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The Effect of Species Choice, Seed Mix Composition, and Microtopography on Native Plant Restoration in Great Salt Lake Wetlands

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THE EFFECT OF SPECIES CHOICE, SEED MIX COMPOSITION, AND MICROTOPOGRAPHY ON NATIVE PLANT RESTORATION IN GREAT SALT LAKE WETLANDS

by

Coryna Hebert

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ABSTRACT

The effect of species choice, seed mix composition, and microtopography on native plant restoration in Great Salt Lake wetlands

by

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Utah State University, 2022

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Wetlands are highly valued for ecosystem services and functions including flood mitigation, groundwater recharge, and wildlife habitat. As such, restoring native plant communities that promote wetland functions is a high priority for land managers. However, there are considerable barriers to the successful restoration of native plant communities. In our study system (Great Salt Lake wetlands), many areas are invaded by the invasive grass, *Phragmites australis. Phragmites* grows in dense, monotypic stands and has displaced thousands of acres of native plant communities. The reduction of native plant communities in Great Salt Lake wetlands is a major concern because these ecosystems provide habitat for millions of native birds. Managers have made successful efforts to suppress large stands of *Phragmites,* but native plant communities do not often reassemble on their own. To address this issue, seed-based restoration is a feasible strategy due to the large scale of restoration needed. Challenges to seed-based restoration include environmental variability, especially unpredictable water levels, and the persistent threat of re-invasion. To improve the success of seed-based restoration, we investigated several restoration strategies novel to our system. Our first strategy was to identify native species that could establish in a broad range of environmental conditions (particularly soil moisture). These species included perennial graminoids that provide high quality avian habitat and annual forbs that were expected to germinate and establish faster than perennial species and have higher tolerances to drier soils. We also tested different compositions of species in seed mixes. We found two annual native species, *Bidens cernua* (nodding beggartick) and *Rumex maritimus* (goldendock) established across a range of moisture conditions and out-competed other natives and *Phragmites* when sown in a mix. *Distichlis spicata* (saltgrass) had the highest establishment success of all perennial graminoids and established at higher rates than other natives in a field setting. Our final restoration strategy was to implement artificial microtopography (elevation change at the scale of individual plants <1m). Microtopography is an important structural feature in wetlands because it affects soil moisture, hydrology, biogeochemical soil properties, and the spatial distribution of plants. We found some evidence to support the use of microtopography as a restoration intervention. Given the vast evidence for the importance of wetland microtopography, we also sought to characterize the relationship between microtopography, wetland types (emergent marsh, wet meadow, playa), and plant communities. We found microtopography was more pronounced in emergent marshes that had not been grazed by cattle.

(101 pages)

PUBLIC ABSTRACT

The effect of species choice, seed mix composition, and microtopography on native plant restoration in Great Salt Lake wetlands

Coryna Hebert

Wetlands are important ecosystems that improve water quality, prevent floods, and provide wildlife habitat. As such, restoring native plants that promote wetland health is a high priority for land managers. However, there are many challenges to the restoration of native plants. In our study system (Great Salt Lake wetlands), many areas are invaded by the European grass, *Phragmites australis. Phragmites* grows in dense stands and displaces native plants. The reduction of native plant communities in Great Salt Lake wetlands is a major concern because these ecosystems provide habitat for millions of native birds. Managers have made successful efforts to reduce large stands of *Phragmites,* but native plant communities do not often return on their own. To address this issue, seeding wetlands with native species is a promising strategy due to the large scale of restoration needed. Seeding is challenging because water levels can be unpredictable in wetlands, and invasive species can spread to restoration sites. To improve seeding success, we investigated several restoration strategies novel to our system. Our first strategy was to identify native species that could establish in a broader range of environmental conditions (particularly soil moisture). These species included perennial grasses and bulrushes that provide high quality avian habitat and forbs that were expected to germinate and establish faster than bulrushes and sedges. We also tested different compositions of species in seed mixes. We found two annual species, *Bidens*

cernua (nodding beggartick) and *Rumex maritimus* (goldendock), established across a range of moisture conditions and out-performed other natives when sown in a mix. *Distichlis spicata* (saltgrass) had the greatest success of all perennial graminoids (grass-like species) and established at higher rates than other natives in a field setting. Our final restoration strategy was to implement artificial microtopography (elevation change at the scale of individual plants <1m). Microtopography is an important feature in wetlands because it affects soil moisture, water levels, soil properties, and the distribution of plants. We found some evidence from a single experiment to support the use of microtopography as a restoration intervention. Given the vast evidence for the importance of wetland microtopography, we also sought to explore the relationship between microtopography, wetland types (emergent marsh, wet meadow, playa), and plant communities. We found microtopography was more abundant in marshes (as opposed to playas and wet meadows) that had not been grazed by cattle.

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Coryna Hebert

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CHAPTER I

INTRODUCTION

In the arid west of the United States, wetlands are critical because they occur infrequently across the landscape. One of these valuable ecosystems are the wetland complexes surrounding the Great Salt Lake of Utah. These wetlands are a mixture of emergent marshes, wet meadows, and playas, with variable hydrology and associated plant communities (Downard et al. 2014; Downard et al. 2017). All these wetland types provide critical habitat for millions of migratory and resident birds (Aldrich & Paul 2002; Downard et al. 2017). As such, restoring native plant communities is a high priority for land managers. One of the biggest challenges to restoration is the prevalence of invasive species. This system is highly invaded and persistently threatened by the non-native grass *Phragmites australis* (Long et al. 2017). *Phragmites* aggressively invades wetlands, establishing itself in dense monotypic stands that displace native vegetation (Ailstock et al. 2001; Long et al. 2017). Previous research has identified strategies to contain large stands of *Phragmites,* but native plant communities do not reestablish on their own (Rohal et al. 2019; Rohal et al. 2021). Here, we tested several restoration interventions to improve native plant establishment from seed in Great Salt Lake wetlands. Improving native plant establishment is a key step in recovering invasion-resistant plant communities that provide valuable wildlife habitat. However, there are significant barriers to success in seed-based restoration including environmental variability, especially unpredictable water levels, and the persistent threat of re-invasion.

In chapter two, we assessed several restoration interventions through four experimental venues (greenhouse, mesocosms, small field plots, large field plots). Our first restoration strategy was to widen species choice to include species that have a wider tolerance of moisture requirements and can germinate and establish fast relative to slower-growing perennial graminoids. These fast-growing species included *Bidens cernua* (nodding beggartick), *Euthamia occidentalis* (western goldentop), *Epilobium ciliatum* (fringe willowherb), *Polygonum lapathafolium* (pale smartweed), *Rumex maritimus* (goldendock), and *Symphiotricum ciliatum* (rayless alkali aster). Related to this, we tested different seed mix compositions. Perennial graminoid species included *Bolboschoenus maritimus* (alkali bulrush), *Distichlis spicata* (saltgrass), *Eleocharis palustris* (common spikerush), *Puccinellia nuttalianna* (nuttall's alkaligrass), and *Schoenoplectus americanus* (threesquare bulrush), *Schoenoplectus acutus* (hardstem bulrush). In three experimental venues, we tested a seed mix comprised entirely of perennial graminoids, and a seed mix containing graminoids and fast-growing forbs.

We also tested microtopography as a potential restoration tool. Microtopography is a small change in the elevation of the soil surfaces at the scale of individual plans (Huenneke & Sharitz 1986; Moser et al. 2007). Microtopography is a distinct feature of many wetland types that influences vegetation structure, biogeochemical cycling, hydrology, and other wetland functions (Chapin III et al. 1979; Diamond et al. 2020). There is evidence that microtopography can improve restoration outcomes in wetlands and increase biodiversity (Vivian-Smith 1995; Moser et al. 2009; Ahn & Dee 2011). In a restoration context, we predicted that microtopography would increase germination microsites, by creating a gradient of soil moisture at small spatial scales, and thus improve the establishment of diverse seed mixes. To assess this, we implemented two distinct types of artificial microtopography (aboveground mounds are belowground ruts) in three experimental venues.

In addition to testing microtopography as a restoration strategy, we sought to characterize microtopography in our study system. In chapter three, we evaluated the relationship between microtopography, plant communities and wetland type. We assessed 14 sites across Great Salt Lake wetlands, where we conducted species level plant surveys and microtopography surveys along transects. To measure microtopography, we used a low-tech tool called a profilometer that enabled us to measure surface roughness and vertical relief (Leatherman 1987). The objective of this research was to document microtopography in this system, which was previously unknown. Establishing weather or not microtopography is important in Great Sale Lake wetlands informs us on ideal reference conditions for this system.

We found that altering species choice and using seed mixes that incorporate fast-growing forb species was the most successful restoration strategy, but the results were highly dependent on experimental context. We found that metrics of microtopography varied by wetland type. Emergent wetlands, particularly those which were dominated by *Schoenoplectus americanus* (threesquare bulrush) and had not been grazed, were more positively associated with microtopography.

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CHAPTER II

THE EFFECTS OF SPECIES CHOICE, SEED MIX COMPOSITION, AND MICROTOPOGRAPHY ON NATIVE PLANT ESTABLISHMENT AND INVADER SUPPRESSION

Abstract

In wetlands, there are major barriers to restoring native plant communities from seed. These barriers include environmental variability, especially soil moisture and hydrology, high invisibility of wetland systems, and propagule pressure of invasive species. We conducted a series of four experiments to test novel restoration strategies in our system (Great Salt Lake wetlands) to determine which strategy could most effectively overcome restoration barriers, resulting in robust native plant communities. Our first strategy was to modify native seed mix compositions to include faster-growing forb species and species with a wider tolerance of moisture conditions. Our second restoration strategy was to alter the physical seeding environment through the creation of microtopography (change of soil surface elevation at the scale of individual plants <1m). Microtopography could buffer against hydrologic extremes and create moisture gradients for a varied native species assemblage. We found that altering seed mix composition was more effective at improving native plant establishment and suppressing an invader (*Phragmites australis*) in controlled experimental venues but was less effective in field settings. We identified several native species in our study system that consistently performed better than other native species or their functional counterparts (e.g. perennial graminoids or annual forbs). These species included *Rumex maritimus*, *Bidens cernua* and *Distichlis spicata*. Microtopography temporarily improved the establishment of a

seeded native species in a field setting, but this effect did not persist nor was it a strong driver in a controlled experiment. This research offers insight into restoration strategies that can be used to improve establishment of native species in highly invaded wetland systems, but inconsistent results between experimental venues demonstrate the complexities in achieving long-term ecosystem recovery.

Introduction

Restoration of wetland plant communities is necessary to recover critical ecosystem functions that wetlands provide, protect biodiversity, and prevent invasion from undesirable species. A promising strategy to restore vast expanses of wetlands is to seed native plant communities (Merritt & Dixon 2011; Kettenring & Tarsa 2020). Seed-based restoration is especially critical when remnant seed banks and nearby seed source wetlands are insufficient to establish habitat-rich, invasion-resistant native communities (Adams & Galatowitsch 2008). In wetlands, there is a considerable knowledge gap on how to best restore native plant communities from seed, and numerous barriers to long-term ecosystem recovery (Kettenring & Tarsa 2020). One such barrier is hydrologic variation and hydrologic extremes, such as drought or flooding events (Middleton 1999). Wetland hydrology is both spatially and temporally dynamic and poses a barrier to restoration because seeds require a specific range of conditions to germinate and establish (Harper 1965). Simply put, it is difficult to synchronize large scale seeding efforts with optimal restoration site conditions. A second major barrier to seed-based restoration is the prevalence of invasive species and their high propagule pressure (Simberloff 2009; Cassey et al. 2018; Carr et al. 2019). Wetlands are environmental sinks due to their landscape position and are particularly susceptible to invasions (Zedler & Kercher 2004).

Invasive species pose a barrier to seed-based restoration because invasive species can outcompete native seedlings when propagule pressure is high or environmental conditions favor the invader. Restoration of native plant communities after the containment of invasive species is a high priority for wetland managers. Here, we investigated several approaches novel to our study system to improve seed-based restoration outcomes and overcome these common barriers to success.

In restoration, species choice is a major determinant of plant community outcomes (Hooper & Dukes 2010; Hulvey & Aigner 2014; Shackelford et al. 2021). Previous research suggests that seed-based restoration should incorporate species that exhibit a diverse array of functional traits (Byun et al. 2013). More specifically, annual species that germinate and establish quickly and produce robust vegetation cover under a broad range of environmental conditions are more likely to outcompete an invader (Byun et al. 2013, Hess et al. 2019). At the same time, wetland hydrology can be variable and at times unpredictable, making it difficult to optimize seed mix composition to coincide with conditions that support native species establishment. To buffer against these uncertainties, seed mixes can include a wider range of species that tolerate different moisture conditions.

In addition to broadening seed mix compositions, it is equally important to ensure there are suitable environments in which native species can successfully co-establish. Different seeds require different abiotic conditions and environmental cues to germinate and establish (Harper 1965), yet it is difficult to ensure success of native species in a field setting because of environmental variability and unpredictable environmental extremes (particularly hydrologic). Microtopography, a change in surface elevation at the scale of individual plants (<1m) (Huenneke & Sharitz; Moser et al. 2007), could improve the establishment of diverse species assemblages by creating more germination microsites. In wetlands, microtopography creates a gradient of temperature, light, moisture, and biogeochemical soil properties at small spatial scales (Diamond et al. 2020; Moser et al. 2009; Diamond et al. 2021). In turn, microtopography may facilitate interspecific coexistence of species with complimentary niches. In wetland mesocosm experiments, microtopography resulted in greater species richness (Vivian-Smith 1995) and higher growth rates of a pioneer species (Fivash et al. 2020). This principle also held true for field studies in artificial wetlands (Moser et al. 2007). There is further evidence suggesting that microtopographic variation can help buffer against environmental uncertainties and improve native species establishment (Doherty and Zedler 2015). This research tested whether microtopography, through creating more variation in soil moisture, along with manipulating species choice in seed mixes, can be utilized to improve restoration outcomes.

We used the vast wetland complexes surrounding the Great Salt Lake, Utah, to evaluate the potential for microtopography and varied seed mix compositions to facilitate native plant community establishment, particularly after invasive species control. The Great Salt Lake is a terminal basin in the Great Basin of western North America. This unique system contains several wetland types, including emergent marshes, wet meadows, and playas (Downard et al. 2017). The lake and its surrounding wetlands rely on freshwater inputs from snowpack-driven watersheds (Null & Wurtsbaugh 2020). As such, these systems are threatened by drought, climate change, development, and increasing upstream demand for a limited water supply (Downard et al. 2014;

Wurtsbaugh et al. 2017). Adding to these many challenges, these wetlands are heavily invaded by a perennial, non-native grass, *Phragmites australis* (Cav.) (common reed) (Ailstock et al. 2001; Rohal et al. 2019) *Phragmites* has rapidly expanded in Great Salt Lake wetlands and threatens all wetland types due to its wide-ranging tolerance of moisture, nutrient, and salinity levels (Chambers et al. 2003; Rickey & Anderson 2004; Kettenring et al. 2015). *Phragmites* covers an estimated 23,000 acres along the Great Salt Lake (Long et al. 2017). Until now, restoration in this system has focused on re-establishing native species that provide optimal avian habitat once *Phragmites* has been contained. These habitat-forming species include several rhizomatous graminoids in the sedge family (e.g. bulrushes, *Schoenoplectus* and *Bolboschoenus* species). Once established, these species form large stands that provide a suite of important habitat functions and nutritious seeds for waterfowl (Intermountain West Joint Venture 2013, Downard et al. 2017). However, perennial graminoids tend to establish slowly from seed, and are poor competitors of *Phragmites* in early life stages (Tarsa unpublished data). The failure of these species to effectively compete against *Phragmites* when seeded is likely because they require a narrow range of environmental conditions for establishment success, usually bare, moist soils (Kettenring 2016; Marty & Kettenring 2017). Thus, this research aims to identify fast-growing species that can better outcompete *Phragmites* across a wider range of environmental conditions, namely moisture. Selecting variable restoration species is critical to maximize the potential for native species to pre-empt resources before an invader (i.e., via the biotic resistance hypothesis; Funk et al. 2008; Byun et al. 2013; Hess et al. 2019). Additionally, it remains unclear how alterations to the physical seeding environment, such as microtopography, can support establishment of a diverse species assemblage by creating soil moisture gradients.

We sought to identify restoration interventions that could overcome environmental uncertainty and invasion pressure, resulting in robust native plant communities. We used multiple experimental venues (two experiments in controlled environments: a greenhouse and outdoor mesocosms and two experiments *in situ* in Great Salt Lake wetlands) to evaluate the effectiveness of restoration interventions. In these four experiments (2020-2021) we (a) screened individual species performance across variable water levels, (b) evaluated different seed mix compositions across variable water levels, and (c) tested if altering the physical environment in which seeds are sown through the creation of microtopography would enhance establishment. We predicted that forb species would perform better across all moisture conditions than perennial graminoids and that seed mixes including forbs would perform better than mixes containing only graminoids. We predicted that microtopography would create more germination microsites to support a higher diversity of species, and thus we would observe higher cover of native species and greater species evenness in treatments with microtopography.

Methods

Seed sourcing, cleaning, and viability testing

We selected species with a range of growth forms, habitat preferences, and wetland indicator statuses for use in the various experiments (Table S2.15). Seeds were hand collected or purchased in 2019 or 2020 from several locations within our study system (Table S2.16). For experiments conducted in 2020, all seeds were collected in

2019. For experiments conducted in 2021, seeds were collected from 2020. Seed lots from different collection years were never mixed. For each seed lot (year x seed collection location), we analyzed viability in three replicates x 100 seeds each, then averaged the results for a mean percent viable (Table S2.15). Instructions for scoring seeds of specific families and concentrations/saturation times were guided by a tetrazolium handbook (Millers and Peters 2010).

Dormancy breaking and sowing

Dormancy was broken following best-known protocols for each species, via either cold stratification at 2°C or bleach scarification (Table S2.15; Marty and Kettenring 2017; Rosbakh et al. 2019). For all experiments, seeds were sown on the soil surface regardless of experimental venue (mesocosm, greenhouse, field) to facilitate the high light levels necessary to trigger germination for wetland species (Kettenring et al. 2006; Kettenring 2016; Marty and Kettenring 2017). Prior to sowing, seeds were mixed with sand to allow even dispersion of seeds across the soil surface.

Monitoring and data collection

For all experiments, response variables were percent cover or biomass of plants by species as a proxy for establishment success. In the 2020 greenhouse experiment cover was estimated to individual percent. In all other experiments percent cover was broken into the following classes: <1%, 1-10%, 11-20%, 21-30%, 31-40%, 41-50%, 51-60%, 61-70%, 71-80%, 81-90%, 91-100% and the cover class midpoint was used for subsequent analysis. We also harvested aboveground biomass by species for the greenhouse and mesocosm experiments.

Statistical analyses

We used R statistical software version 4.1.3 (R Core Team 2021) for all analyses with the "GLMMtmb" package for mixed effects models (Brooks et al. 2017). Unless noted otherwise, we used the midpoint of plant percent cover data and transformed these values to proportions (divided by 100) and fitted with beta distributions (Damgaard and Irvine 2019). To fit the beta, we added a small value (0.01) to zeros and truncated values ≥ 1 to 0.999. For biomass data, we used either a square root or log transformation (whichever resulted in a better model fit) and assumed gaussian distributions. For log-transformed data, a small value (0.01) was added to zeros. We used the "DHARMa" package to inspect residual diagnostics for mixed effects models (Hartig 2016). We used the "emmeans" package to extract and visualize model means and inspect pairwise comparisons between treatments and response variables (Lenth 2022).

Effect of Water Level and Seed Mix Composition on Native Species Performance (Greenhouse experiment 2020)

<u>Experimental design and treatments</u>

From February 10 to March 16, 2020, we conducted a greenhouse experiment to investigate the establishment success of nine native wetland plant species at three different water levels. There were nine single species seed mix treatments and two multi-species seed mix treatments (a graminoid-only mix with five species and a graminoid + forb mix with nine species), for a total of 11 seed treatments each replicated three times (11 seed treatments x 3 water levels x 3 replicates). Each of 33 treatment combinations was assigned randomly to one of 33 tins within each of 3 blocks.

Species included five perennial graminoids: *Bolboschoenus maritimus, Eleocharis palustris, Schoenoplectus acutus*, *Puccinellia nuttalliana,* and *Distichlis spicata.* The other four species were faster-growing forbs, all of which are annuals except for *Epilobium ciliatum*: *Rumex maritimus, Polygonum lapathafolium, Bidens cernua,* and *E. ciliatum* (Table 2.1). In addition to seeding species individually, there were two seed mix treatments. The first mix included the five perennial graminoids in a 1:1 proportion, and the second mix included all nine species in a 1:1 proportion. We used a seeding density of 1,938 seeds m^{-2}. This density was recommended as a standard seeding rate by regional wetland managers and has been used by other researchers as a baseline seeding rate for experiments (Intermountain West Joint Venture; Robinson 2022).

The greenhouse conditions mimicked summer growing conditions in northern Utah with a 32℃ high and 15℃ low temperature range. A 16-hour photoperiod was supplemented with artificial light provided by LED fixtures (Gavita Pro 1000^{e}). Sampling units were aluminum cake tins (29.2 x 22.7 cm) that rested inside plastic dish tubs filled with water. Tins had 5 small holes on the bottom to uptake water. Aluminum trays were filled with a standard potting soil mix (SunGro™). The soil mix did not contain nutrients, so a standard rate (5.9g/L) of slow-release pelleted fertilizer was added following manufacturer's instructions (Osmocote® 15-9-12) to ensure plants were not nutrient-limited.

Water level treatments were achieved by filling plastic dish tubs to different depths, which were refilled daily as needed to counter evapotranspiration and achieve the target depth. The water level treatments represented a dry condition (range of 2 to 6 cm in the water reservoir), a moist soil condition (3 to 7 cm), and a saturated condition (9 to 12 cm). Tins were approximately 5 cm above the bottom of the reservoir, so the dry treatment would absorb 1 cm of water, the moist treatment would absorb 2 cm, and the saturated treatment would never dry out. Water levels were measured in a 4-hour window every morning.

Data collection

Percent cover by species was collected weekly for the length of the experiment. After 40 days, biomass was harvested by clipping plants at the soil surface and separating leaves/stems from inflorescences. The multi-species seed mix treatments was separated by species. Biomass was dried at 65°C for 24 hours and weighed immediately upon removal from the drying oven.

Statistical analyses

We ran generalized linear mixed models on percent cover of individual species and total cover of seed mix treatments on the last monitoring date, 40 days after seeding. Fixed effects included water treatment (3 levels) and seed treatment (11 levels). Random effects included block.

Effect of Seed Mix Composition and Microtopography on Wetland Plant Communities (Field experiment 2020)

Experimental design and study site

In summer 2020, we implemented a field experiment investigating the interactive effects of seed mix treatment (three levels) and artificially created microtopography (four levels) on wetland plant cover. Microtopography treatments were applied in one of four plots (1 m x 3 m) in each of five blocks (2 m x 6 m) in a completely randomized block design. Each microtopography treatment plot was divided into three 1 m^2 sub-plots in which different seed mix treatments were applied for a total of 60 subplots. Fine mesh barriers made of white organza fabric (50 cm high) were installed around each subplot to ensure seeds stayed in place (Figure 2.1b).

The experiment was implemented at Farmington Bay Waterfowl Management Area northwest of the Turpin unit along the eastern shore of Great Salt Lake (Figure 2.2). This area had been treated for removal of *Phragmites* for several years as per management recommendations (Rohal 2018) but did not have extensive native plant recovery and had not been actively revegetated by managers. Additionally, as is customary in many Great Salt Lake wetlands (Downard et al. 2014), there was a water control structure approximately 300 m from the study site, which allowed for release of water to the experiment site if it got too dry (soil no longer saturated or moist). The headgate was periodically opened and closed throughout the length of the growing season to ensure the site did not dry out.

Microtopography treatments

Two treatments consisted of five rectangular mounds with either 5 or 15 cm relief (Figure 2.1a). Mounds (as opposed to depressions) were tested because digging into the soil surface could create compaction, and mounds were predicted to create early season germination microsites when plots were flooded. This treatment is also representative of a hummock-hollow topography that forms naturally in certain wetland types (Doherty and Zedler 2015). The third treatment was a system of linear, parallel ruts with 10-cm relief. This treatment is consistent with microtopography created artificially with machinery, such as a disc roller, sometimes used in mitigation wetlands (Ahn and Dee

2011). The fourth treatment was an untreated control lacking any artificial microtopography.

Seed mix treatments

There were two seed mixes treatments tested: a mixture of habitat-forming perennial graminoids (*D. spicata, P. nuttalliana, B. maritimus, S. acutus,* and *E. palustris*), a graminoid and forb mix (all the graminoid species and several annual and perennial forb species *E. ciliatum R. maritimus*, and *B. cernua)*, and an unseeded control. In the earlier greenhouse study, these perennial graminoid species did not establish when planted in a 1:1 proportion with fast-growing forbs, so we reduced the combined proportion of forb species to 25% in the graminoid + forb mix. The graminoid-only mix contained species in a 1:1 proportion.

Data collection

Plant cover by species was assessed visually within each of the 60 microtopography × seeding treatment sub-plots bi-weekly throughout the growing season of summer 2020. In summer 2021, the same data were collected once during the peak growing season (7/20/2021). We assessed all species present in the subplots, not just seeded species, and categorized species as either native or invasive. Invasive species included *Phragmites australis*, *Polypogon monspeliensis* and *Typha* spp. Although both *Typha* species (*Typha domingensis* and *Typha latifolia*) are considered native to this region, they can displace other desirable native species and 'choke' emergent wetland habitats, and thus are considered undesirable by managers (Rohal 2018). For this reason, we have included *Typha* spp. in the invasive category. Native species included all other species considered native to Great Salt Lake wetlands.

Statistical analyses

For our mixed effects models, fixed effects included seed mix treatment, vegetation component (native or invasive) and microtopography type. Random effects included block, plot within block, and subplot within plot. We ran a generalized linear mixed model on data collected on a peak day in the growing season (7/2/2020). We chose this date because we witnessed forb species, including *R. maritimus*, begin to senesce at the following monitoring date. We ran a separate model on the data collected in 2021 (7/20/2021). We used a summed metric of native and invasive species cover to simplify the model as we could not achieve a satisfactory model fit using individual species cover.

Effect of Microtopography, Water Level, and Seed Mix Composition on Wetland Plant Communities and Invader Suppression (Mesocosm experiment 2021)

Experimental design

In June 2021, we implemented a mesocosm experiment to test the effects of microtopography, water level, and seed mixture on native plant establishment and the suppression of an invader, *Phragmites australis* in a split plot design. Mesocosms were located outside the research greenhouses at Utah State University. The south-facing site received long sun exposure, which is consistent with environmental conditions in Great Salt Lake wetlands where there is little to no shade.

Mesocosms were established in blue plastic children's wading pools with a 1.5 m diameter (1.77 m^2 area) and a 35 cm depth. Microtopography treatment and water level treatment were assigned at the pool level. There were 5 replicates per microtopography (3 levels) x water (2 levels) treatment for a total of 30 pools. Pools were arranged in a completely randomized design in 2 rows of 15 pools. Pools were divided in half with rigid plastic sheets. One half received a graminoid seed mixture, while the other half received a graminoid and forb mixture. Pools were filled with Lambert™ potting soil and mixed with fertilizer (Osmocote™) at the recommended medium rate of 5.9g/L so plants were not nutrient-limited. Soil was measured by volume to ensure uniform amounts between treatments.

Microtopography treatments

There were two distinct microtopography treatments and one untreated control. The microtopography treatments consisted of parallel ruts dug 5 cm and 10 cm below the soil surface and were spaced 10 cm apart. Ruts were chosen because they are more tractable for implementation by restoration practitioners because they can be reproduced at scale in restoration sites with disc rollers.

Water level treatments

There were two water levels, a ‘high’ and a ‘low’. The high-water treatment received 54.5 liters of water a day and the low water treatment received 36.4 liters of water a day. Pools were irrigated automatically each morning with drip tubes that flowed at 9 liters/hour. Water amounts were determined such that the treatment with no microtopography and the low water would have moist soil, while the rutted treatments in low water conditions had saturated soil in the ruts. For the high-water treatment, all pools were flooded. Water levels were monitored daily to ensure the irrigation system was functioning properly and pools were watertight.

Seed mix treatments

Graminoid species sown were *B. maritimus*, *E. palustris*, *S. acutus*, and *D. spicata*. The graminoid and forb mix contained all four perennial species with the addition of five forbs: *E. ciliatum*, *R. maritimus*, *B. cernua*, *S. ciliatum*, and *E. occidentalis*. Seeds were sown at a rate of 5,812 PLS/m^2. This rate was three times the recommended sowing density commonly implemented in the region because this density was shown to suppress *Phragmites* competition more effectively in field experiments (Robinson 2022). Species were mixed in a 1:1 ratio for both seed mix treatments. *Phragmites australis* was sown at a density of 400 PLS/m^2.

Data collection

Percent cover by species was assessed visually once a week. At the end of the experiment (10 weeks after seeding), biomass was harvested, dried at 60°C for 72 hours, and weighed for each species.

Statistical analysis

We ran three mixed effects models on the biomass data. Biomass data were square root transformed and models assumed gaussian distributions. To assess the effect of seed mix treatment, microtopography, and water level on vegetation components, the first model used summed native biomass totals and *Phragmites* biomass between the two seed treatments. In this model, fixed effects included water treatment, microtopography type, seed mix treatment, and vegetation component (native or *Phragmites*). Random effects included pool and pool-half. To assess the success of native species relative to one another, additional models compared individual species biomass within our seed mix treatments. Fixed effects included microtopography, water treatment, and species. Random effects included pool.

Effect of Microtopography on Wetland Plant Communities (Field experiment 2021)

Experimental design

In May 2021, in collaboration with Utah Division of Forestry, Fire & State Lands (FFSL) and the Utah Division of Wildlife Resources (DWR), we implemented and monitored a large-scale seeding to test the effect of artificial microtopography on the establishment of several native wetland species. Approximately 225 kg (496 pounds) of 52% *B. maritimus*, 47% *S. acutus* and *E. palustris* was seeded at a bulk rate of 23.1 kg/acre (47 lbs./acre) near Teal Lake at Farmington Bay WMA, Great Salt Lake, Utah, USA (Figure 2.2). The seeding rate was calculated by dividing kilograms broadcasted seed by the known area covered. This site was chosen because the soil was bare and moist, which has been demonstrated to improve germination success of wetland seeds (Kettenring 2016). Additionally, the site had been previously treated for the removal of *Phragmites* with a three-year cycle of glyphosate application and mowing/trampling remnant litter stands.

Microtopography treatments

Microtopography was implemented with a disc roller, a common tool used in farming to plough soil before sowing seeds. The disc roller created parallel ruts in the soil that are approximately 10 cm deep. This apparatus was attached to a Marsh Master® (Coast Machinery LLC, Baton Rouge, LA) and driven through the site prior to seeding. Then, a broadcast seeder (Herd® 750-3PT), also attached to a Marsh Master® drove adjacent to the disced tracks to ensure seed was broadcast into the created ruts and adjacent areas that were not disced (Figure 2.3a, b) to facilitate comparisons between the microtopography treatments (disced or non-disced).

Data collection

We returned on July 6 and September 20, 2021, to monitor vegetation success (measured by percent cover). We established 50 1-m^2 paired quadrats with half of the quadrats in seeded, disced tracks, and the other half in seeded, un-disced tracks. Paired quadrats were placed 50 cm apart. Two corners were marked with PVC and a flag was placed in the quadrat with no microtopography to ensure relocation for the second monitoring event in September. Quadrat placement was haphazard and spanned a large portion of the seeded area. In each quadrat, we assessed percent cover by species in 10-percent cover classes and standing water depth.

Statistical analyses

We ran a generalized linear mixed model on percent cover of *B. maritimus* at the first monitoring date. We were unable to model *E. palustris* and *S. acutus* because we observed zero to trace cover of both species at both monitoring dates. The fixed effect was microtopography type and the random effect was plot (quadrat pairings were assigned to a plot number). Percent cover was log transformed and the model assumed a normal distribution. We opted for a gaussian distribution (as opposed to the beta used in our other cover models) due to superior model fit. We attempted to include date as a factor in our model but were unable to fit the model without violating assumptions of homogeneous variance, likely because the second monitoring date included too many zero values.

Results

Effect of water level and seed mix on native plant establishment (Greenhouse Experiment 2020)

The model for end-of-experiment cover suggested an interaction between seed treatment and water level (Table 2.1), wherein cover of individual species and total cover of seed mixes was dependent on water level. For most species, cover differed most between the saturated and dry water levels (Table S2.1).

Model results indicated an effect of both seed mix and water level on cover (Table 2.1). All species exhibited highest cover in saturated conditions and lowest cover in dry conditions, with the exception of *Polygonum lapathifolium* (which exhibited the lowest cover in moist conditions) (Figure 2.4). Forb species exhibited higher cover across all water levels than perennial graminoids, and tended to establish and grow faster (Figure 2.6). The graminoid mix exhibited significantly lower cover across all water levels than the graminoid and forb mix. In the graminoid and forb treatment, *Rumex maritimus*, *Polygonum lapathifolium*, *Epilobium ciliatum* and *Bidens cernua* tended to out-grow perennial graminoids across all water levels and account for nearly all of the end-of-experiment cover (Table 2.5). When perennial graminoids were sown in a mix without forbs, *Distichlis spicata* had the highest cover across all water levels (Figure 2.5).

Effect of seed mix and microtopography on plant community dynamics (Field Experiment 2020)

The model from year one (7/22/2020) indicated an interaction between seed mix treatment and vegetation cover (native or invasive) (Table 2.2). Native cover was greater than invasive cover for both seed mixes, but there was no difference between native and invasive cover in the control plots (Table S2.4). There was no evidence for an effect of microtopography on cover (Table S2.3). There was no difference in native cover between the two seeded plots (Table S2.3). Invasive cover did not differ significantly between the treatment plots and the control (Table S2.3).

Native cover in both seeded and control plots was primarily driven by high cover of *R. maritimus* and *D. spicata* (Figure 2.7). Other native species with notable cover (over 10% in some treatments) included *B. maritimus*, *B. cernua*, and forbs of the Chenopodiaceae family (Figure 2.7).

The interaction between seed mix treatment and plant cover (native or invasive) was not observed the following season (Table 2.3). The model for a peak growing season day in 2021 (7/20/2021) indicated no significant interactions between fixed effects (microtopography, seed mix type) and the response variable (percent cover of natives and invasives) (Figure 2.7). Invasive species cover (primarily *Phragmites*, *Typha* spp., and *P. monspeliensis*) increased from 2020 to 2021 regardless of treatment (Figure 2.7). Species seeded the year prior tended to decrease in cover, especially *R. maritimus, B. cernua,* and *D. spicata* (Figure 2.7).

Effect of seed mix, microtopography, invasion pressure, and water level on native plant establishment (Mesocosm Experiment 2021)

The first model (comparing native and *Phragmites* biomass between seed mix *and* microtopography *and* water level) indicated an interaction between seed mix type and water level. Water level (high or low) influenced native biomass, where native biomass was higher in the higher water treatments, but water level did not affect *Phragmites* biomass. Microtopography did not have an observed effect on native or *Phragmites* biomass. There was a difference for both native biomass and *Phragmites* biomass between seed mix treatments. In the graminoid + forb treatment, native biomass that in the graminoid-only treatment. *Phragmites* biomass was higher in the graminoid-only treatment than in the graminoid + forb treatment (Figure 2.9). In the graminoid-only mix, biomass was largely driven by *D. spicata*, *B. maritimus*, and *Phragmites*. The graminoid and forb mixture overall exhibited a different species composition. Biomass and cover in those treatments were largely composed of *B. cernua* and *R. maritimus* (Figure 2.8).

The models comparing individual species biomass within seed treatments also indicated that water treatment influenced end-of-experiment biomass, but not microtopography. In both seed mixes, there was a difference between biomass at the high and low water levels for all species except for *Phragmites* (Figure 2.8). However, for the graminoid and forb treatment, the interaction between biomass and water treatment was weaker. In this treatment, water level only influenced *B. cernua* and *B. maritimus* biomass.

Effect of artificial microtopography on native plant establishment (Field Experiment 2021)

The mixed effects model from the first monitoring date (July 6) indicated an effect of microtopography treatment on *B. maritimus* cover (Table 2.7). On July 6, mean percent cover of alkali bulrush was 2.9% in the disced quadrats compared to 1.4% in the non-disced quadrats. At the first monitoring date, we noticed high rates of *B. maritimus* germination within some disced areas, with the highest observed value at 21-30% cover. At the second monitoring date, cover in both treatments had decreased to less than 1% (Figure 2.10).

Discussion

In disturbed ecosystems, such as extensively invaded wetlands, restoration is complex and requires a multi-faceted approach to establish native plants. Identifying optimal native species to seed, ideal seed mix compositions, and environmental conditions that favor establishment are critical to restore invasion-resistant native plant communities. Here, we tested target restoration species across different seed mix compositions and environmental conditions, specifically moisture and microtopography structure. We identified several native plants (*B. cernua, R. maritimus, D. spicata*) that established well across a range of moisture conditions and suppressed the growth of other sown natives and an invader (*P. australis*). Seed mix composition was also an important determinant of community outcomes—mixes containing forbs *and* graminoids had higher native biomass and lower *P. australis* biomass compared to graminoid-only treatments in the mesocosm experiment. However, in a field setting, sowing native seeds increased native species cover regardless of seed mix composition but was not effective at suppressing invasives as invasive cover did not differ between seeded treatments and the unseeded control. Furthermore, the initial year-1 effect of seeding was temporary as native cover decreased the following year and was far surpassed by invasive cover. To support the establishment of diverse species mixtures and buffer against hydrologic uncertainties, we tested microtopography in three distinct experimental settings (small field plots, mesocosms, and large-scale restoration plots). Although we found that discing (soil ruts) enhanced native species cover (*B. maritimus*) mid-growing season in large-scale restoration plots, the benefit of discing did not persist through the end of the growing season. In the other experimental contexts, microtopography had no observed effect on plant cover or biomass suggesting that this restoration technique may have limited application to restorations in controlled settings. Our findings suggest that species selection, seed mix composition, and soil moisture are significant determinants of plant community reassembly, but their relative importance varies by experimental venue.

Effect of species choice and seed mix composition on native plant establishment and invader suppression

Environmental variability, extreme weather events, and high invasion pressure are barriers to the successful establishment of native plant communities from seed (Byun et al. 2015; Andrus et al. 2018; Shriver et al. 2018). To overcome these barriers, practitioners must identify native species that can establish across a range of different and occasionally extreme environmental conditions and preempt resources from invaders. Our first restoration strategy tested different native species and seed mix compositions with variable growth forms and hydrophytic tolerances across different water levels (Table S2.15). Species were chosen due to their natural abundance in our study system and were often observed growing in dense stands (C. Hebert, *pers. obs.*), indicating high establishment success under natural conditions. We predicted that forb species would generally perform better than perennial monocots across variable water levels.

In some experimental venues (in particular, controlled mesocosm and greenhouse studies), our predictions regarding the performance of faster-growing forbs were supported, but patterns of native community assembly in field settings were less clear. When seeded alone in a greenhouse experiment, forb species emerged faster and had greater cover across all water conditions. In moist and dry conditions in the greenhouse, *D. spicata* was the only graminoid that achieved greater than 25% cover, which was surpassed by all forbs (Figure 2.4). Regarding seed mix composition, we found that the effect of seed mix was also dependent on experimental environment. In controlled environments, seed mixes containing forbs and graminoids had significantly higher biomass and cover than graminoid-only mixes as predicted. In this context, forbs, particularly *B.cernua*, *R. maritimus* and *P. lapathafolium* (greenhouse only) almost entirely suppressed the establishment and growth of graminoids. Seed mixes that included forbs were also more effective at outperforming an invader. Our findings are consistent with other studies showing that utilizing different plant functional groups can suppress invader growth, since increasing functional diversity increases the likelihood that native species niches will overlap with an invader (Byun et al. 2013; Iannone III & Galatowitsch 2008). It should be noted that we used a seeding density of *Phragmites* that is lower than identified seed bank densities in our study system but still represents a level of propagule pressure that could occur at restoration sites (Rohal et al. 2021).

In the field setting (Field experiment in 2020), seeding increased native cover compared to unseeded control plots regardless of seed mix composition. In this experiment, the most prevalent seeded species across both treatments was *D. spicata* (Figure 2.7). Interestingly, *Distlichis spicata* did not compete well against forb species in controlled experiments (Figures 2.5 and 2.8) yet tended to perform well compared to other graminoids and forbs in the field setting. Saltgrass has been documented as a colonizer species after widespread disturbance, which supports its use as a restoration candidate following invasive species control (Allison 1996) and has consistently outperformed other perennial graminoids in similar experimental venues (Robinson 2022). These results demonstrate the importance of testing restoration strategies in different experimental venues (e.g. greenhouse vs. field), because driving mechanisms in greenhouses may be dampened under highly variable field conditions.

Effect of microtopography on native plant establishment

In addition to diversifying the types of species used in restoration, we attempted to buffer against environmental uncertainty by altering the physical environment in which seeds are sown by creating microtopography. In many wetlands, microtopography is an important structural feature that varies moisture and soil chemistry at small spatial scales (Sullivan et al. 2008; Duberstein et al. 2013; Diamond et al. 2020). In wetland restoration, microtopography, often in the form of ruts created by disc rollers, has been shown to improve establishment of native plants (Moser et al 2007). In our experiments, we hypothesized that microtopography would improve germination and establishment success by creating more germination microsites. Hypothetically, ruts would help maintain soil moisture later in the growing season by creating water-retaining depressions while mounds would provide germination sites for species that cannot establish in flooded conditions typically present from spring runoff. In the 2021 field experiment, there was significantly higher cover of *B. maritimus* in disced quadrats compared to un-disced quadrats at the first monitoring date. The seeding area had saturated soils at the time of seeding that subsequently dried out. However, this effect did not persist to the second monitoring date, and high mortality of *B. maritimus* was observed. Seedlings died likely due to soil desiccation at the site. Utah experienced extreme drought conditions in 2021, which likely affected surface water availability in our study system (Williams et al. 2022). The failure of this seeding effort is further support for the use of different species other than hydrophytic graminoids (e.g. bulrushes) when environmental conditions, especially moisture, are uncertain. We observed no effect of microtopography in our 2020 field experiment or 2021 mesocosm experiment. It is unclear why we were unable to replicate the effect we saw at our first monitoring point. In the 2020 field experiment, microtopography may have been ineffective due to the high pressure of invasive species. In the mesocosm experiment, the low water level may have been too moderate to result in strong differences in conditions between the treatments with microtopography and without. In a field setting, more evidence is needed to determine if discing is a useful restoration strategy. At the very least, it is an inexpensive method to help keep seeds in place at a restoration site, which is a critical component to monitoring success.

Future research directions & recommendations for restoration practitioners

Our experiments demonstrate the value of identifying fast-growing, competitive native species to use in restoration. In wetland systems threatened by drought, identifying species that can establish in wider range of moisture conditions is critical. Our research identifies possible first steps in the restoration of native plants in wetlands, but also demonstrated the need for continued intervention. We suggest further research is needed to explore new seeding strategies that build upon these findings. We found that seeding a large mix of species when several outcompete the rest and have a higher tolerance for different moisture conditions may be a waste of seeds, as we observed in multiple experiments where forbs out-competed perennial graminoids. These findings suggest the need to explore a successional seeding approach, wherein sites are seeded multiple times with different seed mixes across growing season and years. For example, once an area has been mostly cleared of an invader, but re-invasion pressure remains high, high seeding densities of fast-growing species could be used to combat high propagule pressure. Then in subsequent years or even later in the same season, re-seeding efforts can focus on higher value species.

Setbacks to our field experiments demonstrate the need to identify optimal environmental conditions to improve establishment of high value (e.g., habitat-forming) species that are difficult to establish from seed. Our findings indicate that for slow-growing perennials, saturated soil conditions throughout the growing season are ideal. Managers will need to be selective when choosing sites and species to optimize performance. Monitoring seeding outcomes can indicate if it will be necessary to re-seed over multiple years to fend off invasion. In addition to re-seeding, other solutions may include increasing sowing density (Adams & Galatowitsch 2008; Barr et al. 2017; Byun et al. 2020) and active management of invasive species. Most likely, a combination of these practices in addition to screening individual species and seed mix compositions is best. Given the scale of restoration needed in wetlands globally, successful interventions are imperative to recover wetland functions and services. Success will depend on multipronged approaches that are unique to site conditions and greater ecosystem settings. Our research offers insights to several approaches and suggests that widening species choice is a promising strategy that can tip the scales of success towards native plant communities.

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Figures & Tables

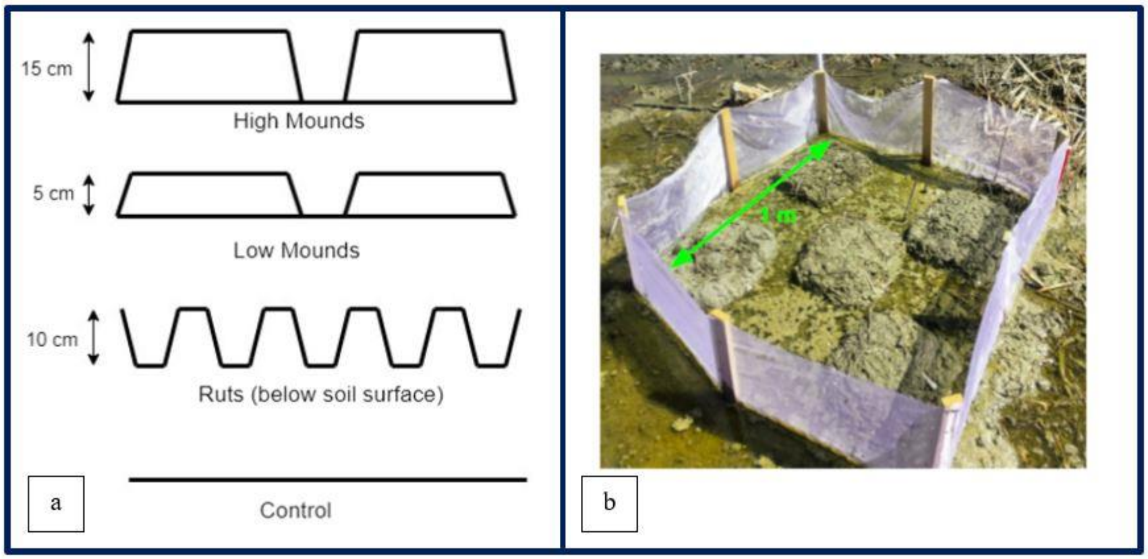

Figure 2.1. (a) The four microtopography treatments and (b) an example of a high mound subplot for the 2020 field experiment testing the effect of microtopography and seed mix composition on native plant establishment (field experiment 2020).

Figure 2.2. Location of the field experiments at Farmington Bay Waterfowl Management Area east of the Great Salt Lake, Utah. The southeast point was the site for the 2020 Field Experiment (small restoration plots) and the northwest point was the site of the 2021 field experiment (largescale discing experiment).

Figure 2.3. (a) The Marsh Master with an attached disc roller; (b) example of broadcast seeding method where machinery was driven adjacent to disced areas and (c) alkali bulrush germination in ruts created by disc roller (Field experiment 2021).

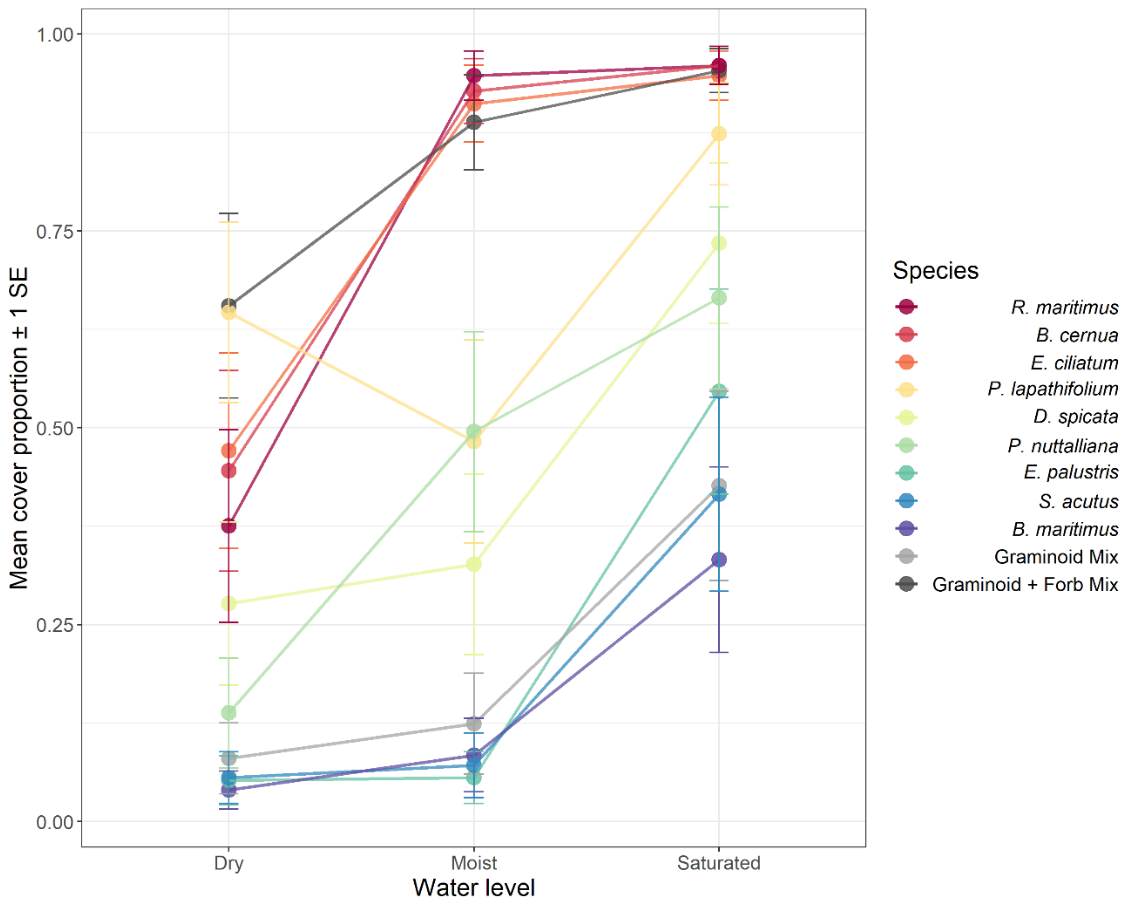

Figure 2.4. Average single species and seed mix treatment cover proportions (model means) across experimental water levels (greenhouse experiment 2020).

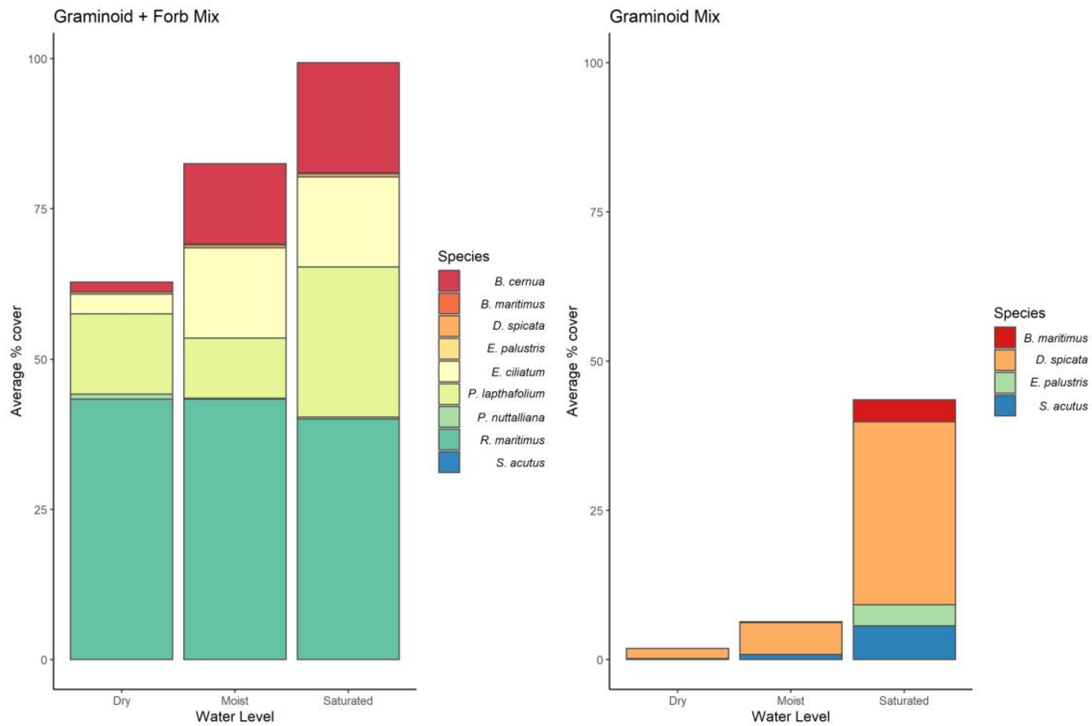

Figure 2.5. Composition of species cover in two seed mix treatments on the last experiment day (*g*reenhouse experiment 2020).

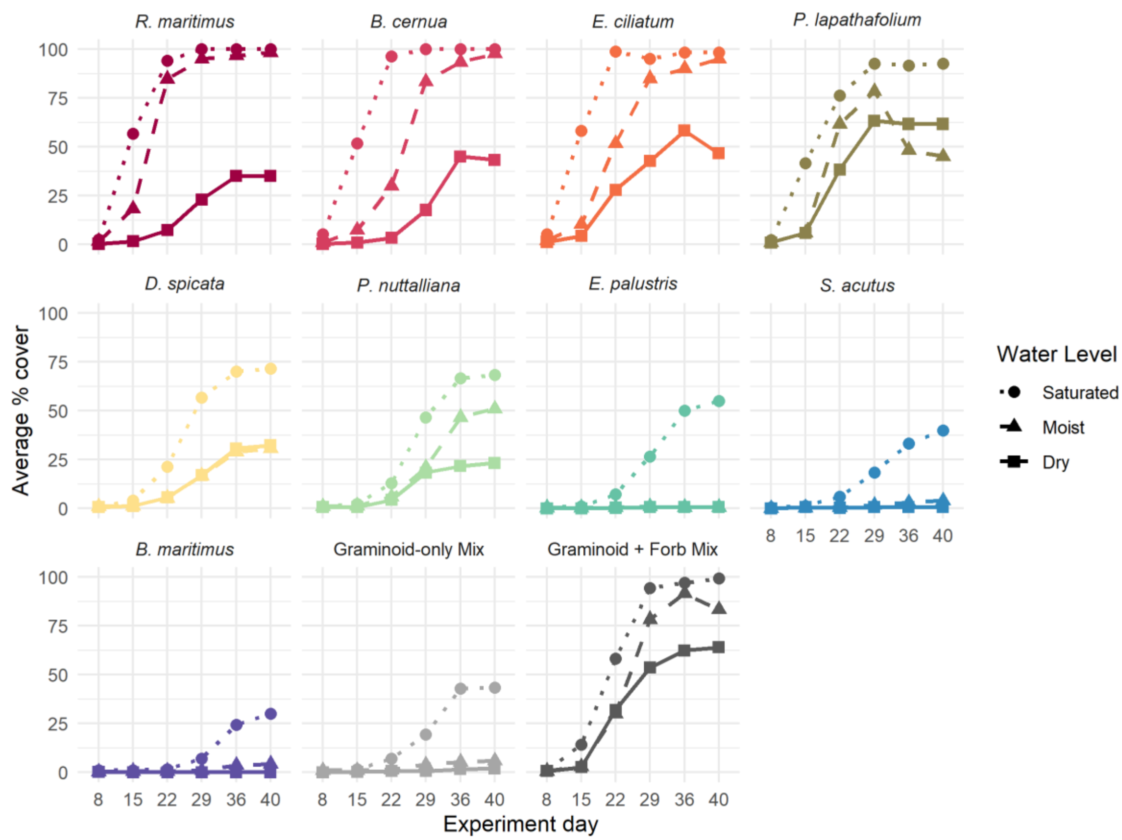

Figure 2.6. Average percent cover of individual species and the two seed mix treatments over time (*g*reenhouse experiment 2020).

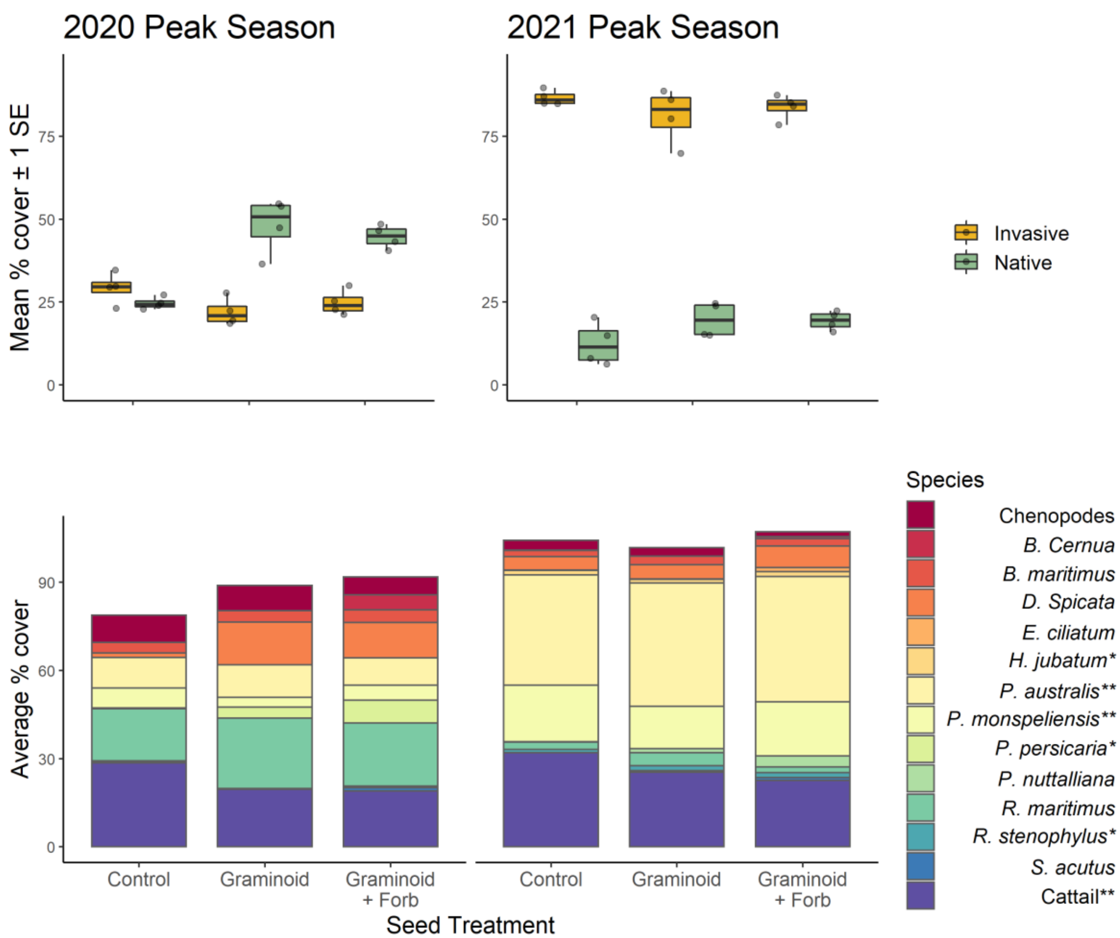

Figure 2.7. Average native and invasive cover (upper panel) and plant community composition (raw means) (lower panel) across seed mix treatments at peak experiment days in 2020 and 2021 as indicated by the mixed effects model. "Control" represents unseeded plots. A single asterisk indicates a non-native species, and two asterisks indicates species considered invasive. All other species are native to Great Salt Lake wetlands (field experiment 2020).

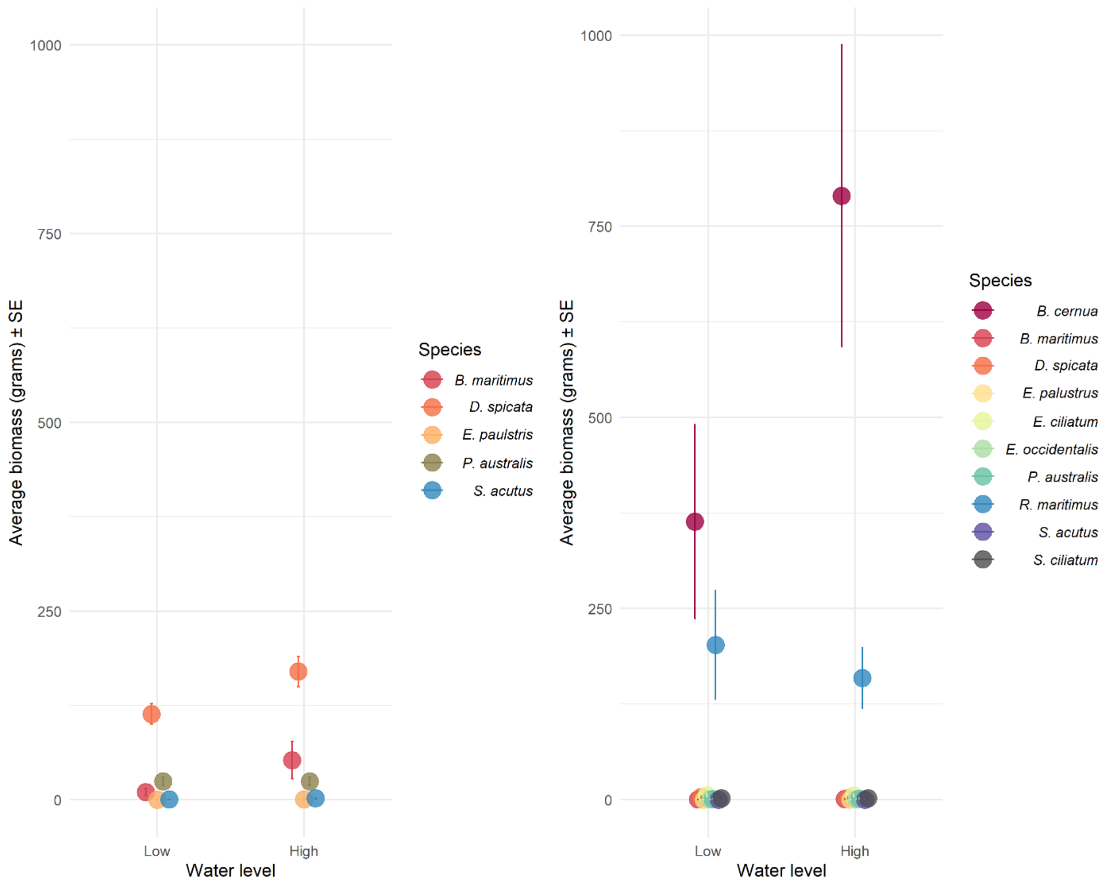

Figure 2.8. Average end-of-experiment biomass for the graminoid seed mix (left) and graminoid + forb mix (right) with values derived from the mixed effects model (mesocosm experiment 2021).

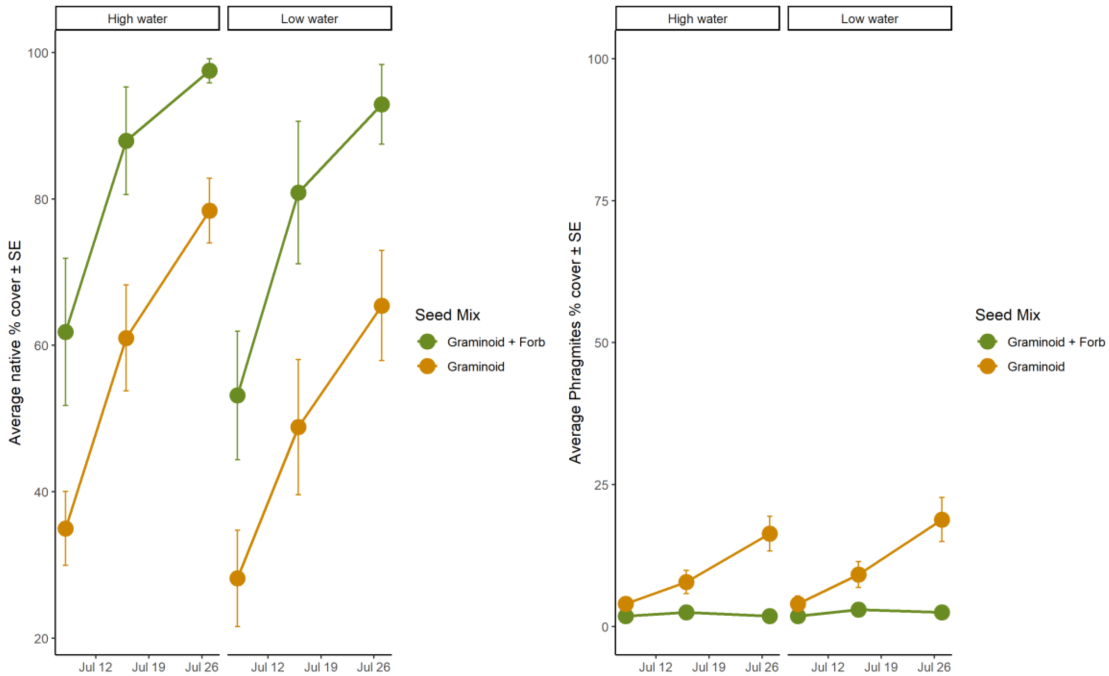

Figure 2.9. (a) Percent cover of native and (b) Phragmites over time at different water levels (mesocosm experiment 2021).

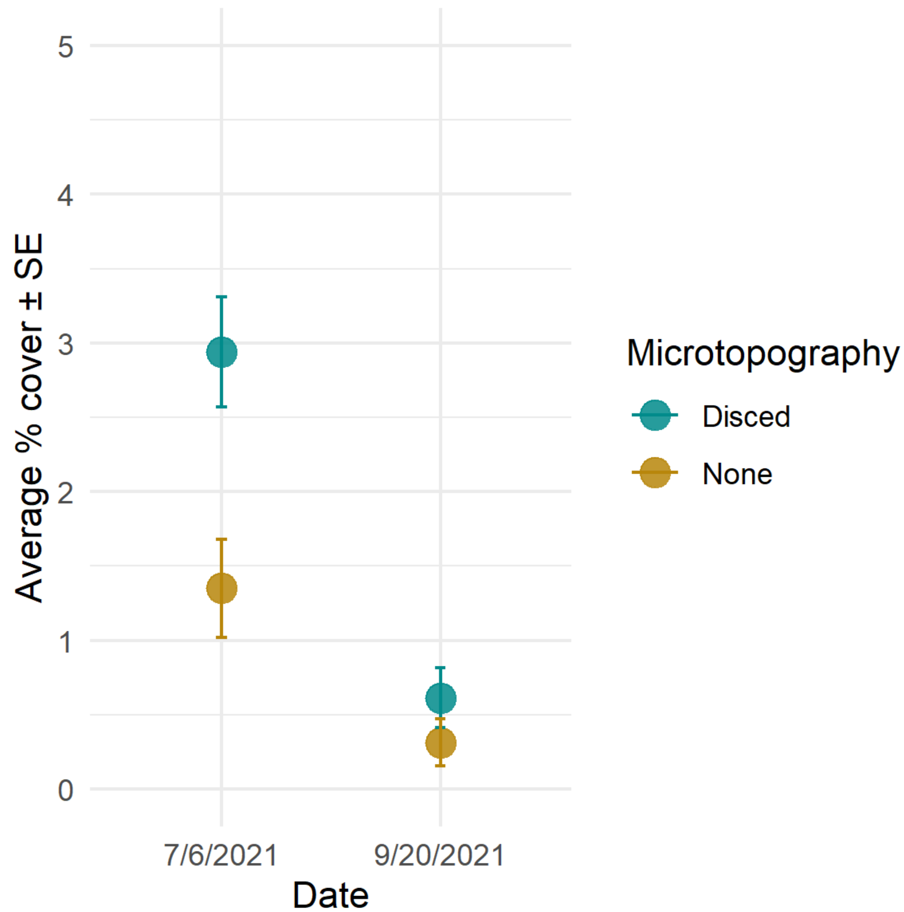

Figure 2.10. Alkali bulrush cover in different microtopography treatments at each monitoring date (field experiment 2021).

Table 2.1. Analysis of Deviance Table (Type II Wald chisquare tests) for mixed effects model on species cover on the last day of the experiment (greenhouse experiment 2020, day 40).

	X^2	***Df***	***Pr(>X^2)***
(Intercept)	0.002298	1	0.96
species	175.7595	10	**<0.001**
water_treatment	102.839	2	**<0.001**
species:water_treatment	31.98388	20	**0.04**

Table 2.2. Analysis of Deviance Table (Type II Wald chisquare tests) for mixed effects model on species cover (field experiment 2020, year 1).

	X^2	***Df***	***Pr(>X^2)***
species	12.15762	1	**<0.001**
seed	3.597453	2	0.17
micro	1.740729	3	0.63
species:seed	12.55937	2	**0.002**
species:micro	0.787241	3	0.85
seed:micro	1.774052	6	0.94
species:seed:micro	0.709183	6	1

Table 2.3. Analysis of Deviance Table (Type II Wald chisquare tests) for mixed effects model on species cover (field experiment 2020, year 2).

	X^2	***Df***	***Pr(>X^2)***
species	177.2135	1	**<0.001**
seed	0.826409	2	0.66
micro	6.367793	3	0.10
species:seed	4.982017	2	0.08
species:micro	2.223464	3	0.53
seed:micro	1.245635	6	0.97
species:seed:micro	2.849947	6	0.82

Table 2.4. Analysis of Deviance Table (Type III Wald chisquare tests) for model comparing total native and *Phragmites* biomass between seed mix treatments (mesocosm experiment 2021).

	X^2	*Df*	*Pr(>X²)*
(Intercept)	2910.305	1	0
seed	152.6218	1	**<0.001**
species	1523.833	1	**<0.001**
water	22.73767	1	**<0.001**
micro	0.042457	2	0.98
seed:species	421.1677	1	**<0.001**
seed:water	2.126216	1	0.14
species:water	26.99702	1	**<0.001**
seed:micro	2.934913	2	0.23
species:micro	2.079189	2	0.35
water:micro	1.277416	2	0.53
seed:species:water	2.423182	1	0.12
seed:species:micro	1.394378	2	0.50
seed:water:micro	0.519292	2	0.77
species:water:micro	4.583309	2	0.10
seed:species:water:micro	0.622138	2	0.73

Table 2.5. Analysis of Deviance Table (Type III Wald chisquare tests) for model comparing species biomass in the graminoid-only seed mix (mesocosm experiment 2021).

	X^2	*Df*	*Pr(>X²)*
(Intercept)	180.4435	1	**<0.001**
species	1667.973	4	0
water	25.26894	1	**<0.001**
micro	0.730254	2	0.69
species:water	36.95006	4	**<0.001**
species:micro	12.33507	8	0.14
water:micro	1.277586	2	0.53
species:water:micro	12.83646	8	0.12

Table 2.6. Analysis of Deviance Table (Type III Wald chisquare tests) for model comparing species biomass in the graminoid and forb seed mix (mesocosm experiment 2021).

	X^2	***Df***	***Pr(>X^2)***
(Intercept)	15.23234	1	**<0.001**
species	2710.718	9	0
water	3.884525	1	**0.05**
micro	3.718894	2	0.16
species:water	17.34438	9	**0.04**
species:micro	23.15356	18	0.18
water:micro	0.219899	2	0.9
species:water:micro	19.5026	18	0.36

Table 2.7. Analysis of Deviance Table (Type III Wald chisquare tests) for model comparing alkali bulrush cover and microtopography treatments (field experiment 2021).

	X^2	***Df***	***Pr(>X^2)***
micro_treatment	13.98123	1	**<0.001**

CHAPTER III

MICROTOPOGRAPHY OF GREAT SALT LAKE WETLANDS

Abstract

Microtopography (change in soil surface elevation at the scale of individual plants) is an important structural feature in many wetland ecosystems. Microtopography affects ecological functions in wetlands and is often driven by particular plant species. In the Intermountain West, there is little information on wetland microtopography and associated plant communities. Here, we conducted an observational study across different wetland types (emergent, wet meadow, playa) in Great Salt Lake wetlands, Utah (n=14 sites). We found that emergent wetlands had higher roughness and relief values than wet meadows and playas. An ordination analysis (NMDS) suggested that metrics of microtopography were positively associated with emergent wetlands that had not been grazed, which were primarily composed of threesquare bulrush (*Schoenoplectus americanus*). These findings suggest that microtopography may be associated with species in this system, but more evidence is needed to strengthen this conclusion. This research is a foundation for the further exploration of microtopography in similar wetland types and provides valuable ecosystem knowledge for a continentally significant wetland system in which conservation and restoration is a high priority.

Introduction

Wetlands are valued for ecosystem services including flood retention, water quality improvement, groundwater recharge, and supporting biodiversity (Zedler & Kercher 2005; Keddy et al. 2009). In wetlands, microtopography is a structural feature that influences many of the ecological functions underlying these services. Microtopography is a small change in elevation at the scale of individual plants (<1 m) which creates vertical relief and increases surface roughness (Huenneke & Sharitz 1986; Titus 1990; Moser et al. 2007) (Figure 3.1). Microtopography influences soil moisture variability, biogeochemical soil properties, nutrient cycling, and vegetation structure (Lindholm & Markkula 1984, Bubier et al. 1993) and has been documented in many wetland types including bogs, forested swamps, coastal marshes, and others (Sullivan et al. 2008; Duberstein et al; 2013; Diamond et al. 2021). In many wetland systems, microtopography appears to be driven by plant species (Fogel et al. 2004; Stribling et al. 2007; Diamond et al. 2020). Despite robust evidence demonstrating the importance of microtopography, structural wetland features and associated plant communities have been seldom described in arid wetlands of the western U.S., a region where naturally scarce aquatic resources are essential to healthy landscapes.

We conducted a study to characterize microtopography in one of the largest wetland complexes in the Great Basin of the Western U.S., Great Salt Lake wetlands. The Great Salt Lake is the largest saline lake in the Western hemisphere (Arnow & Stephens 1990). Along its vast eastern shoreline is a patchwork of emergent marshes, wet meadows, and playas that comprise approximately 70% of Utah’s wetlands (Downard et al. 2017; U.S. Fish & Wildlife Service 2011). Historically, these wetlands were deltas of three major tributaries: the Bear, Weber, and Jordan Rivers (Downard et al. 2014; U.S. Fish and Wildlife Service 2020). Although these rivers still flow into the Great Salt Lake, the surrounding wetlands are maintained by a vast system of impoundments with water control structures like headgates, dikes, and cement channels (Downard et al. 2014; U.S.

Fish and Wildlife Service 2020). Other major alterations to this system include the extensive invasion of Eurasian common reed, *Phragmites australis* (Cav.), which covers an estimated 23,000 acres (Long et al. 2017). *Phragmites* aggressively outcompetes native vegetation and establishes itself in dense, monotypic stands that spread vegetatively and by seed (Kettenring & Mock 2012; Kettenring et al. 2016). *Phragmites* is also an ecosystem engineer due to its high stem density that traps sediment (Rooth & Stevenson 2000). Increased sediment loads in other wetland systems resulted in lower species richness, organic matter, and was correlated with less microtopographic relief (Werner & Zedler 2002). Given the extensive invasion of an ecosystem engineer and prolific hydrologic alterations in Great Salt Lake wetlands, it is possible that microtopographic features present in this system historically have been altered. Thus, the objective of this research was to quantify current microtopography in Great Salt Lake wetlands and determine whether metrics of microtopography are associated with certain plant species, specific wetland types, or other site metrics such as site grazing status. We assessed microtopography as two quantifiable metrics, roughness and relief, and conducted plant surveys across the several wetland types adjacent to the Great Salt Lake. This is the first research effort to formally characterize microtopography in Great Salt Lake wetlands, or any wetland ecosystem in the Great Basin of the United States. By doing so, we enhance knowledge of a valuable wetland ecosystem, which is a continentally significant resource for birds (Aldrich & Paul 2004). Restoration of native plant communities that provide high-value wildlife habitat is a priority in Great Salt Lake wetlands (Kettenring et al. 2020; Tarsa et al. 2022). Determining the relationship between microtopography and plant communities in this system enhances knowledge of reference conditions for planning and implementing restoration objectives.

Methods

Between summer 2020 and fall 2021, we conducted an observational study to characterize microtopography and plant communities across 14 Great Salt Lake wetland sites (Figure 3.1). Sites were chosen based on accessibility (distance to roads), and uniformity of vegetation type. The objective of this study was to discern whether any dominant plant species or specific wetland types (emergent marshes, wet meadow, playa) were associated with microtopography in Great Salt Lake wetlands. Emergent marshes are semi-permanently wetlands flooded with tall, hydrophytic vegetation including bulrushes and cattails. Wet meadows are temporarily to semi-permanently flooded wetlands with shorter vegetation, including grasses, rushes, sedges, and forbs. Playas are temporarily and shallowly flooded areas that typically have short, sparse vegetation (Downward et al. 2017). Most sites were wet meadows, as these contain a larger diversity of plant species (Downward et al. 2017). Only two playa sites were sampled as these areas are often more sparsely vegetated and appear flat. Sampled areas included state (Public Shooting Grounds Wildlife Management Area (WMA), Howard Slough WMA, Ogden Bay WMA, Harold Crane WMA, WMA = Wildlife Management Area), federal (Bear River Migratory Bird Refuge), and private lands (North Point Duck Club, The Nature Conservancy's Great Salt Lake Shorelands Preserve).

At each site, a center point was marked with a GPS unit. Plot centers were chosen to ensure uniformity in the plant community. For example, if a site transitioned from a cattail-dominated emergent marsh to a sedge meadow, the plot center was chosen so the site remained within one wetland type. From the center point, three 25-m transects were laid out at 0°, 120°, and 240°, creating a spoke pattern to guide plant community and microtopography data collection (Figure 3.4d). The plant community was characterized using a line-point intercept method along each transect by counting the number of species and the number of times it is "hit" by the rods to derive species cover. The pin was dropped every 0.5 m for a total of 50 measurements per transect. Each plant was identified to species level. These data were used to determine species richness and abundance by site. Percent cover by species by site was then derived by dividing the number of hits by the total number of points (typically 150 per site) (Godínez-Alvarez et al. 2009).

Microtopography was characterized with a profilometer (Leatherman 1987). There are several advantages to using a profilometer compared to more high-tech remote sensing methods such as LIDAR or terrestrial laser scanning (TLS), where measurements are easily skewed by vegetation and standing water. A profilometer is not impacted by the presence of standing water, and it is apparent when the pins are skewed by dense vegetation. Furthermore, most literature quantifying microtopography with remote sensing methods only measure bare surfaces, which suggests this approach is not ideal for this study system where sites often have dense vegetation (Stovall et al. 2019, Thompsen et al. 2015). The profilometer was 50 cm tall and 1m wide with 250 vertical spring steel rods spaced 3 mm apart (Figure 3.3). It has a small level built into the apparatus to level each measurement to ensure slope does not skew measurements. Once the profilometer was placed on the transect, we adjusted individual pins to ensure they were contacting the soil surface but did not apply enough pressure for pins to penetrate the ground. Once the frame was steadied and each pin was adjusted, a photo was taken of the profile. After photos were collected from each site, image analysis software (ImageJ™) was used to calculate roughness (total length of the pin profile divided by the width of the profilometer) and relief (total change in elevation) (Moser et al. 2007) (Figure 3.2, 3.3). Generally, microtopography measurements were taken at the end of the growing season after plant communities were surveyed, as it was easier to adjust pins once the vegetation senesced.

All statistical analyses were performed in R version 4.0.3 (R Core Team 2021). We used the ‘vegan’ package to conduct non-metric multidimensional scaling (NMDS) of plant communities with topographic metrics (median relief and median roughness) overlaid as environmental vectors using the ‘metaMDS’ function. This allowed us to see if metrics of microtopography were more associated with some sites. We could also assess which dominant plant species are more strongly associated with microtopography. Median values of relief and roughness were chosen due to heterogenous variance between sites, so a non-parametric value was preferred over the mean value. We reduced the number of dimensions to achieve an acceptable stress value (<0.2) and removed rare species (<5% percent cover at a site) (McCune et al. 2002). We investigated additional vegetation and disturbance metrics that might be associated with microtopography and included these data as vectors in the ordination. These metrics included grazing status (indicated by remnant cow dung, grazed vegetation, deep hoof prints e.g. Figure 3.4a), number of species per site, percent cover native, percent cover invasive, percent litter and wetland type. Non-native, invasive species were *Phragmites australis, Lepidium latifolium,* and *Polypogon monspeliensis* (Downard et al. 2017; Kettenring et al. 2020).

Results

Median relief values ranged from 3.9 to 11.2 cm and median roughness values ranged from 1.09 to 1.29 (Figure 3.5). The NMDS (k = 2; stress = 0.15; Figure 6) suggested that most communities of the same wetland type had similar plant community composition since they were closer in the ordination space. Metrics of microtopography (median roughness and median relief) had the longest vectors in the ordination space, suggesting a stronger association with plant communities in the ordination space. Grazing status vectors. Median relief appears to be more strongly associated with emergent wetlands, particularly sites with a higher proportion of *Schoenoplectus americanus*. On the contrary, wet meadow and playa sites appear to be negatively correlated with median relief and median roughness. Some dominant species such as *Bolboschoenus maritimus*, *Salicornia rubra*, and *Distichlis spicata* (which appear more frequently in wet meadows and playas) also appear to be negatively associated with median relief and median roughness. The environmental vectors also suggest some association with sites that were not grazed and median relief.

Composition of plant communities contained mostly native species; the highest percent cover of invasive species was 48.7%. Species richness ranged from 4 to 21 species (Table 3.1). Dominant species at emergent sites included *Typha* spp., *Schoenoplectus americanus,* and *Schoenoplectus acutus.* In wet meadow sites, dominant species included *Distlichlis spicata* and *Bolboschoenus maritimus.* Dominant species at playa sites included *Distichlis spicata* and *Salicornia rubra.* Invasive species *Phragmites australis* and *Polypogon monspeliensis* appeared most frequently in wet meadows. Out of

14 sites, we found evidence of grazing at 12 sites. Two sites at Public Shooting Grounds WMA were un-grazed.

Discussion

Microtopography is an important structural feature in wetlands because it influences nutrient cycling, biogeochemical soil properties, soil moisture variability and hydrology (Sullivan et al. 2008; Zona et al. 2011; Duberstein et al. 2013; Diamond et al. 2020). In many of these systems, microtopography is associated with particular plant species (Fogel et al. 2004, Stribling et al. 2007, Diamond et al. 2019). In arid wetlands of the Great Basin in the Western U.S., there is little information about microtopography and associated plant communities. To address this knowledge gap, we conducted a preliminary observational study to characterize two metrics of microtopography (roughness and relief) and plant communities in Great Salt Lake wetlands. We also sought to test the use of a profilometer, a low-tech methodology for measuring microtopography (Figure 3.3). Our findings indicate some associations between microtopography, wetland types, plant communities, and grazing status in the Great Salt Lake wetland complex. Specifically, we found that metrics of microtopography were positively associated with emergent wetlands, especially those which had not been grazed.

Great Salt Lake wetlands are a patchwork of different wetland types that vary largely due to hydrology and salinity (Downard et al. 2017). As such, different wetlands tend to have differing plant communities and varying degrees of microtopography. Playas and wet meadows had more subtle microtopography while emergent wetlands had average relief values nearly twice as large as playas and wet meadows (although we had a limited sample size of playa sites). Roughness values followed a similar pattern as median relief values per site (Figure 3.5). Given these findings, it is unsurprising that median relief and roughness are more strongly associated with emergent wetlands in the NMDS. This association appears to be driven largely by bulrush species *Schoenoplectus americanus* (Figure 6). We were unable to find specific references to this species or genus and wetland microtopography. However, other species in the same family (Cyperaceae such as *Carex* spp. and *Eriophorum* spp.) are associated with tussock formation in bogs and sedge meadows (Costello 1936; Chapin III et al. 1979; Peach & Zedler 2006). Interestingly, other bulrush species that are common in our study region, *Bolboschoenus maritimus,* and *Schoeoneplectus acutus,* were not strongly associated with metrics of microtopography, but this is likely to low abundance of these species at our sites relative to *S. americanus*.

Our findings also indicated an association between microtopography and sites that had not been grazed. This pattern made us question whether grazing in this system, which occurs across most state- and privately-owned lands in Great Salt Lake wetlands (Duncan et al. 2019; Kettenring et al. 2020), obscures natural patterns of microtopography. In some sites, remnant hoofprints formed their own type of microtopography (Figure 4a). There is limited evidence in the literature regarding the effect of grazing on wetland microtopography. In a swamp meadow, researchers found that grazing altered soil respiration patterns in microtopographic highs and lows (Zhao et al. 2022). In upland systems, there is evidence that grazing erodes microtopography, leading to soil erosion (Nash et al. 2004). Increased erosion and sedimentation in known to degrade microtopography in wetlands, which can in turn alter wetland hydrology (Werner &

Zedler 2002; Doherty & Zedler 2015). Since we did not investigate soil respiration or sedimentation in relation to microtopography, there are remaining questions about how grazing impacts microtopography in this system, and what the broader implications of those effects are to ecosystem functioning. In Great Salt Lake wetlands, there are documented benefits to livestock grazing, namely, to control the invasive grass, *Phragmites australis* (Silliman et al. 2014, Duncan et al. 2019). Land managers may be reluctant to alter grazing practices unless there is a clear negative effect of grazing.

Regarding metrics of roughness and relief, we found the profilometer to be an effective tool for capturing ground surface measurements and recommend its usage in systems with dense vegetation and remnant litter mats. However, we recognize the limitations of this low-tech tool due to the tedious and time-consuming nature of measurements i.e., adjusting the pins at every measurement, which limited the number of sites we were able to sample over two field seasons. Additionally, it was challenging to gather ground surface measurements of emergent wetlands which remained flooded year-round, especially if the surface substrate was mucky.

More sites should be surveyed to strengthen or disprove the association between emergent wetlands and bulrush species with microtopography in this system. Sites should be surveyed that have higher proportions of other bulrush species, not just *Schoenoplectus americanus*. Expanding this study to other wetland complexes in the arid West would also increase the generalizability of these findings to the broader region. The more we know about these ecosystems, the more we can improve management and conservation strategies. There is evidence that microtopography can be a useful restoration tool by increasing biodiversity and buffering against hydrologic uncertainties in [add brief naming of wetland types] wetlands in other regions in North America (Vivian-Smith 1995, Doherty and Zedler 2005, Moser et al. 2009). An additional research opportunity is to quantify the specific functions of microtopography in Great Salt Lake wetlands, where restoration is a major priority for managers and researchers (Rohal et al. 2019, Rohal et al. 2021). If structural features such as microtopography add demonstrable ecosystem functions to wetlands, microtopography could be considered part of an ideal reference state when developing restoration objectives and in choosing restoration interventions (e.g., discing).

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Figures and Tables

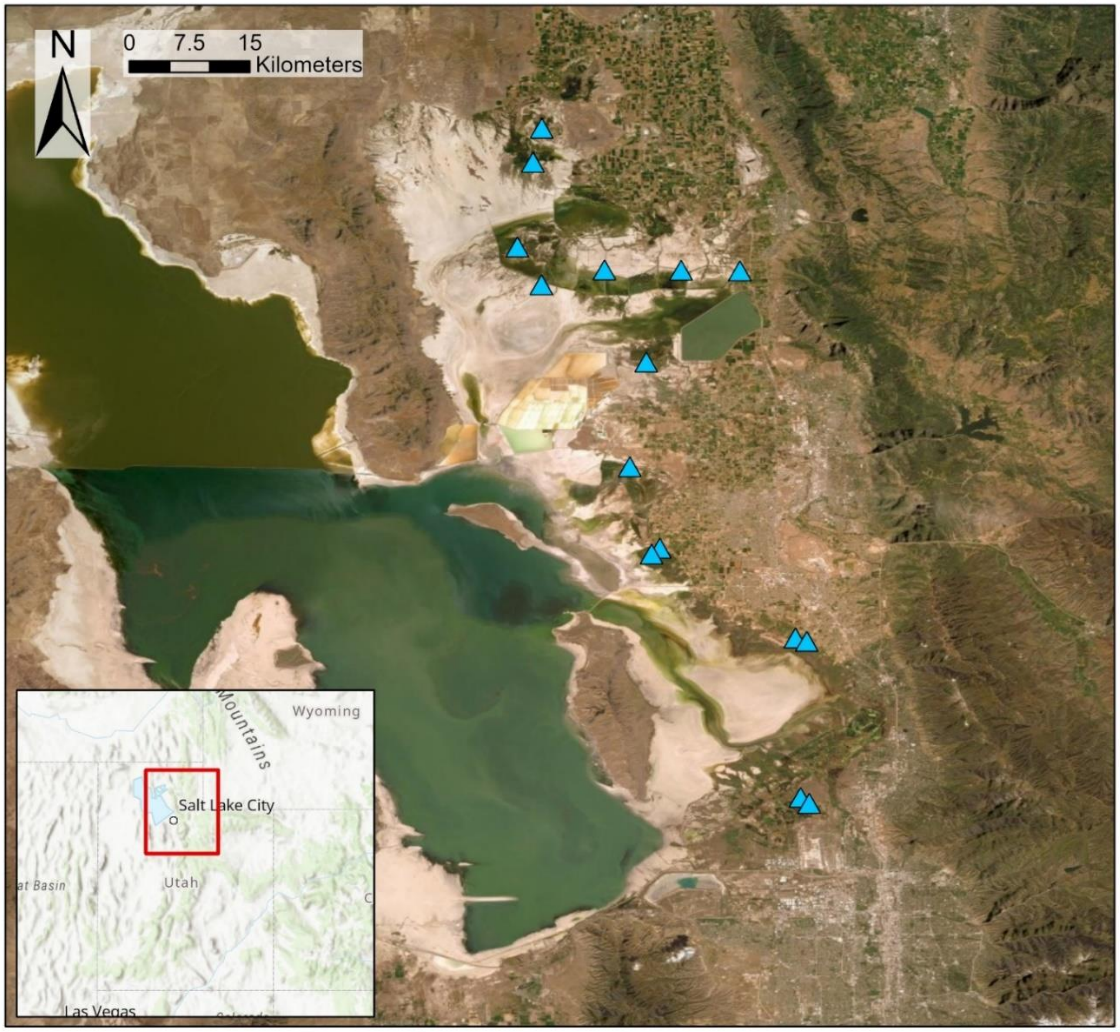

Figure 3.1. Sampled sites (denoted with blue triangles) across Great Salt Lake wetlands (n = 14).

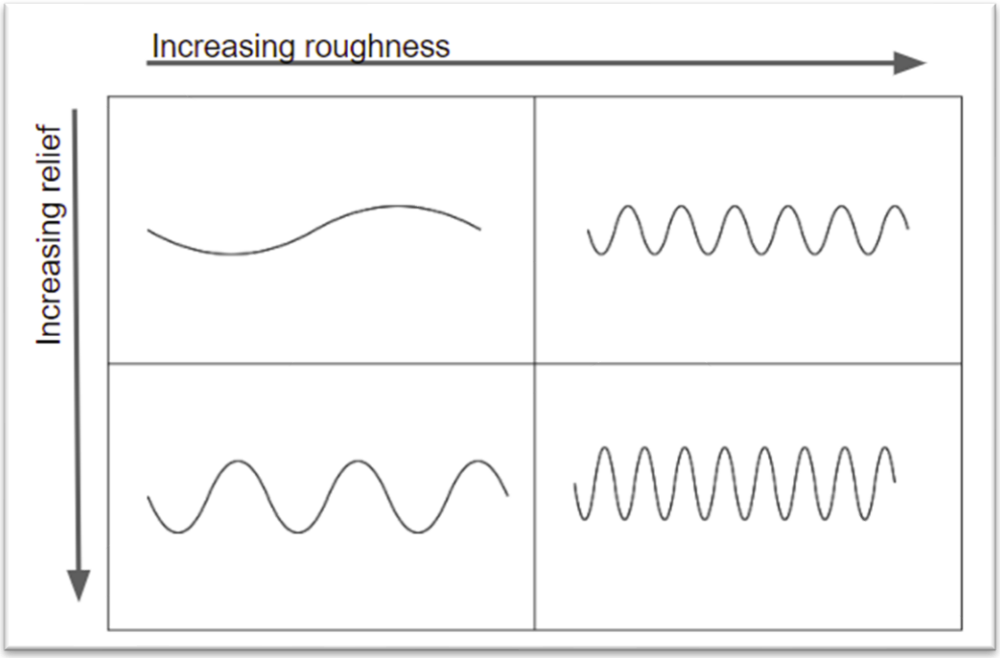

Figure 3.2. Relief and roughness are used to quantify microtopography (Adapted from Moser et al. 2007).

Figure 3.3. A profilometer was used to measure microtopography shown here with examples of roughness and relief.

Figure 3.4. Example of microtopography created by (a) hoofprints, (b) alkali bulrush (*Bolboschoenus maritimus*) and (c) hardstem bulrush (*Schoenoplectus acutus*). (d) an example of the site center point with spoke-pattern transects used in the sampling design.

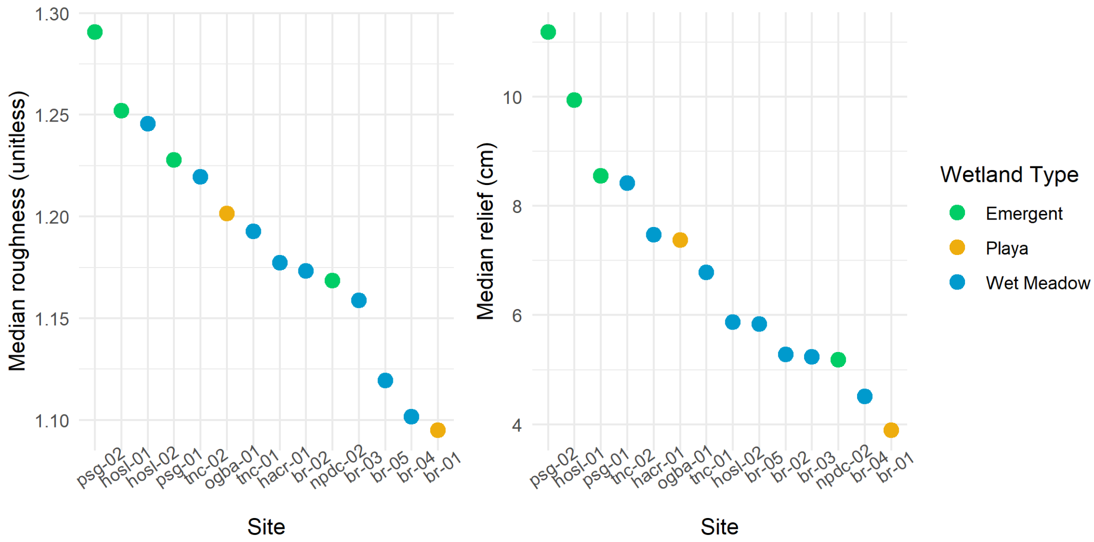

Figure 3.5. Median relief and roughness values for each site with wetland type denoted.

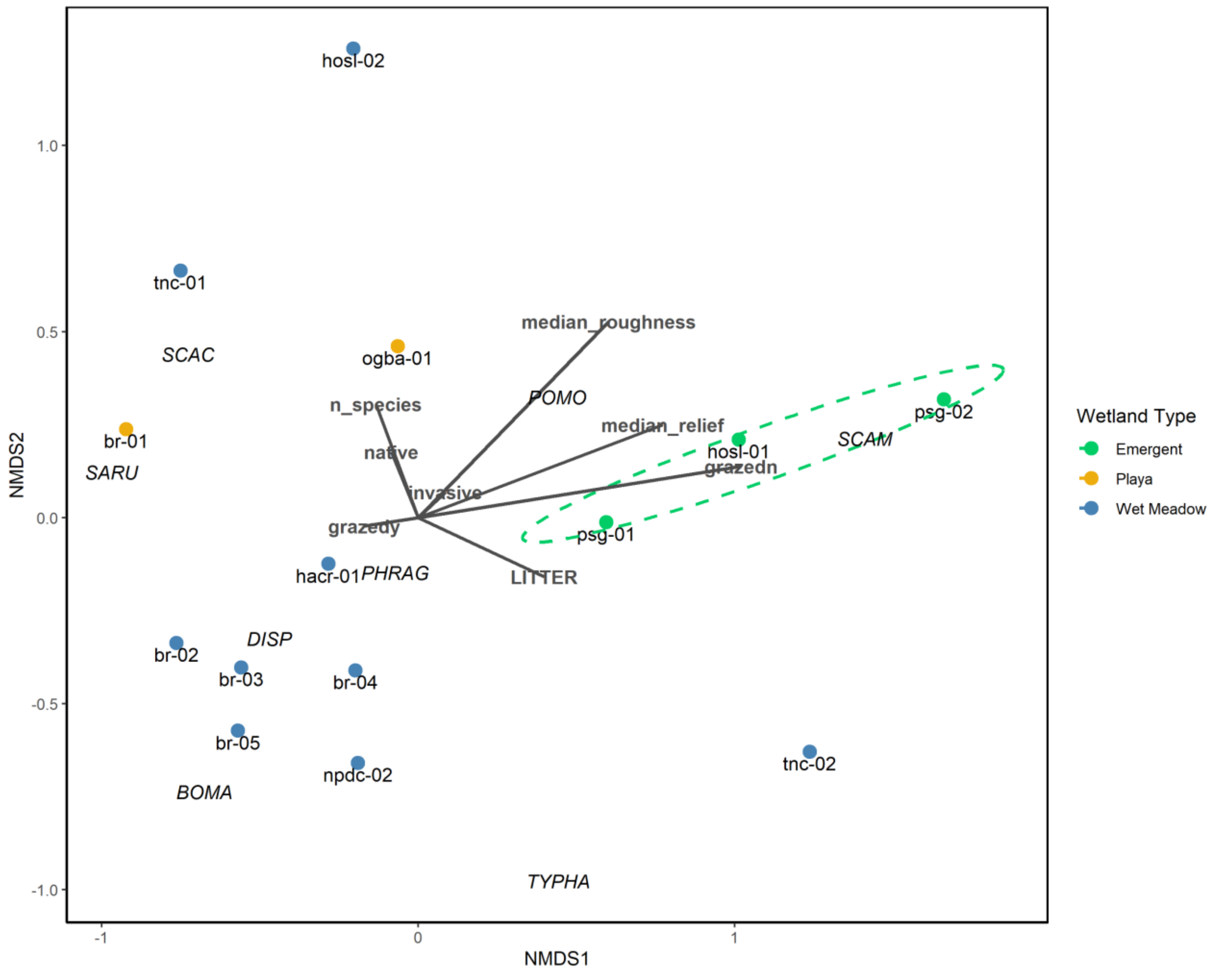

Figure 3.6. NMDS of plant communities grouped by wetland type. Species codes are: BOMA: *Bolboschoenus maritimus*, DISP: *Distichlis spicata*, PHRAG: *Phragmites australis*, POMO: *Polypogon monspeliensis*, SARU: *Salicornia rubra*, SCAC: *Schoenoplectus acutus*, SCAM: *Schoenoplectus americanus*. LITTER: litter (dead, un-decomposed plant material).

Table 3.1. Site characteristics used as environmental vectors in NMDS.

Site	# Species	% Native	% Invasive	% Litter	Grazed	Wetland type	Site name
br-01	6	89	0	29	yes	playa	Bear River Migratory Bird Refuge
br-02	5	80	0.5	53	yes	wet meadow	Bear River Migratory Bird Refuge
br-03	5	53	1	99	yes	wet meadow	Bear River Migratory Bird Refuge
br-04	11	87	1	98	yes	wet meadow	Bear River Migratory Bird Refuge
br-05	10	85	20	87	yes	wet meadow	Bear River Migratory Bird Refuge
hacr-01	5	62	33	8	yes	wet meadow	Harold Crane WMA
hosl-01	10	147	35	88	yes	emergent	Howard Slough WMA
hosl-02	12	45	1	89	yes	wet meadow	Howard Slough WMA
npdc-02	10	53	0.5	95	yes	wet meadow	North Point Duck Club
ogba-01	10	28	47	74	yes	playa	Ogden Bay WMA
psg-01	4	67	0	100	no	emergent	Public Shooting Grounds WMA
psg-02	4	71	0	94	no	emergent	Public Shooting Grounds WMA
tnc-01	21	141	0	98	yes	wet meadow	Nature Conservancy Shorelands Preserve
tnc-02	11	24	13	100	yes	wet meadow	Nature Conservancy Shorelands Preserve

CHAPTER IV

SUMMARY AND CONCLUSIONS

Restoration of native plant communities is hard to achieve, in part due to environmental uncertainty and high likelihood of re-invasion by non-native species (Simberloff 2009; Cassey et al. 2018; Carr et al. 2019). To overcome these barriers, we investigated several restoration strategies novel to our study system. The first of these strategies was to identify species that could germinate, establish, and grow faster in a wider range of soil moisture conditions, and to test different seed mix compositions. Lastly, we explored whether artificial microtopography could improve native plant establishment. To augment our investigation of microtopography, we conducted an observational study to characterize microtopography and associated wetland types and plant communities in Great Salt Lake wetlands, as little was known about microtopography in this system.

In our second chapter, we identified several species native to our study system that appear to perform well in a variety of conditions. These species include *Bidens cernua*, *Rumex maritimus,* and *Distichlis spicata. Bidens cernua* and *R. maritimus* performed especially well in the greenhouse and mesocosm studies, where they suppressed the growth of other seeded species, including an invader (*Phragmites australis*). *Distichlis spicata* performed best out of all the perennial graminoids and had higher establishment success in the field than other sown natives. The remaining species that we tested tended to perform poorly in both field and experimental contexts. Our findings support widening species choice and using more functionally diverse seed mixes (perennial graminoids and annual forbs together) as promising restoration strategies.

Regarding the use of microtopography as a restoration strategy, discing appeared promising initially given the higher germination rates of *B. maritimus* in disced tracks, but the effect did not persist, and seeded species had high mortality at the end of the growing season. The desiccation of our restoration site confirms the challenges of environmental unpredictability, especially concerning soil moisture. However, discing is an inexpensive, low-effort method. Given the findings at our first monitoring date, discing should not be ruled out as a restoration intervention.

In our third chapter, we conducted an observational study to identify the relationship between microtopography, wetland types, and plant community composition in Great Salt Lake wetlands. We identified an association between metrics of microtopography (roughness and relief), grazing status, and emergent wetlands with high proportions of *Schoenoplectus americanus*. Given the documented importance of microtopography in wetlands, further observational studies should be conducted to investigate natural patterns of microtopography in the various wetlands around the Great Salt Lake and determine the extent to which grazing affects vegetation structure. Furthermore, the specific ecosystem functions associated with microtopography (e.g., nutrient cycling, soil moisture variability, and respiration etc.) should be identified to understand how they may relate to microtopography.

The successful, long-term restoration of native plant communities in necessary to improve wetland functioning. Here, we offer strategies to increase the likelihood of native plant establishment and invader suppression. Managers will likely have to employ several techniques, in addition to the ones identified in this research, across multiple growing seasons to ultimately achieve invasion-resistant plant communities.

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APPENDIX

Appendix A: Supplemental Information for Chapter II

Table S2.1. Pairwise comparisons from the mixed effects model showing water comparisons of individual species cover and total cover of seed mixes (greenhouse experiment 2020).

contrast	species	estimate	SE	df	t.ratio	p.value
WP1 - WP2	BICE	0.62961	0.823804	97	0.764272	0.73
WP1 - WP3	BICE	3.400043	0.777179	97	4.37485	**<0.001**
WP2 - WP3	BICE	2.770433	0.764259	97	3.62499	**<0.001**
WP1 - WP2	BOMA	1.68723	0.765109	97	2.205215	0.08
WP1 - WP3	BOMA	2.48388	0.779898	97	3.184878	**0.01**
WP2 - WP3	BOMA	0.79665	0.821475	97	0.96978	0.6
WP1 - WP2	DISP	1.739802	0.699175	97	2.488365	**0.04**
WP1 - WP3	DISP	1.97697	0.698137	97	2.831781	**0.02**
WP2 - WP3	DISP	0.237169	0.692188	97	0.342636	0.94
WP1 - WP2	ELPA	3.016825	0.780433	97	3.865579	**<0.001**
WP1 - WP3	ELPA	3.076634	0.786259	97	3.913001	**<0.001**
WP2 - WP3	ELPA	0.059809	0.828252	97	0.072211	1
WP1 - WP2	EPCI	0.555973	0.81801	97	0.679666	0.78
WP1 - WP3	EPCI	3.004733	0.763347	97	3.93626	**<0.001**
WP2 - WP3	EPCI	2.448759	0.745141	97	3.286304	**<0.001**
WP1 - WP2	MIX	0.955881	0.81959	97	1.166292	0.48
WP1 - WP3	MIX	2.383211	0.77625	97	3.070161	**0.01**
WP2 - WP3	MIX	1.42733	0.760795	97	1.876103	0.15
WP1 - WP2	PMIX	1.65571	0.727293	97	2.276536	0.06
WP1 - WP3	PMIX	2.139881	0.743892	97	2.876603	**0.01**
WP2 - WP3	PMIX	0.484171	0.801327	97	0.604211	0.82
WP1 - WP2	POLA	1.999332	0.745247	97	2.682778	**0.02**
WP1 - WP3	POLA	1.326551	0.733099	97	1.80951	0.17
WP2 - WP3	POLA	-0.67278	0.677945	97	-0.99238	0.58
WP1 - WP2	PUNU	0.703705	0.685138	97	1.0271	0.56
WP1 - WP3	PUNU	2.519296	0.74571	97	3.378385	**<0.001**
WP2 - WP3	PUNU	1.815592	0.736178	97	2.466241	**0.04**
WP1 - WP2	RUMA	0.292172	0.828577	97	0.352619	0.93
WP1 - WP3	RUMA	3.689532	0.785144	97	4.699178	**<0.001**
WP2 - WP3	RUMA	3.39736	0.782852	97	4.339721	**<0.001**
WP1 - WP2	SCAC	2.223376	0.761794	97	2.918604	**0.01**
WP1 - WP3	SCAC	2.492006	0.763906	97	3.262189	**<0.001**
WP2 - WP3	SCAC	0.26863	0.823126	97	0.326353	0.94

Table S2.2. Pairwise comparisons from the mixed effects model showing species/seed mix comparisons across water levels (greenhouse experiment 2020).

contrast	water_treatment	estimate	SE	df	t.ratio	p.value
BICE - BOMA	WP1	3.877137	0.792282	97	4.893633	**<0.001**
BICE - DISP	WP1	2.164036	0.775926	97	2.788973	0.18
BICE - ELPA	WP1	2.995275	0.780626	97	3.837015	**0.01**
BICE - EPCI	WP1	0.292172	0.828577	97	0.352619	1
BICE - MIX	WP1	0.156163	0.829802	97	0.188193	1
BICE - PMIX	WP1	3.47761	0.760645	97	4.571925	**<0.001**
BICE - POLA	WP1	1.25032	0.810821	97	1.542041	0.9
BICE - PUNU	WP1	2.495444	0.773233	97	3.227285	0.06
BICE - RUMA	WP1	-1.24E-16	0.828989	97	-1.50E-16	1
BICE - SCAC	WP1	3.520094	0.772315	97	4.557849	**<0.001**
BOMA - DISP	WP1	-1.7131	0.705469	97	-2.42831	0.36
BOMA - ELPA	WP1	-0.88186	0.708141	97	-1.24532	0.98
BOMA - EPCI	WP1	-3.58497	0.790028	97	-4.53777	**<0.001**
BOMA - MIX	WP1	-3.72097	0.79466	97	-4.68247	**<0.001**
BOMA - PMIX	WP1	-0.39953	0.681546	97	-0.58621	1
BOMA - POLA	WP1	-2.62682	0.758952	97	-3.46111	0.03
BOMA - PUNU	WP1	-1.38169	0.703442	97	-1.96419	0.67
BOMA - RUMA	WP1	-3.87714	0.792282	97	-4.89363	**<0.001**
BOMA - SCAC	WP1	-0.35704	0.692927	97	-0.51527	1
DISP - ELPA	WP1	0.831239	0.701229	97	1.185403	0.98
DISP - EPCI	WP1	-1.87186	0.774971	97	-2.4154	0.37
DISP - MIX	WP1	-2.00787	0.778552	97	-2.57898	0.27
DISP - PMIX	WP1	1.313574	0.676148	97	1.94273	0.69
DISP - POLA	WP1	-0.91372	0.745705	97	-1.22531	0.98
DISP - PUNU	WP1	0.331408	0.6947	97	0.477052	1
DISP - RUMA	WP1	-2.16404	0.775926	97	-2.78897	0.18
DISP - SCAC	WP1	1.356058	0.687729	97	1.971792	0.67
ELPA - EPCI	WP1	-2.7031	0.778959	97	-3.47015	**0.03**
ELPA - MIX	WP1	-2.83911	0.782089	97	-3.63016	**0.02**
ELPA - PMIX	WP1	0.482335	0.677862	97	0.711554	1
ELPA - POLA	WP1	-1.74496	0.750514	97	-2.32501	0.43
ELPA - PUNU	WP1	-0.49983	0.698125	97	-0.71596	1
ELPA - RUMA	WP1	-2.99528	0.780626	97	-3.83702	**0.01**
ELPA - SCAC	WP1	0.524819	0.689883	97	0.760737	1
EPCI - MIX	WP1	-0.13601	0.829746	97	-0.16392	1
EPCI - PMIX	WP1	3.185438	0.758233	97	4.201133	**<0.001**
EPCI - POLA	WP1	0.958148	0.810881	97	1.181614	0.98
EPCI - PUNU	WP1	2.203273	0.772075	97	2.853701	0.15
EPCI - RUMA	WP1	-0.29217	0.828577	97	-0.35262	1
EPCI - SCAC	WP1	3.227922	0.770072	97	4.191713	**<0.001**

MIX - PMIX	WP1	3.321447	0.762336	97	4.356934	**<0.001**
MIX - POLA	WP1	1.094157	0.812061	97	1.347382	0.96
MIX - PUNU	WP1	2.339281	0.774883	97	3.018882	0.1
MIX - RUMA	WP1	-0.15616	0.829802	97	-0.18819	1
MIX - SCAC	WP1	3.363931	0.774209	97	4.34499	**<0.001**
PMIX - POLA	WP1	-2.22729	0.728685	97	-3.05659	0.09
PMIX - PUNU	WP1	-0.98217	0.672831	97	-1.45975	0.93
PMIX - RUMA	WP1	-3.47761	0.760645	97	-4.57193	**<0.001**
PMIX - SCAC	WP1	0.042484	0.663043	97	0.064075	1
POLA - PUNU	WP1	1.245125	0.743565	97	1.674533	0.84
POLA - RUMA	WP1	-1.25032	0.810821	97	-1.54204	0.9
POLA - SCAC	WP1	2.269774	0.74016	97	3.066598	0.09
PUNU - RUMA	WP1	-2.49544	0.773233	97	-3.22729	0.06
PUNU - SCAC	WP1	1.02465	0.684881	97	1.496098	0.92
RUMA - SCAC	WP1	3.520094	0.772315	97	4.557849	**<0.001**
BICE - BOMA	WP2	4.934757	0.840511	97	5.871139	**<0.001**
BICE - DISP	WP2	3.274228	0.770588	97	4.249002	**<0.001**
BICE - ELPA	WP2	5.38249	0.857221	97	6.278996	**<0.001**
BICE - EPCI	WP2	0.218535	0.810167	97	0.269741	1
BICE - MIX	WP2	0.482434	0.814774	97	0.592108	1
BICE - PMIX	WP2	4.50371	0.826847	97	5.446846	**<0.001**
BICE - POLA	WP2	2.620041	0.763819	97	3.430188	**0.03**
BICE - PUNU	WP2	2.569539	0.758512	97	3.387607	**0.04**
BICE - RUMA	WP2	-0.33744	0.82215	97	-0.41043	1
BICE - SCAC	WP2	5.11386	0.854688	97	5.983304	**<0.001**
BOMA - DISP	WP2	-1.66053	0.757941	97	-2.19084	0.52
BOMA - ELPA	WP2	0.447733	0.819493	97	0.546353	1
BOMA - EPCI	WP2	-4.71622	0.832245	97	-5.66687	**<0.001**
BOMA - MIX	WP2	-4.45232	0.835797	97	-5.32704	**<0.001**
BOMA - PMIX	WP2	-0.43105	0.79892	97	-0.53954	1
BOMA - POLA	WP2	-2.31472	0.758321	97	-3.05242	0.1
BOMA - PUNU	WP2	-2.36522	0.753143	97	-3.14046	0.08
BOMA - RUMA	WP2	-5.2722	0.851492	97	-6.19172	**<0.001**
BOMA - SCAC	WP2	0.179103	0.819233	97	0.218622	1
DISP - ELPA	WP2	2.108262	0.771219	97	2.733673	0.2
DISP - EPCI	WP2	-3.05569	0.762748	97	-4.00616	**0.01**
DISP - MIX	WP2	-2.79179	0.765532	97	-3.64687	**0.02**
DISP - PMIX	WP2	1.229481	0.745765	97	1.648617	0.86
DISP - POLA	WP2	-0.65419	0.692695	97	-0.94441	1
DISP - PUNU	WP2	-0.70469	0.686678	97	-1.02623	0.99
DISP - RUMA	WP2	-3.61167	0.781331	97	-4.62245	**<0.001**
DISP - SCAC	WP2	1.839632	0.769594	97	2.390391	0.38
ELPA - EPCI	WP2	-5.16395	0.848084	97	-6.08897	**<0.001**

ELPA - MIX	WP2	-4.90006	0.84786	97	-5.77932	**<0.001**
ELPA - PMIX	WP2	-0.87878	0.808855	97	-1.08645	0.99
ELPA - POLA	WP2	-2.76245	0.772345	97	-3.5767	**0.02**
ELPA - PUNU	WP2	-2.81295	0.765926	97	-3.67261	**0.02**
ELPA - RUMA	WP2	-5.71993	0.871038	97	-6.5668	**<0.001**
ELPA - SCAC	WP2	-0.26863	0.823126	97	-0.32635	1
EPCI - MIX	WP2	0.263899	0.8106	97	0.32556	1
EPCI - PMIX	WP2	4.285174	0.818343	97	5.236402	**<0.001**
EPCI - POLA	WP2	2.401506	0.756589	97	3.174124	0.07
EPCI - PUNU	WP2	2.351004	0.750907	97	3.130884	0.08
EPCI - RUMA	WP2	-0.55597	0.81801	97	-0.67967	1
EPCI - SCAC	WP2	4.895325	0.845449	97	5.790209	**<0.001**
MIX - PMIX	WP2	4.021275	0.821046	97	4.897749	**<0.001**
MIX - POLA	WP2	2.137607	0.757757	97	2.820967	0.17
MIX - PUNU	WP2	2.087105	0.751981	97	2.775475	0.18
MIX - RUMA	WP2	-0.81987	0.822121	97	-0.99727	1
MIX - SCAC	WP2	4.631426	0.843557	97	5.490354	**<0.001**
PMIX - POLA	WP2	-1.88367	0.7456	97	-2.52638	0.3
PMIX - PUNU	WP2	-1.93417	0.739721	97	-2.61473	0.26
PMIX - RUMA	WP2	-4.84115	0.838804	97	-5.77149	**<0.001**
PMIX - SCAC	WP2	0.61015	0.807627	97	0.755485	1
POLA - PUNU	WP2	-0.0505	0.683108	97	-0.07393	1
POLA - RUMA	WP2	-2.95748	0.773791	97	-3.82206	**0.01**
POLA - SCAC	WP2	2.493819	0.770392	97	3.237077	0.06
PUNU - RUMA	WP2	-2.90698	0.769411	97	-3.77819	**0.01**
PUNU - SCAC	WP2	2.544321	0.763475	97	3.332552	**0.05**
RUMA - SCAC	WP2	5.451298	0.869259	97	6.271204	**<0.001**
BICE - BOMA	WP3	2.960974	0.773931	97	3.825889	**0.01**
BICE - DISP	WP3	0.740964	0.689019	97	1.07539	0.99
BICE - ELPA	WP3	2.671866	0.774673	97	3.449026	**0.03**
BICE - EPCI	WP3	-0.10314	0.675416	97	-0.1527	1
BICE - MIX	WP3	-0.86067	0.689664	97	-1.24795	0.97
BICE - PMIX	WP3	2.217447	0.759873	97	2.918181	0.13
BICE - POLA	WP3	-0.82317	0.676881	97	-1.21613	0.98
BICE - PUNU	WP3	1.614698	0.740799	97	2.179672	0.52
BICE - RUMA	WP3	0.289489	0.693186	97	0.417621	1
BICE - SCAC	WP3	2.612057	0.769725	97	3.393493	**0.04**
BOMA - DISP	WP3	-2.22001	0.7736	97	-2.86971	0.15
BOMA - ELPA	WP3	-0.28911	0.829566	97	-0.3485	1
BOMA - EPCI	WP3	-3.06411	0.764324	97	-4.00892	**0.01**
BOMA - MIX	WP3	-3.82164	0.780928	97	-4.89372	**<0.001**
BOMA - PMIX	WP3	-0.74353	0.822045	97	-0.90448	1
BOMA - POLA	WP3	-3.78415	0.768177	97	-4.92614	**<0.001**

BOMA - PUNU	WP3	-1.34628	0.810054	97	-1.66196	0.85
BOMA - RUMA	WP3	-2.67148	0.776609	97	-3.43993	**0.03**
BOMA - SCAC	WP3	-0.34892	0.827428	97	-0.42169	1
DISP - ELPA	WP3	1.930902	0.775385	97	2.490251	0.32
DISP - EPCI	WP3	-0.8441	0.676988	97	-1.24685	0.98
DISP - MIX	WP3	-1.60163	0.691419	97	-2.31644	0.43
DISP - PMIX	WP3	1.476484	0.759377	97	1.944335	0.69
DISP - POLA	WP3	-1.56414	0.680272	97	-2.29928	0.44
DISP - PUNU	WP3	0.873734	0.742742	97	1.176363	0.98
DISP - RUMA	WP3	-0.45147	0.694913	97	-0.64969	1
DISP - SCAC	WP3	1.871093	0.769864	97	2.43042	0.36
ELPA - EPCI	WP3	-2.775	0.765133	97	-3.62683	**0.02**
ELPA - MIX	WP3	-3.53254	0.780694	97	-4.52487	**<0.001**
ELPA - PMIX	WP3	-0.45442	0.823098	97	-0.55208	1
ELPA - POLA	WP3	-3.49504	0.768025	97	-4.55068	**<0.001**
ELPA - PUNU	WP3	-1.05717	0.812233	97	-1.30156	0.97
ELPA - RUMA	WP3	-2.38238	0.777151	97	-3.06553	0.09
ELPA - SCAC	WP3	-0.05981	0.828252	97	-0.07221	1
EPCI - MIX	WP3	-0.75753	0.677466	97	-1.11818	0.99
EPCI - PMIX	WP3	2.320586	0.749801	97	3.094934	0.09
EPCI - POLA	WP3	-0.72003	0.664663	97	-1.08331	0.99
EPCI - PUNU	WP3	1.717837	0.730436	97	2.351795	0.41
EPCI - RUMA	WP3	0.392628	0.681476	97	0.576143	1
EPCI - SCAC	WP3	2.715195	0.760011	97	3.572576	**0.02**
MIX - PMIX	WP3	3.078117	0.76643	97	4.016176	**0.01**
MIX - POLA	WP3	0.037496	0.677317	97	0.05536	1
MIX - PUNU	WP3	2.475367	0.751024	97	3.295988	**0.05**
MIX - RUMA	WP3	1.150158	0.695876	97	1.652821	0.85
MIX - SCAC	WP3	3.472726	0.77747	97	4.4667	**<0.001**
PMIX - POLA	WP3	-3.04062	0.753691	97	-4.0343	**<0.001**
PMIX - PUNU	WP3	-0.60275	0.798566	97	-0.75479	1
PMIX - RUMA	WP3	-1.92796	0.763374	97	-2.52558	0.3
PMIX - SCAC	WP3	0.394609	0.819496	97	0.481527	1
POLA - PUNU	WP3	2.43787	0.73453	97	3.318953	**0.05**
POLA - RUMA	WP3	1.112662	0.682999	97	1.629082	0.87
POLA - SCAC	WP3	3.435229	0.763937	97	4.496743	**<0.001**
PUNU - RUMA	WP3	-1.32521	0.745123	97	-1.77851	0.79
PUNU - SCAC	WP3	0.997359	0.804923	97	1.239073	0.98
RUMA - SCAC	WP3	2.322568	0.772711	97	3.00574	0.11

Table S2.3. Pairwise comparisons from the mixed effects model showing species comparisons across microtopography levels (field experiment 2020, year 1).

contrast_species	micro	estimate	SE	df	t.ratio	p.value
invasive - native	control	-0.59989	0.34367	116	-1.74553	0.08
invasive - native	high	-0.78756	0.345326	116	-2.28061	**0.02**
invasive - native	low	-0.72557	0.346197	116	-2.09584	**0.04**
invasive - native	ruts	-0.38594	0.346007	116	-1.11541	0.27

Table S2.4. Pairwise comparisons from the mixed effects model showing species comparisons across see mix treatments (field experiment 2020, year 1).

contrast	seed	estimate	SE	df	t.ratio	p.value
invasive - native	control	0.225872	0.298958	116	0.755531	0.45
invasive - native	high	-0.90336	0.296659	116	-3.04512	**0.003**
invasive - native	pmix	-1.19672	0.305272	116	-3.92018	<**0.001**
invasive - native	control	0.225872	0.298958	116	0.755531	0.45
invasive - native	high	-0.90336	0.296659	116	-3.04512	**0.003**
invasive - native	pmix	-1.19672	0.305272	116	-3.92018	<**0.001**

Table S2.5. Pairwise comparisons from the mixed effects model showing seed mix comparisons across species levels (field experiment 2020, year 1).

contrast_seed-mix	species	estimate	SE	df	t.ratio	p.value
control - high	invasive	0.224082	0.30038	116	0.745995	0.74
control - pmix	invasive	0.383712	0.306277	116	1.252824	0.42
high - pmix	invasive	0.15963	0.30843	116	0.517556	0.86
control - high	native	-0.90515	0.293417	116	-3.08487	<**0.001**
control - pmix	native	-1.03888	0.294212	116	-3.53107	**0.002**
high - pmix	native	-0.13373	0.286268	116	-0.46715	0.89

Table S2.6. Pairwise comparisons from the mixed effects model showing seed mix comparisons across species levels (field experiment 2020, year 2).

contrast_seed-mix	species	estimate	SE	df	t.ratio	p.value
control - high	invasive	0.21296	0.326658	115	0.651935	0.79
control - pmix	invasive	0.345081	0.33253	115	1.037745	0.55
high - pmix	invasive	0.132121	0.329226	115	0.401308	0.92
control - high	native	-0.6273	0.32543	115	-1.9276	0.14
control - pmix	native	-0.62808	0.32454	115	-1.93529	0.13
high - pmix	native	-0.00078	0.320939	115	-0.00243	1

Table S2.7. Pairwise comparisons from the mixed effects model showing species comparisons across seed mix levels (field experiment 2020, year 2).

contrast	seed	estimate	SE	df	t.ratio	p.value
invasive - native	control	3.931345	0.377724	115	10.40798	**<0.001**
invasive - native	high	3.091084	0.353892	115	8.734535	**<0.001**
invasive - native	pmix	2.958185	0.355643	115	8.31784	**<0.001**

Table S2.8. Pairwise comparisons from the mixed effects model seed mix treatment comparisons across species levels (mesocosm experiment 2021).

contrast_seed-mix	species	estimate	SE	df	t.ratio	p.value
h - p	native_biomass	15.02525	0.82678	115	18.17321	**<0.001**
h - p	phau_grams	-3.73312	0.38976	115	-9.578	**<0.001**

Table S2.9. Pairwise comparisons from the mixed effects model showing water level comparisons across species levels (mesocosm experiment 2021).

contrast_water	species	estimate	SE	df	t.ratio	p.value
high - low	native_biomass	4.553896	0.82678	115	5.507988	**<0.001**
high - low	phau_grams	-0.19536	0.38976	115	-0.50123	0.62

Table S2.10. Pairwise comparisons from the mixed effects model showing water level comparisons across species levels (mesocosm experiment 2021).

contrast_water	species	estimate	SE	df	t.ratio	p.value
high - low	boma_grams	1.670719	0.665877	144	2.50905	**0.01**
high - low	disp_grams	0.401707	0.167563	144	2.397343	**0.02**
high - low	elpa_grams	2.245057	0.574942	144	3.904841	**<0.001**
high - low	phau_grams	0.005098	0.305689	144	0.016677	0.98
high - low	scac_grams	2.1033	0.420803	144	4.9983	**<0.001**

Table S2.11. Pairwise comparisons from the mixed effects model showing species comparisons across water levels (mesocosm experiment 2021).

contrast	water	estimate	SE	df	t.ratio	p.value
boma_grams - disp_grams	high	-1.17438	0.455694	144	-2.57712	0.08
boma_grams - elpa_grams	high	5.07353	0.599081	144	8.468858	**<0.001**
boma_grams - phau_grams	high	0.773176	0.490246	144	1.577118	0.51
boma_grams - scac_grams	high	3.328539	0.531184	144	6.266266	**<0.001**

disp_grams - elpa_grams	high	6.247908	0.388896	144	16.06574	0
disp_grams - phau_grams	high	1.947555	0.180788	144	10.7726	0
disp_grams - scac_grams	high	4.502918	0.272945	144	16.49754	0
elpa_grams - phau_grams	high	-4.30035	0.428864	144	-10.0273	0
elpa_grams - scac_grams	high	-1.74499	0.47512	144	-3.67273	**0.003**
phau_grams - scac_grams	high	2.555363	0.327388	144	7.805297	<**0.001**
boma_grams - disp_grams	low	-2.44339	0.455694	144	-5.36191	<**0.001**
boma_grams - elpa_grams	low	5.647867	0.599081	144	9.427556	0
boma_grams - phau_grams	low	-0.89244	0.490246	144	-1.8204	0.37
boma_grams - scac_grams	low	3.76112	0.531184	144	7.080638	<**0.001**
disp_grams - elpa_grams	low	8.091258	0.388896	144	20.80569	0
disp_grams - phau_grams	low	1.550946	0.180788	144	8.578824	<**0.001**
disp_grams - scac_grams	low	6.20451	0.272945	144	22.73174	0
elpa_grams - phau_grams	low	-6.54031	0.428864	144	-15.2503	0
elpa_grams - scac_grams	low	-1.88675	0.47512	144	-3.97109	<**0.001**
phau_grams - scac_grams	low	4.653564	0.327388	144	14.21421	0

Table S2.12. Pairwise comparisons from the mixed effects model showing water level comparisons across species levels (mesocosm experiment 2021).

contrast	species	estimate	SE	df	t.ratio	p.value
high - low	bice_grams	0.7757	0.429485	297	1.806116	0.07
high - low	boma_grams	1.457435	0.429485	297	3.393445	<**0.001**
high - low	disp_grams	-0.39675	0.429485	297	-0.92378	0.36
high - low	elpa_grams	0.293781	0.429485	297	0.684031	0.49
high - low	epci_grams	-0.12566	0.429485	297	-0.29258	0.77
high - low	euoc_grams	0.545821	0.429485	297	1.270871	0.2
high - low	phau_grams	0.211452	0.429485	297	0.492337	0.62
high - low	ruma_grams	-0.24123	0.429485	297	-0.56168	0.57

high - low	scac_grams	0.844138	0.429485	297	1.965465	0.05
high - low	syci_grams	-0.06598	0.429485	297	-0.15363	0.87

Table S2.13. Pairwise comparisons from the mixed effects model showing species comparisons across water levels (mesocosm experiment 2021).

contrast	water	estimate	SE	df	t.ratio	p.value
bice_grams - boma_grams	high	7.046719	0.337828	297	20.85891	**<0.001**
bice_grams - disp_grams	high	5.933634	0.337828	297	17.56408	**<0.001**
bice_grams - elpa_grams	high	11.49419	0.337828	297	34.02382	**<0.001**
bice_grams - epci_grams	high	5.003118	0.337828	297	14.80967	**<0.001**
bice_grams - euoc_grams	high	7.376102	0.337828	297	21.83391	**<0.001**
bice_grams - phau_grams	high	6.404193	0.337828	297	18.95697	**<0.001**
bice_grams - ruma_grams	high	1.602881	0.337828	297	4.744667	**<0.001**
bice_grams - scac_grams	high	10.86357	0.337828	297	32.15712	**<0.001**
bice_grams - syci_grams	high	6.079927	0.337828	297	17.99712	**<0.001**
boma_grams - disp_grams	high	-1.11308	0.337828	297	-3.29483	0.04
boma_grams - elpa_grams	high	4.447473	0.337828	297	13.16491	**<0.001**
boma_grams - epci_grams	high	-2.0436	0.337828	297	-6.04924	**<0.001**
boma_grams - euoc_grams	high	0.329383	0.337828	297	0.975002	0.99
boma_grams - phau_grams	high	-0.64253	0.337828	297	-1.90193	0.67
boma_grams - ruma_grams	high	-5.44384	0.337828	297	-16.1142	**<0.001**
boma_grams - scac_grams	high	3.816851	0.337828	297	11.29821	**<0.001**
boma_grams - syci_grams	high	-0.96679	0.337828	297	-2.86179	0.12
disp_grams - elpa_grams	high	5.560557	0.337828	297	16.45974	**<0.001**
disp_grams - epci_grams	high	-0.93052	0.337828	297	-2.75441	0.16
disp_grams - euoc_grams	high	1.442467	0.337828	297	4.26983	0.01
disp_grams - phau_grams	high	0.470559	0.337828	297	1.392895	0.93
disp_grams - ruma_grams	high	-4.33075	0.337828	297	-12.8194	**<0.001**
disp_grams - scac_grams	high	4.929935	0.337828	297	14.59304	**<0.001**
disp_grams - syci_grams	high	0.146293	0.337828	297	0.433041	1
elpa_grams - epci_grams	high	-6.49107	0.337828	297	-19.2141	**<0.001**
elpa_grams - euoc_grams	high	-4.11809	0.337828	297	-12.1899	**<0.001**
elpa_grams - phau_grams	high	-5.09	0.337828	297	-15.0668	**<0.001**
elpa_grams - ruma_grams	high	-9.89131	0.337828	297	-29.2792	**<0.001**
elpa_grams - scac_grams	high	-0.63062	0.337828	297	-1.8667	0.69
elpa_grams - syci_grams	high	-5.41426	0.337828	297	-16.0267	**<0.001**
epci_grams - euoc_grams	high	2.372984	0.337828	297	7.024241	**<0.001**
epci_grams - phau_grams	high	1.401075	0.337828	297	4.147305	0.01
epci_grams - ruma_grams	high	-3.40024	0.337828	297	-10.065	**<0.001**
epci_grams - scac_grams	high	5.860452	0.337828	297	17.34745	**<0.001**
epci_grams - syci_grams	high	1.07681	0.337828	297	3.187452	0.05
euoc_grams - phau_grams	high	-0.97191	0.337828	297	-2.87694	0.12
euoc_grams - ruma_grams	high	-5.77322	0.337828	297	-17.0892	**<0.001**
euoc_grams - scac_grams	high	3.487468	0.337828	297	10.32321	**<0.001**
euoc_grams - syci_grams	high	-1.29617	0.337828	297	-3.83679	0.01
phau_grams - ruma_grams	high	-4.80131	0.337828	297	-14.2123	**<0.001**
phau_grams - scac_grams	high	4.459377	0.337828	297	13.20015	**<0.001**

phau_grams - syci_grams	high	-0.32427	0.337828	297	-0.95985	0.99
ruma_grams - scac_grams	high	9.260689	0.337828	297	27.41245	**<0.001**
ruma_grams - syci_grams	high	4.477047	0.337828	297	13.25245	**<0.001**
scac_grams - syci_grams	high	-4.78364	0.337828	297	-14.16	**<0.001**
bice_grams - boma_grams	low	7.728453	0.483248	297	15.99271	**<0.001**
bice_grams - disp_grams	low	4.761182	0.483248	297	9.852454	**<0.001**
bice_grams - elpa_grams	low	11.01227	0.483248	297	22.78802	**<0.001**
bice_grams - epci_grams	low	4.101758	0.483248	297	8.487889	**<0.001**
bice_grams - euoc_grams	low	7.146222	0.483248	297	14.78789	**<0.001**
bice_grams - phau_grams	low	5.839944	0.483248	297	12.08477	**<0.001**
bice_grams - ruma_grams	low	0.585946	0.483248	297	1.212515	0.97
bice_grams - scac_grams	low	10.93201	0.483248	297	22.62192	**<0.001**
bice_grams - syci_grams	low	5.238245	0.483248	297	10.83965	**<0.001**
boma_grams - disp_grams	low	-2.96727	0.483248	297	-6.14026	**<0.001**
boma_grams - elpa_grams	low	3.283819	0.483248	297	6.795303	**<0.001**
boma_grams - epci_grams	low	-3.62669	0.483248	297	-7.50483	**<0.001**
boma_grams - euoc_grams	low	-0.58223	0.483248	297	-1.20483	0.97
boma_grams - phau_grams	low	-1.88851	0.483248	297	-3.90795	**0.01**
boma_grams - ruma_grams	low	-7.14251	0.483248	297	-14.7802	**<0.001**
boma_grams - scac_grams	low	3.203554	0.483248	297	6.629209	**<0.001**
boma_grams - syci_grams	low	-2.49021	0.483248	297	-5.15306	**<0.001**
disp_grams - elpa_grams	low	6.25109	0.483248	297	12.93556	**<0.001**
disp_grams - epci_grams	low	-0.65942	0.483248	297	-1.36456	0.94
disp_grams - euoc_grams	low	2.38504	0.483248	297	4.935433	**<0.001**
disp_grams - phau_grams	low	1.078762	0.483248	297	2.232314	0.44
disp_grams - ruma_grams	low	-4.17524	0.483248	297	-8.63994	**<0.001**
disp_grams - scac_grams	low	6.170825	0.483248	297	12.76947	**<0.001**
disp_grams - syci_grams	low	0.477063	0.483248	297	0.9872	**<0.001**
elpa_grams - epci_grams	low	-6.91051	0.483248	297	-14.3001	**<0.001**
elpa_grams - euoc_grams	low	-3.86605	0.483248	297	-8.00013	**<0.001**
elpa_grams - phau_grams	low	-5.17233	0.483248	297	-10.7033	**<0.001**
elpa_grams - ruma_grams	low	-10.4263	0.483248	297	-21.5755	**<0.001**
elpa_grams - scac_grams	low	-0.08026	0.483248	297	-0.16609	1
elpa_grams - syci_grams	low	-5.77403	0.483248	297	-11.9484	**<0.001**
epci_grams - euoc_grams	low	3.044464	0.483248	297	6.299998	**<0.001**
epci_grams - phau_grams	low	1.738186	0.483248	297	3.596878	**0.01**
epci_grams - ruma_grams	low	-3.51581	0.483248	297	-7.27537	**<0.001**
epci_grams - scac_grams	low	6.830249	0.483248	297	14.13403	**<0.001**
epci_grams - syci_grams	low	1.136487	0.483248	297	2.351765	0.36
euoc_grams - phau_grams	low	-1.30628	0.483248	297	-2.70312	0.18
euoc_grams - ruma_grams	low	-6.56028	0.483248	297	-13.5754	**<0.001**
euoc_grams - scac_grams	low	3.785785	0.483248	297	7.834037	**<0.001**
euoc_grams - syci_grams	low	-1.90798	0.483248	297	-3.94823	**0.01**
phau_grams - ruma_grams	low	-5.254	0.483248	297	-10.8723	**<0.001**
phau_grams - scac_grams	low	5.092063	0.483248	297	10.53716	**<0.001**
phau_grams - syci_grams	low	-0.6017	0.483248	297	-1.24511	0.96
ruma_grams - scac_grams	low	10.34606	0.483248	297	21.40941	**<0.001**
ruma_grams - syci_grams	low	4.652299	0.483248	297	9.627139	**<0.001**
scac_grams - syci_grams	low	-5.69376	0.483248	297	-11.7823	**<0.001**

Table S2.14. Pairwise comparisons from the mixed effects model showing microtopography treatment comparisons (field experiment 2021).

contrast	estimate	SE	df	t.ratio	p.value
disked - no_disk	0.997171	0.266684	95	3.739148	**<0.001**

Table S2.15. Restoration species characteristics and results of viability tests. Experiment codes are Greenhouse 2020 (GH20), Field experiment 2020 (FE20), and Mesocosm experiment 2021 (MS21), or classified as “ALL” if used in all experiments. Wetland indicator status is a federal plant designation indicating how hydrophytic a species is with ‘obligate’ being the most hydrophytic and ‘upland’ being the least. Forb species are in bold.

Species	Common name	Experiments	Growth form (USDA, NRCS 2022)	Family	Great Salt Lake habitat (Downard 2017)	Wetland indicator status (USDA, NRCS 2022)	Viability ± SE (2019)	Viability± SE (2020)	Dormancy breaking technique
Bolboschoenus maritimus	alkali bulrush	ALL	Perennial, rhizomatous graminoid	Cyperaceae	Emergent/meadow	Obligate	0.93 ± 0.01	0.87 ± 0.004	24-48 hour 3% bleach scarification
Schoenoplectus acutus	hardstem bulrush	ALL	Perennial, rhizomatous graminoid	Cyperaceae	Emergent	Obligate	0.74 ± 0.02	0.83 ± 0.01	6 weeks cold stratification (2°C)
Eleocharis palustris	common spikerush	ALL	Perennial, rhizomatous graminoid	Cyperaceae	Meadow/emergent	Obligate	0.72 ± 0.02	0.80 ± 0.02	24-hour 3% bleach scarification
Distichlis spicata	saltgrass	GH20, FE20, MS21	Perennial, rhizomatous graminoid	Poaceae	Meadow/playa	Facultative	0.90 ± 0.02	0.80 ± 0.05	6 weeks cold stratification (2°C)
Puccinellia nuttalliana	Nuttall’s alkaligrass	GH20, FE20	Perennial, rhizomatous graminoid	Poaceae	Meadow/emergent	Facultative-wet	0.88 ± 0.02	NA	6 weeks cold stratification (2°C)
Polygonum lapathifolium	pale smartweed	GH20	Annual forb	Polygonaceae	Emergent	Facultative-wet	0.94 ± 0.01	NA	6 weeks cold stratification (2°C)
Rumex maritimus	golden dock	GH20, FE20, MS21	Annual/biennial, rhizomatous forb	Polygonaceae	Emergent	Facultative-wet	0.82 ± 0.03	0.76 ± 0.03	

									6 weeks cold stratification (2°C)
Epilobium ciliatum	fringe willowherb	GH20, FE20, MS21	Perennial forb	Onagraceae	Emergent/meadow	Facultative-wet	0.94 ± 0.01	0.38 ± 0.04	6 weeks cold stratification (2°C)
Bidens cernua	nodding beggartick	GH20, FE20, MS21	Annual forb	Asteraceae	Meadow	Obligate	0.80 ± 0.06	0.75 ± 0.03	6 weeks cold stratification (2°C)
Symphyotrichum ciliatum	rayless alkali aster	MS21	Annual forb	Asteraceae	Meadow	Facultative-wet	NA	0.88	6 weeks cold stratification (2°C)
Euthamia occidentalis	western goldentop	MS21	Perennial forb	Asteraceae	Emergent	Facultative-wet	NA	0.84 ± 0.01	6 weeks cold stratification (2°C)

Table S2.16. Seed collection year and location for native wetland species used in all experiments. WMA = Waterfowl Management Area.

	Farmington Bay WMA	Howard Slough WMA	Bear River Migratory Bird Refuge	Salt Creek WMA	Public Shooting Grounds WMA	Ogden Bay WMA	North Point Duck Club	Harold Crane WMA	Granite Seed	TNC Shorelands Preserve	Sterner Collections
Bolboschoenus maritimus	2020	2019 2020	2019			2020	2020	2019 2020			
Schoenoplectus acutus				2020		2020		2020	2019	2020	
Eleocharis palustris					2020				2019	2020	2020
Distichlis spicata									2019		2020
Puccinellia nuttalliana									2019		
Polygonum lapathifolium		2019	2020								
Rumex maritimus	2019 2020	2019 2020		2019 2020							
Epilobium ciliatum	2019 2020	2019 2020	2019 2020								
Bidens cernua	2019	2019 2020	2019 2020			2020					
Symphyotrichum ciliatum		2020						2020		2020	
Euthamia occidentalis			2020			2020		2020		2020	