help to eliminate any potential bias introduced by differences in elevation affecting factors such as water drainage, nutrient availability, and microclimate.

Secondly, incorporating drone technology to measure the percent cover of *Spartina alterniflora* could provide more precise and consistent data compared to visual estimation methods. While visual estimation was utilized in the absence of drone imagery, the use of drones would offer advantages such as high-resolution aerial imagery, standardized data collection protocols, and the ability to cover large areas efficiently. By capturing images of the experimental plots from above, researchers could assess the extent of *S. alterniflora* cover and monitor changes over time without the need for extensive fieldwork which would streamline the data collection process. However, the accuracy of such methods still needs to be tested.

Additionally, implementing a more robust experimental design with increased replication and randomized plot selection could strengthen the statistical power of the study. By increasing the number of replicate plots and randomizing their placement within the study area, researchers can reduce the potential for sampling bias and improve the generalizability of the findings. This would enhance the robustness of the conclusions drawn from the study and increase confidence in the validity of the results.

Conclusion

The expansion of invasive *P. australis* into salt marshes dominated by the native *S. alterniflora* represents a significant threat to the biodiversity, ecosystem functions, and resilience of these valuable coastal wetlands. This study, conducted in the Great Sippewissett Marsh in Falmouth, Massachusetts, has provided valuable insights into the competitive interactions between these two species and the potential for targeted management actions to facilitate the restoration of native vegetation.

The experimental clipping of *P. australis* stems resulted in a striking increase in the percent cover of *S. alterniflora*, leading to growth that was almost double that observed in control plots. This finding highlights the inhibitory effect of the invasive species on the growth of the native salt marsh vegetation, likely due to a combination of shading and potential belowground competition factors.

As sea levels continue to rise, the encroachment of *P. australis* into potential migration zones for native salt marsh vegetation poses a severe threat, potentially resulting in the loss of some of these important ecosystems. Proactive measures, including the preservation of migration corridors, habitat restoration efforts, and potential assisted migration or relocation of native species, may be necessary to ensure the long-term survival and resilience of salt marsh ecosystems.

This study has highlighted the potential effectiveness of one physical control method, clipping, in managing invasive species and promoting the recovery of native vegetation. However, future research should explore additional physical control approaches as well as methods to scale up and optimize these approaches and integrate them with other management strategies, such as introducing other native plant species into the restored area.

By addressing the multifaceted threats posed by invasive species and sea level rise, and by adopting an ecosystem-based approach to restoration, researchers and land managers may contribute to the protection and conservation of salt marsh ecosystems, potentially safeguarding their invaluable ecosystem services and promoting their resilience in the face of environmental change. While the short-term results are promising, long-term monitoring and research are crucial to understand the trajectories of native vegetation recovery, the resilience of the restored ecosystem, and the potential for reinvasion by invasive species. Thus, this project serves as a first step and offers a solid foundation for further exploration of this topic. Drawing from the lessons and experiences acquired throughout this endeavor, I am committed to ongoing research in this area. It is my aspiration to deepen the comprehension of the interaction between native and invasive plant species within salt marsh ecosystems and to develop effective restoration protocols that may contribute to global conservation efforts.

References:

Almeida, C. M. R., A. P. Mucha, and M. T. Vasconcelos. 2011. “Role of Different Salt Marsh Plants on Metal Retention in an Urban Estuary (Lima Estuary, NW Portugal).” *Estuarine, Coastal and Shelf Science* 91 (2): 243–49. https://doi.org/10.1016/j.ecss.2010.10.037.

Back, C. L., and J. R. Holomuzki. 2008. “Long-Term Spread and Control of Invasive, Common Reed (*Phragmites australis*) in Sheldon Marsh, Lake Erie,” *The Ohio Journal of Science*, 108 (5): 108-112.. http://hdl.handle.net/1811/48452.

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. “The Value of Estuarine and Coastal Ecosystem Services.” *Ecological Monographs* 81 (2): 169–93. https://doi.org/10.1890/10-1510.1.

Beaumont, N. J., L. Jones, A. Garbutt, J. D. Hansom, and M. Toberman. 2014. “The Value of Carbon Sequestration and Storage in Coastal Habitats.” *Estuarine, Coastal and Shelf Science* 137 (January): 32–40. https://doi.org/10.1016/j.ecss.2013.11.022.

Bertness, M. D. 1984. “Ribbed Mussels and Spartina Alterniflora Production in a New England Salt Marsh.” *Ecology* 65 (6): 1794–1807. https://doi.org/10.2307/1937776.

———. 1991. “Zonation of *Spartina patens* and *Spartina alterniflora* in New England Salt Marsh.” *Ecology* 72 (1): 138–48. https://doi.org/10.2307/1938909.

Bertness, M.D., and T. Miller. 1984. “The Distribution and Dynamics of *Uca Pugnax* (Smith) Burrows in a New England Salt Marsh.” *Journal of Experimental Marine Biology and Ecology* 83 (3): 211–37. https://doi.org/10.1016/S0022-0981(84)80002-7.

Blum, M. J., K. J. Bando, M. Katz, and D. R. Strong. 2007. “Geographic Structure, Genetic Diversity and Source Tracking of *Spartina alterniflora*.” *Journal of Biogeography* 34 (12): 2055–69. https://doi.org/10.1111/j.1365-2699.2007.01764.x.

Bowen, J. L., A. C. Spivak, A.E. Bernhard, R. W. Fulweiler, and A. E. Giblin. 2023. “Salt Marsh Nitrogen Cycling: Where Land Meets Sea.” *Trends in Microbiology* 0 (0). https://doi.org/10.1016/j.tim.2023.09.010.

Burden, A., R. A. Garbutt, C. D. Evans, D. L. Jones, and D. M. Cooper. 2013. "Carbon Sequestration and Biogeochemical Cycling in a Saltmarsh Subject to Coastal Managed Realignment." *Estuarine, Coastal and Shelf Science* 120 (March): 12–20. https://doi.org/10.1016/j.ecss.2013.01.014.

Carlson, M. L., K. P. Kowalski, and D. A. Wilcox. 2009. "Promoting Species Establishment in a *Phragmites*-Dominated Great Lakes Coastal Wetland." *Natural Areas Journal* 29 (3): 263–80. https://doi.org/10.3375/043.029.0306.

Carrion, S. 2016. "Determining Factors That Influence Smooth Cordgrass (*Spartina alterniflora* Loisel) Transplant Success In Community-Based Living Shoreline Projects." *Honors Undergraduate Theses*, January. https://stars.library.ucf.edu/honorstheses/68.

Chambers, R. M., L. A. Meyerson, and K. Saltonstall. 1999. "Expansion of *Phragmites australis* into Tidal Wetlands of North America." *Aquatic Botany* 64 (3–4): 261–73. https://doi.org/10.1016/S0304-3770(99)00055-8.

Cheng, C., Z. Liu, Y. Zhang, Q. He, B. Li, and J. Wu. 2024. "Leaf Litter Decomposition and Its Drivers Differ between an Invasive and a Native Plant: Management Implications." *Ecological Applications* 34 (1): e2739. https://doi.org/10.1002/eap.2739.

Chmura, G. L., S. C. Anisfeld, D. R. Cahoon, and J. C. Lynch. 2003. "Global Carbon Sequestration in Tidal, Saline Wetland Soils." *Global Biogeochemical Cycles* 17 (4). https://doi.org/10.1029/2002GB001917.

Christiansen, T., P. L. Wiberg, and T. G. Milligan. 2000. "Flow and Sediment Transport on a Tidal Salt Marsh Surface." *Estuarine, Coastal and Shelf Science* 50 (3): 315–31. https://doi.org/10.1006/ecss.2000.0548.

Davis, J. L., C. A. Currin, C. O'Brien, C. Raffenburg, and A. Davis. 2015. "Living Shorelines: Coastal Resilience with a Blue Carbon Benefit." *PLOS ONE* 10 (11): e0142595. https://doi.org/10.1371/journal.pone.0142595.

Der Toorn, J. V., and J. H. Mook. 1982. "The Influence of Environmental Factors and Management on Stands of *Phragmites australis*. I. Effects of Burning, Frost and Insect Damage on Shoot Density and Shoot Size." *Journal of Applied Ecology* 19 (2): 477–99. https://doi.org/10.2307/2403481.

Drake, K., H. Halifax, S. C. Adamowicz, and C. Craft. 2015. "Carbon Sequestration in Tidal Salt Marshes of the Northeast United States." *Environmental*

Management 56 (4): 998–1008. https://doi.org/10.1007/s00267-015-0568-z.

Duarte, C. M., J. J Middelburg, and N. F. Caraco. 2005. “Major Role of Marine Vegetation on the Oceanic Carbon Cycle.” *Biogeosciences* 2 (1): 1–8.

Engloner, A. I. 2009. “Structure, Growth Dynamics and Biomass of Reed (*Phragmites australis*) – A Review.” *Flora - Morphology, Distribution, Functional Ecology of Plants* 204 (5): 331–46. https://doi.org/10.1016/j.flora.2008.05.001.

Ermgassen, P. S. E. zu, R. Baker, M. W. Beck, K. Dodds, S. O. S. E. zu Ermgassen, D. Mallick, M. D. Taylor, and R. E. Turner. 2021. “Ecosystem Services: Delivering Decision-Making for Salt Marshes.” *Estuaries and Coasts* 44 (6): 1691–98. https://doi.org/10.1007/s12237-021-00952-z.

Evgenidou, A., and I. Valiela. 2002. “Response of Growth and Density of a Population of Geukensia Demissa to Land-Derived Nitrogen Loading, in Waquoit Bay, Massachusetts.” *Estuarine, Coastal and Shelf Science* 55 (1): 125–38. https://doi.org/10.1006/ecss.2001.0891.

Feagin, R. A., S. M. Lozada-Bernard, T. M. Ravens, I. Möller, K. M. Yeager, and A. H. Baird. 2009. “Does Vegetation Prevent Wave Erosion of Salt Marsh Edges?” *Proceedings of the National Academy of Sciences* 106 (25): 10109–13. https://doi.org/10.1073/pnas.0901297106.

Ferrón, S., T. Ortega, and J. M. Forja. 2009. “Benthic Fluxes in a Tidal Salt Marsh Creek Affected by Fish Farm Activities: Río San Pedro (Bay of Cádiz, SW Spain).” *Marine Chemistry* 113 (1): 50–62. https://doi.org/10.1016/j.marchem.2008.12.002.

Fox, L., I. Valiela, and E. L. Kinney. 2012. “Vegetation Cover and Elevation in Long-Term Experimental Nutrient-Enrichment Plots in Great Sippewissett Salt Marsh, Cape Cod, Massachusetts: Implications for Eutrophication and Sea Level Rise.” *Estuaries and Coasts* 35 (2): 445–58. https://doi.org/10.1007/s12237-012-9479-x.

Friedrichs, C. T., and J. E. Perry. 2001. “Tidal Salt Marsh Morphodynamics: A Synthesis.” *Journal of Coastal Research*, 7–37. https://www.jstor.org/stable/25736162.

Gallardo, B., M. Clavero, M. I. Sánchez, and M. Vilà. 2016. “Global Ecological Impacts of Invasive Species in Aquatic Ecosystems.” *Global Change Biology* 22 (1): 151–63. https://doi.org/10.1111/gcb.13004.

Gjerdrum, C., C.S. Elphick, and M. Rubega. 2005. “Nest Site Selection and Nesting Success in Saltmarsh Breeding Sparrows: The Importance of Nest Habitat, Timing, and Study Site Differences.” *The Condor* 107 (4): 849–62. https://doi.org/10.1093/condor/107.4.849.

Guo, W., C. Lambertini, L. X. Nguyen, X. Li, and H. Brix. 2014. “Preadaptation and Post-Introduction Evolution Facilitate the Invasion of *Phragmites australis* in North America.” *Ecology and Evolution* 4 (24): 4567–77. https://doi.org/10.1002/ece3.1286.

Gutiérrez, J. L., C. G. Jones, P. M. Groffman, S. E. G. Findlay, O. O. Iribarne, P. D. Ribeiro, and C. M. Bruschetti. 2006. “The Contribution of Crab Burrow Excavation to Carbon Availability in Surficial Salt-Marsh Sediments.” *Ecosystems* 9 (4): 647–58. https://doi.org/10.1007/s10021-006-0135-9.

Hazelton, E. L. G., T. J. Mozdzer, D. M. Burdick, K. M. Kettenring, and D. F. Whigham. 2014. “*Phragmites australis* Management in the United States: 40 Years of Methods and Outcomes.” *AoB PLANTS* 6 (January). https://doi.org/10.1093/aobpla/plu001.

Hellings, S. E., and J. L. Gallagher. 1992. “The Effects of Salinity and Flooding on *Phragmites australis*.” *Journal of Applied Ecology* 29 (1): 41–49. https://doi.org/10.2307/2404345.

Hierro, J. L., J. L. Maron, and R. M. Callaway. 2005. “A Biogeographical Approach to Plant Invasions: The Importance of Studying Exotics in Their Introduced and Native Range.” *Journal of Ecology* 93 (1): 5–15. https://doi.org/10.1111/j.0022-0477.2004.00953.x.

Hirtreiter, J., and D. Potts. 2012. “Canopy Structure, Photosynthetic Capacity and Nitrogen Distribution in Adjacent Mixed and Monospecific Stands of *Phragmites australis* and *Typha latifolia*.” *Plant Ecology* 213 (May). https://doi.org/10.1007/s11258-012-0044-2.

Howes, B. L., J. W. H. Dacey, and J. M. Teal. 1985. “Annual Carbon Mineralization and Belowground Production of *Spartina alterniflora* in a New England Salt Marsh.” *Ecology* 66 (2): 595–605. https://doi.org/10.2307/1940408.

Keller, R. P., J. Geist, J. M. Jeschke, and I. Kühn. 2011. “Invasive Species in Europe: Ecology, Status, and Policy.” *Environmental Sciences Europe* 23 (1): 23. https://doi.org/10.1186/2190-4715-23-23.

Kettenring, K. M., K. E. Mock, B. Zaman, and M. McKee. 2016. "Life on the Edge: Reproductive Mode and Rate of Invasive *Phragmites australis* Patch Expansion." *Biological Invasions* 18 (9): 2475–95. https://doi.org/10.1007/s10530-016-1125-2.

Kidson, C. 1959. "The Uses and Limitations of Vegetation in Shore Stabilization." *Geography* 44 (4): 241–50. https://www.jstor.org/stable/40565071.

Kirk, H., J. Paul, J. Straka, and J. R. Freeland. 2011. "Long-Distance Dispersal and High Genetic Diversity Are Implicated in the Invasive Spread of the Common Reed, *Phragmites australis* (Poaceae), in Northeastern North America." *American Journal of Botany* 98 (7): 1180–90. https://doi.org/10.3732/ajb.1000278.

Kostka, J. E., A. Roychoudhury, and P. V. Cappellen. 2002. "Rates and Controls of Anaerobic Microbial Respiration across Spatial and Temporal Gradients in Saltmarsh Sediments." *Biogeochemistry* 60 (1): 49–76. https://doi.org/10.1023/A:1016525216426.

Li, Z., W. Wang, and Y. Zhang. 2014. "Recruitment and Herbivory Affect Spread of Invasive *Spartina alterniflora* in China." *Ecology* 95 (7): 1972–80. https://doi.org/10.1890/13-2283.1.

Lyons, J. E., M. C. Runge, H. P. Laskowski, and W. L. Kendall. 2008. "Monitoring in the context of structured decision-making and adaptive management." Journal of Wildlife Management 72 (8): 1683–92. https://doi.org/10.2193/2008-141

Maricle, B. R., D. R. Cobos, and C. S. Campbell. 2007. "Biophysical and Morphological Leaf Adaptations to Drought and Salinity in Salt Marsh Grasses." *Environmental and Experimental Botany* 60 (3): 458–67. https://doi.org/10.1016/j.envexpbot.2007.01.001.

Martin, L. J., and B.Blossey. 2013. "The Runaway Weed: Costs and Failures of *Phragmites australis* Management in the USA." *Estuaries and Coasts* 36 (3): 626–32. https://doi.org/10.1007/s12237-013-9593-4.

McCormick, M. K., K. M. Kettenring, H. M. Baron, and D. F. Whigham. 2010. "Spread of Invasive *Phragmites australis* in Estuaries with Differing Degrees of Development: Genetic Patterns, Allee Effects and Interpretation." *Journal of Ecology* 98 (6): 1369–78. https://doi.org/10.1111/j.1365-2745.2010.01712.x.

Meyerson, L.A., K. Saltonstall, L. Windham, E. Kiviat, and S. Findlay. 2000. "A

Comparison of *Phragmites australis* in Freshwater and Brackish Marsh Environments in North America." *Wetlands Ecology and Management* 8 (2): 89–103. https://doi.org/10.1023/A:1008432200133.

Meyerson, L. A., D. V. Viola, and R. N. Brown. 2010. "Hybridization of Invasive *Phragmites australis* with a Native Subspecies in North America." *Biological Invasions* 12 (1): 103–11. https://doi.org/10.1007/s10530-009-9434-3.

Moore, G. E., D. M. Burdick, C. R. Peter, and D. R. Keirstead. 2012. "Belowground Biomass of *Phragmites australis* in Coastal Marshes." *Northeastern Naturalist* 19 (4): 611–26. https://doi.org/10.1656/045.019.0406.

Mozdzer, T. J., C. J. Hutto, P. A. Clarke, and D. P. Field. 2008. "Efficacy of Imazapyr and Glyphosate in the Control of Non-Native *Phragmites australis*." *Restoration Ecology* 16 (2): 221–24. https://doi.org/10.1111/j.1526-100X.2008.00386.x.

Nelson, J. L. and E. S. Zavaleta. 2012. "Salt Marsh as a Coastal Filter for the Oceans: Changes in Function with Experimental Increases in Nitrogen Loading and Sea-Level Rise." *PLOS ONE* 7 (8): e38558. https://doi.org/10.1371/journal.pone.0038558.

Nie, M., W. Liu, S. C. Pennings, and B. Li. 2023. "Lessons from the Invasion of *Spartina alterniflora* in Coastal China." *Ecology* 104 (1): e3874. https://doi.org/10.1002/ecy.3874.

Okoye, O. K., H. Li, and Z. Gong. 2020. "Retraction of Invasive *Spartina alterniflora* and Its Effect on the Habitat Loss of Endangered Migratory Bird Species and Their Decline in YNNR Using Remote Sensing Technology." *Ecology and Evolution* 10 (24): 13810–24. https://doi.org/10.1002/ece3.6971.

Pejchar, L., and H. A. Mooney. 2009. "Invasive Species, Ecosystem Services and Human Well-Being." *Trends in Ecology & Evolution* 24 (9): 497–504. https://doi.org/10.1016/j.tree.2009.03.016.

Pennings, S. C., and M. D. Bertness. 2001. "Salt Marsh Communities." In , 289–316. 11. Marine Community Ecology. https://scholar.googleusercontent.com/scholar?q=cache:C_Jhm1A-TSkJ:scholar.google.com/&hl=en&as_sdt=0,22.

Pennings, S. C., and R. M. Callaway. 1992. "Salt Marsh Plant Zonation: The Relative Importance of Competition and Physical Factors." *Ecology* 73 (2): 681–90. https://doi.org/10.2307/1940774.

Portnoy, J.W., and A.E. Giblin. 1997. “Effects of Historic Tidal Restrictions on Salt Marsh Sediment Chemistry.” *Biogeochemistry* 36 (3): 275–303. https://doi.org/10.1023/A:1005715520988.

Reboreda, R., and I. Caçador. 2007. “Halophyte Vegetation Influences in Salt Marsh Retention Capacity for Heavy Metals.” *Environmental Pollution* 146 (1): 147–54. https://doi.org/10.1016/j.envpol.2006.05.035.

Rice, D., J. Rooth, and J. C. Stevenson. 2000. “Colonization and Expansion of *Phragmites australis* in Upper Chesapeake Bay Tidal Marshes.” *Wetlands* 20 (2): 280–99. https://doi.org/10.1672/0277-5212(2000)020[0280:CAEOPA]2.0.CO;2.

Riley, L. A., M. F. Dybdahl, and R. O. Hall. 2008. “Invasive Species Impact: Asymmetric Interactions between Invasive and Endemic Freshwater Snails.” *Journal of the North American Benthological Society* 27 (3): 509–20. https://doi.org/10.1899/07-119.1.

Rohal, C. B., C. Cranney, E. L. G. Hazelton, and K. M. Kettenring. 2019. “Invasive *Phragmites australis* Management Outcomes and Native Plant Recovery Are Context Dependent.” *Ecology and Evolution* 9 (24): 13835–49. https://doi.org/10.1002/ece3.5820.

Rolletschek, H., A. Rolletschek, T. Hartzendorf, and J. G. Kohl. 2000. “Physiological Consequences of Mowing and Burning of *Phragmites australis* stands for Rhizome Ventilation and Amino Acid Metabolism.” *Wetlands Ecology and Management* 8 (6): 425–33. https://doi.org/10.1023/A:1026562002388.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, et al. 2001. “The Population Biology of Invasive Species.” *Annual Review of Ecology, Evolution and Systematics* 32 (Volume 32, 2001): 305–32. https://doi.org/10.1146/annurev.ecolsys.32.081501.114037.

Saltonstall, K. 2002. “Cryptic Invasion by a Non-Native Genotype of the Common Reed, *Phragmites australis*, into North America.” *Proceedings of the National Academy of Sciences* 99 (4): 2445–49. https://doi.org/10.1073/pnas.032477999.

Schroeder, C. S., S. Halbrook, C. Birnbaum, P. Waryszak, W. Wilber, and E. C. Farrer. 2020. “*Phragmites australis* Associates with Belowground Fungal Communities Characterized by High Diversity and Pathogen Abundance.” *Diversity* 12 (9): 363. https://doi.org/10.3390/d12090363.

Teal, J. M., and S. Peterson. 2005. “The Interaction Between Science and Policy in the Control of *Phragmites* in Oligohaline Marshes of Delaware Bay." *Restoration Ecology* 13 (1): 223–27. https://doi.org/10.1111/j.1526-100X.2005.00027.x.

Thomas, M. B., and A. M. Reid. 2007. "Are Exotic Natural Enemies an Effective Way of Controlling Invasive Plants?" *Trends in Ecology & Evolution* 22 (9): 447–53. https://doi.org/10.1016/j.tree.2007.03.003.

Townend, I., C. Fletcher, M. Knappen, and K. Rossington. 2011. "A Review of Salt Marsh Dynamics." *Water and Environment Journal* 25 (4): 477–88. https://doi.org/10.1111/j.1747-6593.2010.00243.x.

Tu, M., C. Hurd, and J. Randall. 2001. "Weed Control Methods Handbook: Tools & Techniques for Use in Natural Areas." *All U.S. Government Documents (Utah Regional Depository)*, April. https://digitalcommons.usu.edu/govdocs/533.

Uddin, M. N., and R. W. Robinson. 2017. "Changes Associated with *Phragmites australis* Invasion in Plant Community and Soil Properties: A Study on Three Invaded Communities in a Wetland, Victoria, Australia." *Limnologica* 66 (September): 24–30. https://doi.org/10.1016/j.limno.2017.07.006.

Valiela, I. 2015. "The Great Sippewissett Salt Marsh Plots—Some History, Highlights, and Contrails from a Long-Term Study." *Estuaries and Coasts* 38 (4): 1099–1120. https://doi.org/10.1007/s12237-015-9976-9.

Valiela, I., J. Lloret, T. Bowyer, S. Miner, D. Remsen, E. Elmstrom, C. Cogswell, and E. R. Thieler. 2018. "Transient Coastal Landscapes: Rising Sea Level Threatens Salt Marshes." *Science of The Total Environment* 640–641 (November): 1148–56. https://doi.org/10.1016/j.scitotenv.2018.05.235.

Valiela, I., J. Lloret, and K. Chenoweth. 2023. "Effects of Climate Change on Salt Marshes." In *Climate Change and Estuaries*, by Michael J. Kennish, Hans W. Paerl, and Joseph R. Crosswell, 1st ed., 355–80. Boca Raton: CRC Press. https://doi.org/10.1201/9781003126096-21.

Valiela, I., J.Lloret, K. Chenoweth, and Y. Wang. 2024. "An Example of Accelerated Changes in Current and Future Ecosystem Trajectories: Unexpected Rapid Transitions in Salt Marsh Vegetation Forced by Sea Level Rise." *Environmental Challenges* 14 (January): 100842. https://doi.org/10.1016/j.envc.2024.100842.

Valiela, I., J. M. Teal, and N. Y. Persson. 1976. "Production and Dynamics of Experimentally Enriched Salt Marsh Vegetation: Belowground Biomass1." *Limnology and Oceanography* 21 (2): 245–52.

https://doi.org/10.4319/lo.1976.21.2.0245.

Vasquez, E. A., E. P. Glenn, J. J. Brown, G. R. Guntenspergen, and S. G. Nelson. 2005. “Salt Tolerance Underlies the Cryptic Invasion of North American Salt Marshes by an Introduced Haplotype of the Common Reed *Phragmites australis* (Poaceae).” *Marine Ecology Progress Series* 298 (August): 1–8. https://doi.org/10.3354/meps298001.

Vernberg, F. J. 1993. “Salt-Marsh Processes: A Review.” *Environmental Toxicology and Chemistry* 12 (12): 2167–95. https://doi.org/10.1002/etc.5620121203.

Wails, C. N., K. Baker, R. Blackburn, A. D. Vallé, J. Heise, H. Herakovich, W. A. Holthuijzen, et al. 2021. “Assessing Changes to Ecosystem Structure and Function Following Invasion by *Spartina alterniflora* and *Phragmites australis*: A Meta-Analysis.” *Biological Invasions* 23 (9): 2695–2709. https://doi.org/10.1007/s10530-021-02540-5.

Wan, S., P. Qin, J. Liu, and H. Zhou. 2009. “The Positive and Negative Effects of Exotic *Spartina alterniflora* in China.” *Ecological Engineering*, Wetland restoration and ecological engineering, 35 (4): 444–52. https://doi.org/10.1016/j.ecoleng.2008.05.020.

Wang, G., P. Qin, S. Wan, W. Zhou, X. Zai, and D. Yan. 2008. “Ecological Control and Integral Utilization of *Spartina alterniflora*.” *Ecological Engineering* 32 (3): 249–55. https://doi.org/10.1016/j.ecoleng.2007.11.014.

Wang, J., X. Zhang, L. Jiang, M. D. Bertness, C. Fang, J. Chen, T. Hara, and B. Li. 2010. “Bioturbation of Burrowing Crabs Promotes Sediment Turnover and Carbon and Nitrogen Movements in an Estuarine Salt Marsh.” *Ecosystems* 13 (4): 586–99. https://doi.org/10.1007/s10021-010-9342-5.

Webb, J. M., R. Quintã, S. Papadimitriou, L. Norman, M. Rigby, D. N. Thomas, and L. Le Vay. 2012. “Halophyte Filter Beds for Treatment of Saline Wastewater from Aquaculture.” *Water Research* 46 (16): 5102–14. https://doi.org/10.1016/j.watres.2012.06.034.

Weis, P, L Windham, D. J Burke, and J. S Weis. 2002. “Release into the Environment of Metals by Two Vascular Salt Marsh Plants.” *Marine Environmental Research* 54 (3): 325–29. https://doi.org/10.1016/S0141-1136(02)00131-9.

Windham, L., and R. G. Lathrop. 1999. “Effects of *Phragmites australis* (Common Reed) Invasion on Aboveground Biomass and Soil Properties in Brackish Tidal

Marsh of the Mullica River, New Jersey." *Estuaries* 22 (4): 927–35. https://doi.org/10.2307/1353072.

Xia, S., W. Wang, Z. Song, Y. Kuzyakov, L. Guo, L. V. Zwieten, Q. Li, et al. 2021. "*Spartina alterniflora* Invasion Controls Organic Carbon Stocks in Coastal Marsh and Mangrove Soils across Tropics and Subtropics." *Global Change Biology* 27 (8): 1627–44. https://doi.org/10.1111/gcb.15516.

Yan, X., L. Zhenyu, W. P. Gregg, and L. Dianmo. 2001. "Invasive Species in China — an Overview." *Biodiversity & Conservation* 10 (8): 1317–41. https://doi.org/10.1023/A:1016695609745.

Zhang, G., J. Bai, Q. Zhao, J. Jia, X. Wang, W. Wang, and X. Wang. 2021. "Soil Carbon Storage and Carbon Sources under Different *Spartina alterniflora* Invasion Periods in a Salt Marsh Ecosystem." *CATENA* 196 (January): 104831.
https://doi.org/10.1016/j.catena.2020.104831.

Zhao, Y., H. Qing, C. jiao Zhao, C. fang Zhou, W. Zhang, Y. Xiao, and S. An. 2010. "Phenotypic Plasticity of *Spartina alterniflora* and *Phragmites australis* in Response to Nitrogen Addition and Intraspecific Competition." *Hydrobiologia* 637 (1): 143–55. https://doi.org/10.1007/s10750-009-9992-5.

Figures:

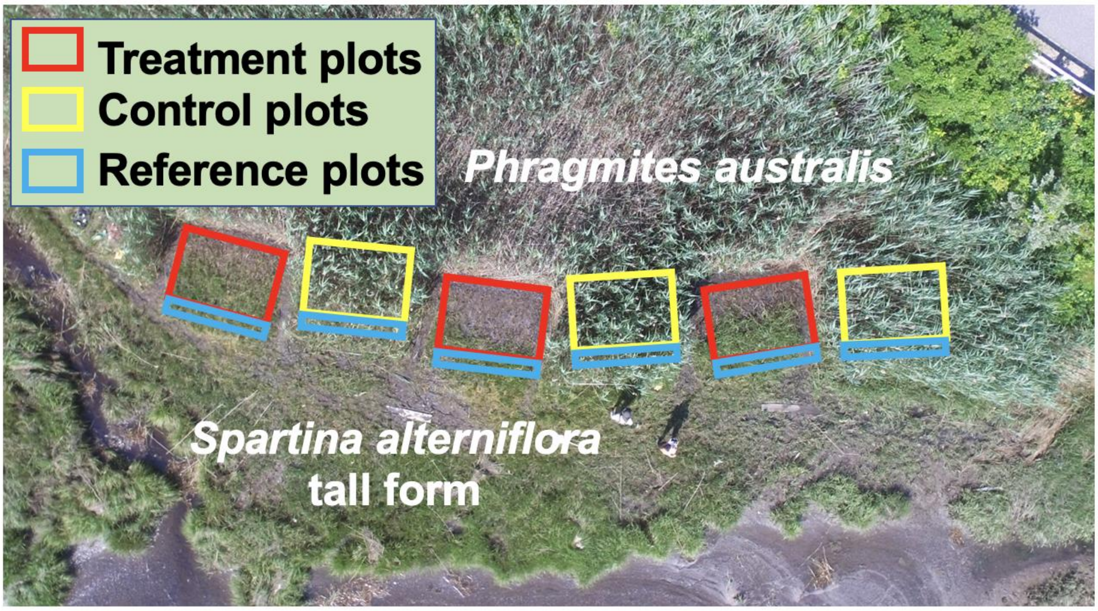

Figure 1: arrangement of two types of experiment plots, treatment and control plots, and reference plots, which are the lower extension of the experiment plots, took on July 5th.

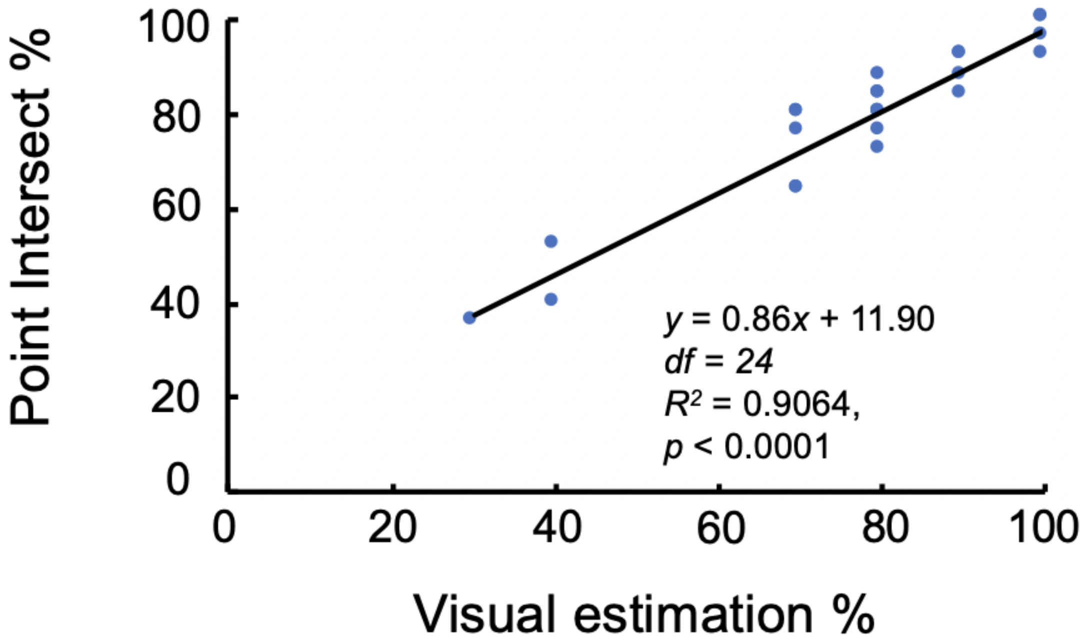

Figure 2: Comparison of point intercept method with visual estimates of cover. Data shown are the visual estimation of percent cover in a 25x25cm patch versus cover values determined with a 25-point-intercept method.

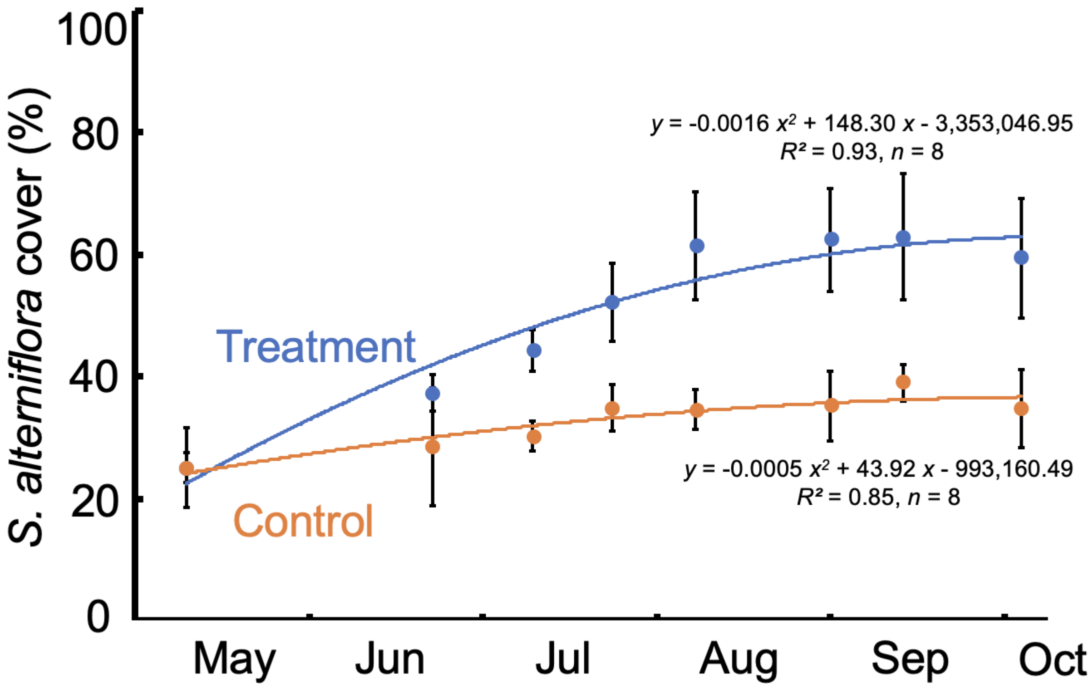

Figure 3: *Spartina alterniflora* % cover, during the growing season, in treatment and control plots. Dots represent means in a sampling period across the three plots in the respective treatment, and error bars represent±SE.

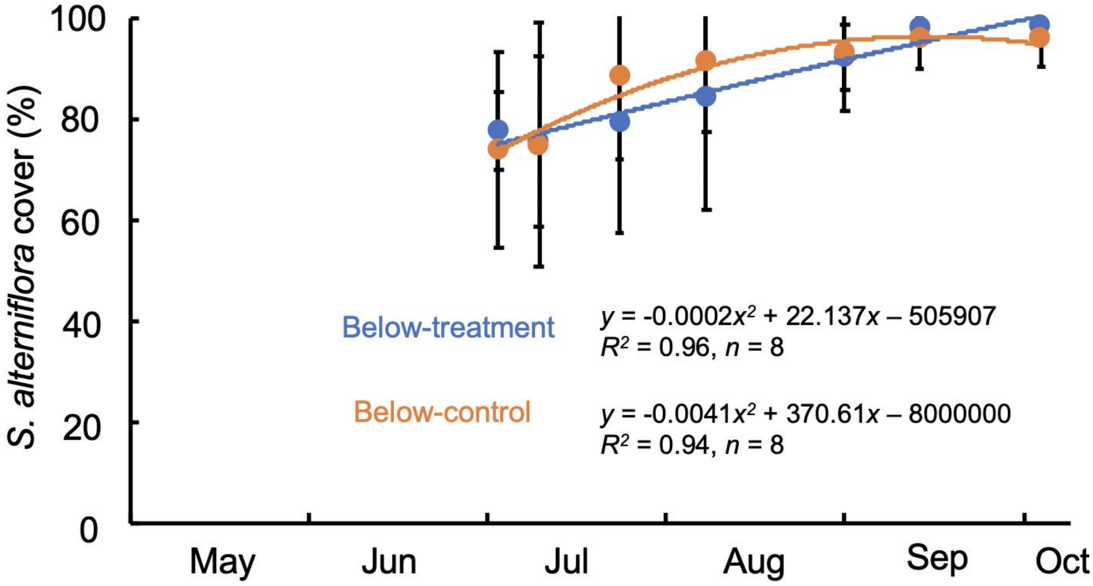

Figure 4: *Spartina alterniflora* % cover, during the growing season, in the reference plots below the treatment and control plots. Dots represent means in a sampling period across the three plots in the respective treatment, and error bars represent ±SE.

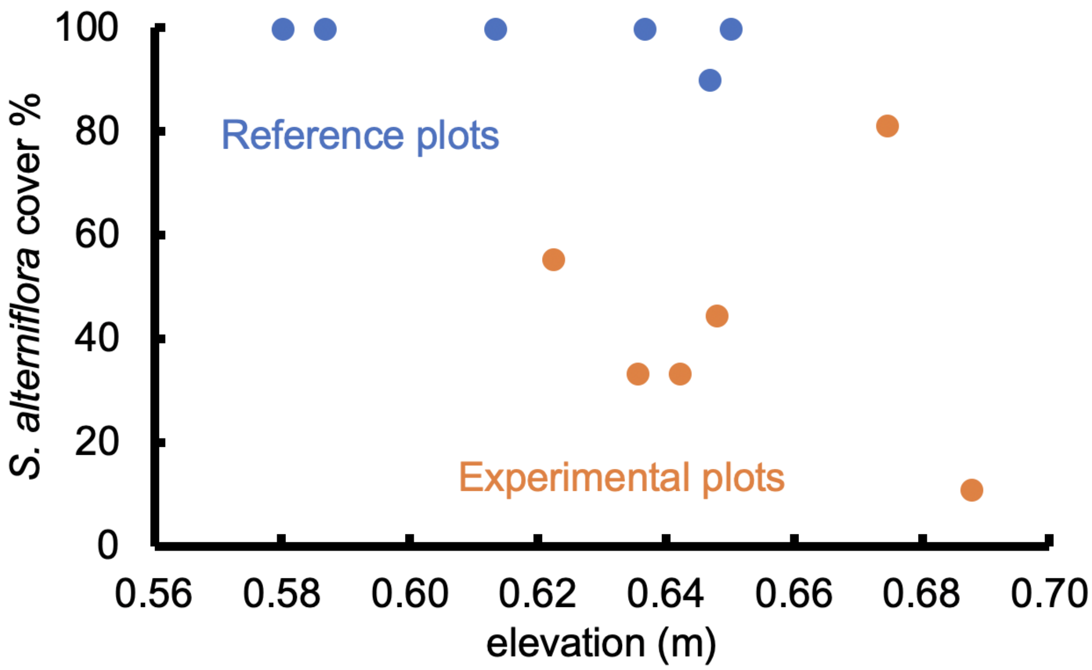

Figure 5: *S. alterniflora* cover(%) vs elevation (m) across reference plots and experimental plots. (*S. alterniflora* cover (%) measured on Oct. 13th, at the end of the growing season.)

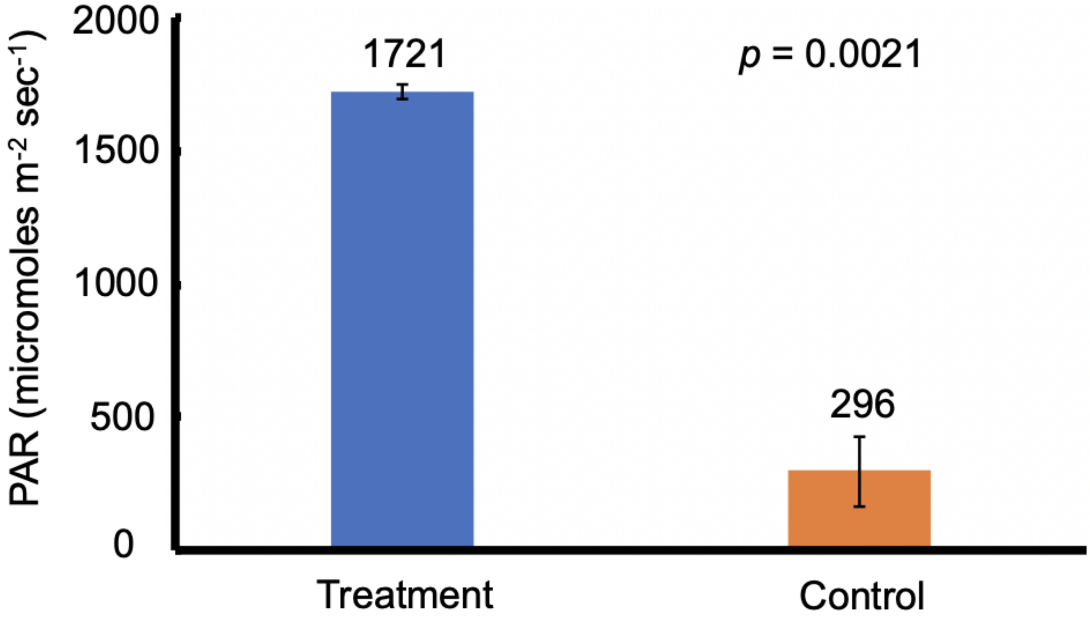

Figure 6: Average photosynthetically active radiation (PAR, micromoles m^{-2} sec-^{1}), *S. alterniflora* accepted, in experimental plots, and their ± 1 standard errors. Treatment plots have a mean of 1721±24SE. Control plots have a mean of 296±131SE.

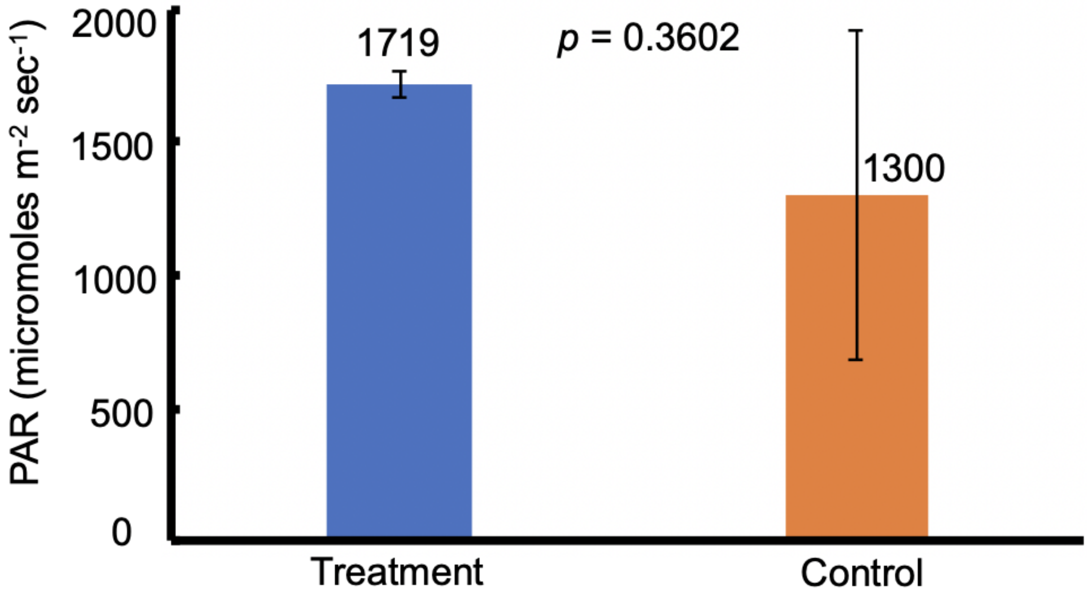

Figure 7: Average photosynthetically active radiation (PAR, micromoles m^{-2} sec^{-1}), *S. alterniflora* accepted, in reference plots, and their ± 1 standard errors. Reference plots associate with treatment plots have a mean of 1719±50. Reference plots associate with control plots have a mean of 1300±617.

Tables:

Table 1: Linear regression and non-linear regression R^2s of *S. alterniflora* percent cover in experimental plots.

Experimental Plots R^2

	Treatment	Control
Linear	0.86	0.79
Non-linear	0.93	0.85

Table 2: Linear regression and non-linear regression R^2s of *S. alterniflora* percent cover in reference plots.

Reference Plots R^2

	Below-Treatment	Below-Control
Linear	0.96	0.79
Non-linear	0.96	0.94

Table 3: Repeated Measures ANOVA test for means of experimental plots *S. alterniflora* percent cover during the growing season.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*
Time Effect	3509.115110	7	501.302159	3.982618	0.003095
Treatment Effect	3817.477725	1	3817.477725	30.328130	0.000005
Interaction	998.946107	7	142.706587	1.133739	0.367188
Error	4027.920184	32	125.872506		
Total	12353.459126	47			

Table 4: Repeated Measures ANOVA test for means of reference plots *S. alterniflora* percent cover during the growing season.

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*
Time Effect	3066.082	6	511.014	2.381	0.055
Treatment Effect	10.667	1	10.667	0.050	0.825
Interaction	223.157	6	37.193	0.173	0.982
Error	6008.260	28	214.581		
Total	9308.166	41			