SEED ECOLOGY AND REGENERATION PROCESSES TO INFORM SEED-BASED WETLAND RESTORATION

by

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ABSTRACT

Seed ecology and regeneration processes to inform seed-based wetland restoration

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Revegetation of native wetland plants is critical following invasive species removal to return wetland functions and services. Sowing seeds of native species can be a financially and logistically feasible restoration approach. However, in practice, seeding efforts often fail to meet restoration goals due to limited information on best practices that maximize native plant recruitment. Further, high mortality at the seed and seedling stages of plant growth can stifle restoration outcomes. We asked: 1) what native sowing density maximizes performance for native wetland communities across environmental conditions, invasive propagule pressure, and seed sowing timing? 2) how do functional regeneration traits vary across species, populations, and abiotic conditions in multivariate trait space? and 3) how do species and populations contribute to invasion resistance through plant cover and clonal production in early life stages? To answer 'Question 1', we conducted a series of mesocosm experiments assessing plant cover and biomass across native seed sowing density, *Phragmites australis* propagule pressure, abiotic filters, and native sowing timing. To answer 'Question 2', we sourced seeds from 6 species and 37 populations across the Intermountain West, USA. In the lab, we measured

seed functional traits and grew out seeds from each species × population in 6 abiotic regimes. We tracked germination and harvested seedlings at set intervals to calculate seedling traits. To answer 'Question 3', we grew 12 species × populations across abiotic conditions in the greenhouse. We tracked germination, survival, mortality, and clonal production of a subset of seedlings in each treatment, and measured percent cover weekly. Through a series of principal components analysis and mixed effects models, we found that increasing native seed sowing density can benefit native plant establishment, particularly when sown early in the season, but this was far less impactful than the role that *P. australis* propagule pressure had in shaping plant communities. Further, competitive interactions shifted across conditions such that low water levels favored *P. australis* suppression when drought-tolerant native (e.g., *D. spicata*) were included in the seed mix. We also identified significant variation in morphological and physiological seed traits, germination traits, and seedlings traits at the species and population level that appeared to provide adaptive value for species-specific habitat requirements. Further, we found unexpected relationships among seedling traits that ran contrary to the well-known leaf economic spectrum. Finally, we found that *Phragmites australis* experienced the highest probability of germination across abiotic conditions relative to the other tested species, followed by *D. spicata*. Both species achieved high native cover and developed clones during the first eight-weeks, though the variation in clonal transitions was be mediated by water availability and temperature. *Eleocharis palustris*, a slow-growing Cyperaceae, achieved high end-of-season cover largely from extensive clonal production in high water levels, making it an ideal restoration candidate to impose biotic resistance in certain contexts. The findings from these studies provide guidance for wetland

managers seeking to maximize seed-based wetland restoration outcomes and offers important insight into early wetland plant dynamics.

(314 pages)

PUBLIC ABSTRACT

Seed ecology and regeneration processes to inform seed-based wetland restoration

Emily E. Tarsa

Wetlands provide immense value to wildlife and humans but have been degrading rapidly around the world. One major challenge is the loss of native plant species in wetlands, which limits the ability of wetlands to function as they should. Restoring wetlands requires a combination of removing the cause of degradation (such as invasive plant species) and, in many cases, actively returning native plants to the site especially via seeding. Further, early plant life stages are the most vulnerable for plants and is often the time in which sown species die and fail to establish. Thus, understanding how and why seeds die or survive across species and environmental conditions can provide guidance for seed-based wetland restoration. Here, we sought to answer these important knowledge gaps through a series of greenhouse and lab experiments. First, we sought to answer what native sowing rate was needed to maximize native plant performance across a gradient of invasive species seed density, environmental conditions, and timing of seed addition. Separately, we performed a lab and growth chamber experiment in which we measured important characteristics about seeds and seedlings (grown in different environmental conditions) to better understand (and ultimately predict) why some species do well and in what conditions that can occur. Finally, in a separate greenhouse experiment, we grew native and invasive wetland plants for eight-weeks and tracked whether seeds germinated, survived, or died in order to quantify plant transitions through these early life stages. We also assessed ‘end-of-season’ percent cover and the rate of

clonal production to gauge how early stages of plant growth contributes to invasion resistance. We found native plant establishment increased with higher native sowing densities, especially when native seeds were sown early in the season. However, the biggest driver in plant community composition following seeding was the density of invasive *Phragmites australis* seeds in the soil. Low water levels yielded higher native plant performance and more effectively suppressed *P. australis* growth. We also identified characteristics of seeds and seedlings that explained their germination and early growth patterns—species that had light seeds with thin seed coats and shallow seed dormancy had faster time to germination and higher growth rates, while species with heavy seeds had thick seed coats, deep seed dormancy, slower germination, and higher resource allocation to plant structures. Finally, we found that high-water levels enhanced the probability of seed germination, and that high temperatures lead to higher clonal development in seedlings. Overall, *Phragmites australis* was a superior performer is early life stages, but *Distichlis spicata* performed well due to high germination probabilities and *Eleocharis palustris* performed well due to extensive clonal production. As seed-based wetland restoration becomes increasingly necessary, the findings from this dissertation provide guidance on which native species should be used, where seeds should be sourced, and what environmental conditions should be targeted to maximize native plant establishment and restore wetland functions.

DEDICATION

This work is dedicated to my children, who helped me maintain perspective and never failed to brighten my days. I hope you find simplicity, joy, and serenity in all that life brings you, as I have found in the wetlands.

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CHAPTER 1

INTRODUCTION

Despite covering less than 10% of the Earth's surface, wetlands are among the most biologically diverse and productive ecosystems in the world (Zedler, 2000; Millennium Ecosystem Assessment, 2005). Degradation of wetland ecosystems is occurring rapidly and disproportionately relative to their land cover—over 70% of wetlands have been destroyed or impaired, which has detrimental impacts to the water quality, flood mitigation, nutrient cycling, carbon sequestration, and habitat provisioning functions that wetlands provide (Zedler & Kercher, 2005; Kingsford et al. 2016). Restoration of degraded wetlands has traditionally relied on passive revegetation of native plant species following the removal or alteration of biological or physical barriers to the site (e.g., removal of invasive plant species; restoring hydrological regime; Galatowitsch, 2012). Passive revegetation approaches have been advocated for in wetland restoration (Mitsch et al. 1998), but, in practice, this approach often leads to plant communities that lack characteristic species or guilds as the result of depleted native seed banks, adjacent land use, or site disturbance history (Zedler, 2000; Seabloom & van der Valk, 2003; De Steven et al. 2006; Luckeydoo et al. 2006; Aronson & Galatowitsch, 2008; Carlson et al. 2009; Rohal et al. 2019). Further, in wetlands that have been previously invaded by invasive plant species, invasive propagule pressure can overwhelm the ability of native plant species to return on their own (Holle & Simberloff, 2005; Lockwood et al. 2009). Thus, continued degradation and alteration of wetlands (and their native seed banks) limits the utility of passive recolonization in many wetland systems

and necessitates active revegetation approaches to restore wetland plant communities (Kettenring & Tarsa, 2020).

Rapidly returning native species to wetlands via active revegetation has many benefits including ensuring resilience to future disturbance or invasion (Cardinale et al., 2012), restoring ecosystem functions and services (Benayas et al. 2009), and providing an 'insurance effect' to improve ecosystem stability in the face of a rapidly changing climate (Loreau et al. 2001; Yachi & Loreau, 1999; Tilman et al. 2006; Aitken & Whitlock, 2013). Active revegetation of native wetland plant species exists in many forms, such as through the installation of sod mats, planting plugs, transplanting rhizomes, or introducing native seeds to the site (Galatowitsch, 2012; Kettenring & Tarsa, 2020). Seed-based restoration is logistically and financially feasible relative to other active revegetation strategies (Tilley & St. John, 2013; Tilley & Hoag, 2006; Menges, 2008), and several studies have demonstrated ecological benefits and cost-savings associated with seed-based restoration (e.g., Palmerlee & Young, 2010). In addition to financial and logistical advantages, seed-based restoration can increase the adaptive potential of a restored plant community as it is easier to collect a wider range of plant genotypes (Menges, 2008). Having diverse plant populations can yield ecosystems that are more resilient to a changing climate, more productive, and better at resisting invasive species (re)invasion (Aitken & Whitlock, 2013; Cardinale *et al.* 2012).

Despite the advantages of seed-based wetland restoration, there are several challenges that limit its success and application. The first challenge is that evidence-based guidance on seeding practices in wetlands is limited due to the paucity of comprehensive research in this area (Perry & Galatowitsch, 2003; Kettenring & Tarsa,

2020). Specifically, wetland environments are highly dynamic and vary over relatively small spatiotemporal scales (Euliss et al. 2004; Jackson, 2006), thus seed-based restoration guidance must account for the interactions of (1) biotic (e.g., seed sowing densities and invasive propagule pressure), (2) abiotic (e.g., variation in water and nutrients), and (3) temporal (e.g., timing of seed introduction) factors that influence community assembly from seed (Kettenring & Tarsa, 2020). Here, I focus on each of these points.

First, guidelines for optimal seed sowing densities in wetland restoration that suppress invasive species, while minimizing the impact to native species establishment, are sparse in the literature (but see van der Valk & Baalman, 2018; Reinhardt Adams & Galatowitsch, 2008), despite having potentially large implications for long-term plant community assembly (Grman et al. 2015; Van Katwijk et al. 2016). For example, sowing densities that are too low result in the failure of native species to occupy available niche space, thus preventing full acquisition of resources at the site (Harper, 1977), which can ultimately allow invasive or undesirable species to establish. Additionally, low densities can result in plant communities that are unable to reach self-sustaining feedbacks (e.g., enough individuals to reproduce at a high enough rate to grow the population or replace individuals that have died), which are necessary to support population growth (Drake & Lodge, 2006; Van Katwijk et al. 2016). Conversely, high sowing densities may result in high competition and density-dependent interactions between and within species, leading to die-offs of individual plants that could open space for subsequent invasions (Burton et al. 2006; Harper, 1977). Further, high sowing densities leads to wasted seed, which is

costly for managers and makes poor use of resources that are often in limited quantity to begin with (Merritt & Dixon, 2011).

Identifying the optimal native seeding density for native species is particularly important when restoring systems that have been previously invaded or have a high likelihood of invasive species propagules being introduced (Reinhardt Adams & Galatowitsch, 2008). Research has shown that functional trait values of plant species that determine overall performance, such as growth rate, size, fitness, and biomass allocation, are typically higher in species that invade ecosystems compared to native, non-invading species (van Kleunen et al., 2010; Kolar & Lodge, 2001; Grotkopp et al., 2002). Additionally, invasive species propagule pressure (i.e., invasive seeds in the seed bank; invasive seeds 'raining' into the restoration site) is likely high at many restoration sites (Holle & Simberloff, 2005; Reinhardt Adams & Galatowitsch, 2008; Byun et al. 2015). As such, a key focus in restoration should be to minimize the (re)invasion of invasive species at a site. To do so, managers must be equipped with the knowledge to better understand and predict how native-invader interactions can be manipulated by adjusting native seed sowing densities.

Second, identifying the abiotic and biotic feedbacks that maintain an ecosystem in a particular state, as well as the thresholds that need to be crossed to flip the system into a more desirable state, can be a valuable restoration tool (Suding et al. 2004). These feedbacks vary widely and can include invasive species propagule pressure that maintains the system in an invasive-dominated state (Reinhardt Adams and Galatowitsch, 2008), changes in landscape connectivity that results in the loss of local seed sources (Suding et al. 2004), and abiotic conditions (e.g., low water availability) that prevent the

establishment of desired species (Hobbs & Norton, 2006). Furthermore, the thresholds that allow ecosystems to shift to a native-dominated state likely vary across space (Suding et al. 2004; Reinhardt Adams and Galatowitsch, 2008). This relationship is due to the variation of resource availability, disturbance regimes, or stressors that influence competitive interactions and abiotic constraints that maintain the ecosystem in one state or another (Wilson and Keddy, 1986; Tilman, 1982; Suding et al. 2004). As such, identifying the optimal native seeding density needed to outcompete invasive species must consider how these densities interact with various environmental conditions. In other words, simply studying them under one set of conditions is not representative of the abiotic heterogeneity that species are exposed to in the field.

Third, the timing of when seeds arrive at a site can have long-standing consequences for plant community assembly via priority effects—that is the effect of earlier arriving species on the germination, growth, and survival of later arriving species in a community (Young et al. 2017; Hess et al. 2019). This effect occurs through two mechanisms: (1) niche preemption, in which available niche space is filled by earlier arriving species and no longer available to later arriving species, and (2) niche modification, in which early arriving species change the biotic or abiotic factors at a site, making the site less conducive to growth of later arriving species (Fukami et al. 2015). It is well-documented that invasive species germinate earlier in the season and grow rapidly relative to native species (e.g., Perkins & Hatfield, 2016; Gioria & Pysék, 2017), so sowing native seeds earlier in the season can provide an advantage to species that typically underperform in restoration (Hess et al. 2019). Utilizing priority effects in seed-based restoration has been shown to increase native dominance and invasion resistance in

restored plant communities (Young et al. 2016; Schantz et al. 2018; Hess et al. 2019; Byun, 2022), but the strength of priority effects is not universal and has relatively unexplored in wetlands (Chase, 2003; Weidlich et al. 2021). Further, there is limited knowledge with how priority effects interact with other restoration manipulations, such as sowing density, which limits its application in the field.

Beyond limited guidance on seeding practices in wetlands, challenges arise in seed-based restoration due to high mortality seeds and seedlings (Merritt & Dixon, 2011). Demographic research on upland plants has identified the stage between germination and emergence as the most limiting stage in a plant's life cycle, making seeds especially vulnerable in restoration (James *et al.* 2011; Barrett-Lennard et al. 2016). Low establishment rates are common, which are partially attributed to lack of biological and physiological knowledge of target species, as well as challenging environmental conditions that impede the transition from seed germination to seedling establishment (Perring et al. 2015; Kildisheva et al. 2016; Larson & Funk, 2016). Thus, there is a critical need to improve our understanding of the processes and conditions that drive seed-based restoration outcomes to improve our ability to control and predict plant community assembly.

In recent years, ecologists have drawn on plant functional traits—morphological or physiological traits that influence plant fitness and ecosystem functioning—to explain vegetation responses to restoration efforts across species (Funk *et al.* 2008). Functional traits can shape community assembly in response to ecological filters, which are abiotic (e.g., moisture) or biotic (e.g., competition) factors that favor the recruitment of some species or traits over others (Keddy, 1992). However, functional trait research has been

limited by its focus on adult plant traits, thus disregarding traits that drive recruitment during the most critical stage of a plant's life cycle. Regeneration traits—traits that drive regeneration processes (e.g., germination, establishment)—are understudied, but have the potential to explain plant community patterns and predict restoration outcomes (Larson and Funk, 2016). For example, seed traits that drive seed persistence (e.g., seed coat thickness) and dispersal (e.g., seed buoyancy) can inform how plant populations adapt to spatial and temporal environmental changes (Gardarin et al. 2010; Hamilton et al. 2013; van Den Broek et al. 2005; Soons et al. 2017), while seed traits that influence seedling growth, such as seed mass (Moles & Westoby, 2004; Lebrija-Trejos et al. 2016), can improve prediction of how a species might perform in restoration. Further, traits that drive early seedling growth, such as traits related to growth rate and biomass allocation, can be used to predict how species respond to abiotic conditions at the restoration site and compete with neighboring plants (Rowe & Leger, 2011; Larson et al. 2021; Stears et al. 2022). Understanding the multidimensional trade-offs of seed and seedling functional trait expression (i.e., a seed or seedling's 'strategy') across abiotic conditions is a critical step to mechanistically explain seed-based restoration outcomes.

To date, regeneration trait research has largely been explored in terrestrial upland species, which limits the generalizability of seed and seedling strategies across habitats (de Bello et al. 2010; Moor et al. 2017). Wetlands are distinctive in that they vary hydrologically on a relatively small spatiotemporal scale (Mitsch & Gosselink, 2015); thus, wetland plants exhibit unique adaptations that allow for survival in wet, dynamic environments (Cronk & Fennessey, 2016). Consequently, we would expect that wetland regenerative strategies might be markedly different than that of upland seeds and

seedlings, but very few studies have been conducted assessing a comprehensive suite of wetland seed and seedling trait responses across environmental conditions.

Additionally, understanding the variation of regeneration traits both between species (interspecific variation) and within species (intraspecific variation) allows for more targeted knowledge of strategies to maximize seed-based wetland restoration outcomes (Albert *et al.* 2010; Clark et al. 2012; Siefert et al. 2015; Funk et al. 2017). For example, interspecific differences in regeneration traits may highlight certain environmental conditions that promote the germination and establishment of some species (e.g., native bulrushes seeded at the site) while inhibiting the establishment of *Phragmites australis,* a highly invasive wetland plant in North America, from the seed bank. Furthermore, intraspecific variation in regeneration traits can inform seed source selection to improve restoration outcomes under changing environmental conditions (e.g., regeneration traits that perform better under drought conditions).

While the last decade has brought about a heightened interest in regeneration traits that drive seedling dynamics (e.g., Larson et al. 2021; James et al. 2011), less attention has focused on the contribution of plant clonality to plant community outcomes (i.e., final plant cover; Kun & Orbony, 2003; Albert et al. 2022). In clonal plants, seed germination and subsequent seedling survival (or seedling mortality) are only part of early processes that contribute to first-year plant cover, and thus, invasion resistance (Gough et al. 2002). As such, incorporating the probability of clonal production across target species in addition to germination and survival probabilities can provide a more realistic picture of the regenerative stages of clonal plants.

The primary objectives of this research are to: (1) identify seed-based wetland restoration techniques that promote native-dominated plant communities (**Chapter 2**), (2) investigate the inter- and intraspecific variation in functional regeneration traits of target wetland species across abiotic conditions (**Chapter 3**), and (3) quantify germination and survival probabilities, clonal development production, and end-of-season cover among target wetland species across abiotic conditions (**Chapter 4**). To date, seed-based revegetation research has been primarily focused on terrestrial upland species and less on wetlands, despite the urgent need to restore wetland ecosystem function paired with the inability for many wetlands to passively revegetate. The research in this dissertation fills this knowledge gap by furthering our understanding of how wetland plants regenerate through seed and how managers can use this information to maximize seed-based restoration outcomes.

In Chapter 2 – **Tipping the balance: the role of seed density, abiotic filters, and priority effects in seed-based wetland restoration –** I manipulated native sowing density, invasive species propagule pressure, abiotic conditions, and sowing timing to quantify native-invader dynamics and outcomes across potential restoration manipulations in the field. I measured percent cover and end-of-season aboveground biomass of native species and *P. australis* in each of these treatments to understand the influence of biotic and abiotic factors on plant performance. My findings from this chapter provide evidence-based recommendations for managers performing seed-based wetland restoration in the field.

In Chapter 3 – **Inter- and intraspecific regeneration traits of wetland plants: emerging patterns and unexpected trade-offs** – I explored the variation in the seed and

seedling traits of 7 focal wetland species from a total of 36 populations to identify strategies, trade-offs, and responses to abiotic conditions. Seed trait measurements were conducted in a lab, followed by a series of growth chamber experiments from which I collected germination metrics and seedling trait measurements. I then used principal component analyses, ANOVA modelling, and standard major axis regressions to explore multivariate trait-trait and trait-environment relationships. Findings from this chapter contribute to the larger field of functional regeneration research but offer a unique perspective in inter- and intraspecific regeneration traits in wetland species.

In Chapter 4 – **Modeling germination, survival, and clonal development: implications for invasion resistance following seed-based wetland restoration** – I grew 6 wetland species sourced from a total of 12 populations across temperature and water regimes for the first 8-weeks of growth. I tracked germination, seedling survival (or mortality), the number of clones produced by each seedling, and population-level percent cover. Generalized linear mixed effects models and logistic regressions were conducted to estimate transition probabilities and percent cover outcomes across treatments. The findings from this chapter enhance understanding of early regenerative dynamics of clonal wetland plants, thus allowing for targeted seed-based wetland restoration decisions on which species to seed, where seeds should be sourced, and what site conditions should be targeted to maximize outcomes.

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CHAPTER 2

TIPPING THE BALANCE: THE ROLE OF SEED DENSITY, ABIOTIC FILTERS, AND PRIORITY EFFECTS IN SEED-BASED WETLAND RESTORATION[1]

Abstract

Sowing native seeds is a common approach to reintroduce native plants to degraded systems. However, this method is often overlooked in wetland restoration despite the immense global loss of diverse native wetland vegetation. Developing guiding principles for seed-based wetland restoration is critical to maximize native plant recovery, particularly in previously invaded wetlands. Doing so requires a comprehensive understanding of how restoration manipulations, and their interactions, influence wetland plant community assembly. With a focus on the invader *Phragmites australis,* we established a series of mesocosm experiments to assess how native sowing density, invader propagule pressure, abiotic filters (water and nutrients), and native sowing timing (i.e., priority effects) interact to influence plant community cover and biomass in wetland habitats. Increasing the density of native seeds yielded higher native cover and biomass, but *P. australis* suppression with increasing sowing densities was minimal. Rather, community outcomes were largely driven by invader propagule pressure—*Phragmites australis* densities of $\leq$ 500 seeds/m^2 maintained high native cover and biomass. Low-water conditions increased the susceptibility of *P. australis* to dominance by native competitors. Early sowing of native seeds showed a large and significant benefit to native cover and biomass, regardless of native sowing density, suggesting that priority effects can be an effective restoration manipulation to enhance native plant establishment. Given

[1]Tarsa, E. E., Holdaway, B. M., & Kettenring, K. M. (2022). Tipping the balance: The role of seed density, abiotic filters, and priority effects in seed-based wetland restoration. *Ecological Applications*, e2706.

the urgent wetland restoration need combined with the limited studies on seed-based wetland restoration, these findings provide guidance on restoration manipulations that are grounded in ecological theory to improve seed-based wetland restoration outcomes.

Keywords: abiotic filters, *Phragmites australis*, plant community assembly, priority effects, propagule pressure, seed addition, sowing density, wetland restoration

Introduction

Revegetation of degraded ecosystems is a critical step in restoring lost ecosystem functions and services. However, this goal is often elusive in systems that have been previously invaded by non-native species due to a complex interaction of biotic and abiotic factors that contribute to high reinvasion potential (Suding et al. 2004; Byun et al. 2015). Biotic factors include the depletion of native seeds from the seed bank that limit passive recolonization (e.g., Seabloom et al. 2003; Kettenring & Galatowitsch, 2011), as well as high invader propagule pressure (Holle and Simberloff, 2005; Byun et al. 2015). Abiotic factors that limit revegetation of degraded ecosystem include abiotic invasive legacies (e.g., litter accumulation, alteration of nutrient cycling; Ehrenfeld, 2003; Farrer & Goldberg, 2009) and abiotic conditions at the site that favor invasive over native species recruitment (Yelenik & D'Antonio, 2013). Identifying restoration manipulations (e.g., native sowing densities, restoration site conditions, and timing of native sowing) that can overcome these factors and shift plant communities from an invaded to a native-dominated state are needed. Doing so requires an understanding of how native-invader interactions change both spatially and temporally to improve predictions of community

assembly processes and translate ecological theory into guiding principles for restoration (Török & Helm, 2017; Brudvig, 2017).

Wetland ecosystems are experiencing immense degradation at a global scale (>50% globally; Zedler & Kercher, 2005), partially due to rapid invasive plant spread that has resulted in loss of critical ecosystem functions and services (Zedler & Kercher, 2005; Moomaw et al. 2018). While traditional approaches to wetland revegetation involve passively allowing native species to recruit from the seed bank following invader removal (Galatowitsch, 2012), this approach often does not result in recolonization of desired native species (Carlson et al., 2009; Rohal et al. 2019*b*). Seed-based restoration (i.e., sowing native seeds on site) is a promising active revegetation approach that has numerous logistical and financial benefits (Menges, 2008; Godefroid et al. 2011), but research and application of this technique in the field has been primarily limited to upland systems (e.g., James et al. 2011; Kildeshiva et al. 2016). In contrast, little research has been conducted regarding seed-based restoration of wetlands (but see e.g., Xiong et al. 2003; Adams & Galatowitsch, 2008), which limits robust generalizations on restoring degraded wetlands through seed (Kettenring & Tarsa, 2020).

The density at which to sow native seeds has large implications for plant community assembly and is a common restoration manipulation (Burton et al. 2006), yet guidance for wetlands is lacking (Kettenring & Tarsa, 2020; but see e.g., Adams & Galatowitsch, 2008; van der Valk & Baalman, 2018). Low seeding densities can prevent full acquisition of resources by native communities, which opens opportunities for further invasion and limits self-sustaining feedbacks necessary for population growth (Drake & Lodge, 2006; Pearson et al. 2016; Van Katwijk et al., 2016). High native sowing

densities may mitigate the negative effects of competitors or abiotic filters in the community but can result in intra- and interspecific competition and density-dependent mortality (Burton et al., 2006). Further, in areas with high invader propagule pressure, the native sowing density must be adjusted to ensure that native species suppress growth of invasive plants (Lockwood et al. 2009).

Understanding how abiotic conditions influence native-invader plant interactions can inform restoration manipulations that achieve high native recovery and limit successful invader recolonization by seed (Wilson & Keddy, 1986; Tillman, 1994). Hydrology is a defining abiotic factor in wetlands that influences germination, establishment, and the overall structure and function of a wetland (Weiher & Keddy, 1995; Cronk & Fennessy, 2001; Rosbakh et al. 2020). Furthermore, wetlands are prone to nutrient accumulation due to their position in the landscape and soil legacy effects (Zedler & Kercher, 2004). Invasive species proliferation in high nutrient conditions is well-documented (Davis et al. 2000), and methods of reducing nutrient levels to manage invasive species growth and spread has been tested with mixed success (e.g., Perry et al. 2004*a*; Iannone & Galatowitsch, 2008). Taken together, measuring how native and invasive species respond to water and nutrient conditions across sowing densities is critical to understanding the context-dependency of these restoration manipulations.

Temporal manipulation of community assembly—achieved by altering the order and timing in which species join a community—is a promising frontier to improve seed-based restoration outcomes (i.e., “priority effects”; Young et al. 2017; Hess et al. 2019). Native priority effects, whereby early arriving native species affect the germination, establishment, survival, and growth of later-arriving invasive species, can provide an

advantage to species that typically underperform in restoration. This advantage occurs via the preemption of resources that limits subsequent resource acquisition by invaders ("niche preemption"; Fukami et al. 2015) or alteration of the abiotic environment, making it less hospitable to subsequent invaders ("niche modification"; Fukami et al. 2015). The strength and importance of priority effects are not expected to be universal across all systems (Chase, 2003); weaker priority effects have been demonstrated in systems with extreme environmental harshness, such as low fertility environments, relative to high fertility environments (Kardol et al. 2013; Young et al. 2016; D'Antonio et al. 2017). Although priority effects are relatively unexplored in wetland systems (Weidlich et al. 2021), we might expect priority effects to play a large role in plant community assembly in less harsh, high-nutrient wetlands due to greater strength of competition filtering relative to habitat filtering (Grime, 2006; Villéger et al. 2008; Laliberté & Legendre, 2010). However, the strength of priority effects has been linked to disturbance, connectivity, and productivity (Chase, 2003) which vary substantially in wetland systems and may result in unexpected plant community outcomes. Furthermore, while there is mounting evidence that priority effects can be a useful restoration tool, less is known about how priority effects interact with other restoration manipulations, such as manipulating seed sowing density (but see Hess et al. 2020), which limits the application of this approach in a restoration context.

Phragmites australis Cav. (Trin.) ex. Steud., the focal invader of this study, is a perennial rhizomatous grass species with broad distribution in diverse aquatic habitats (Saltonstall, 2002; Eller et al. 2017). An invasive *P. australis* lineage, originating in Eurasia, has experienced rapid spread in North American wetlands (Saltonstall 2002;

Lambertini et al. 2012) with deleterious ecological impacts (Meyerson et al. 1999; Pendleton et al. 2020; Wails et al. 2021). Relative to the native subspecies (*americanus*; *sensu* Saltonstall et al. 2004), the invasive lineage of *P. australis* (subsp. *australis*; comprised of multiple non-native haplotypes) is substantially more productive above- and belowground, even during the first year of growth (Saltonstall & Stevenson, 2007; Price et al. 2014). Invasive *P. australis* also spreads substantially more by seed than the native subspecies (Kettenring & Mock, 2012) and seed production and seedling establishment is particularly high with elevated nutrients (Saltonstall & Stevenson, 2007; Kettenring et al. 2011; Kettenring and Whigham 2018). Vegetative spread is also an important driver of *P. australis* spread at the local scale, while sexual reproduction and establishment of new populations often occurs via seed which can be accelerated in bare, disturbed soil often associated with restoration sites (Alvarez et al. 2005; Belzile et al. 2010; Saltonstall et al. 2010; Kettenring & Mock, 2012). Preventing *P. australis* seed reinvasion is a high priority for restoration practitioners following *P. australis* control (Bertness et al. 2002; Rohal et al. 2018). Best practices for controlling *P. australis* are a multi-year application of herbicide to kill the plant aboveground (stems, leaves, and stolons) and belowground (roots and rhizomes) followed by mowing, grazing, or burning to reduce seed output and break down its abundant litter (Rohal et al. 2019*a*). However, natural recolonization of desired native wetland plants has been limited post-*P. australis* management (Carlson et al. 2009; Rohal et al. 2019*b*; Elsey-Quirk & Leck, 2021).

Great Salt Lake wetlands, the focal system in this study, are globally significant for millions of migratory birds and have experienced rapid *P. australis* invasion (Evans and Martinson, 2008; Long et al. 2017). Management efforts have effectively reduced *P.*

australis cover, but native plant recovery has been limited, in part due to challenging abiotic conditions that preclude seedling survival (Rohal et al. 2019*b*). Hydrologically, early-onset drought conditions are a management reality in many Great Salt Lake wetlands as upstream water diversions increase and annual precipitation decreases (Downard et al. 2014; Wurtsbaugh et al. 2017). Furthermore, the proximity of Great Salt Lake wetlands to urban development results in areas of high eutrophication (Wurtsbaugh & Marcarelli, 2006; Long et al. 2017). Eutrophication and drought are not unique to Great Salt Lake wetlands; this problem is increasingly occurring in freshwater and coastal wetlands around the globe (Junk et al. 2013). Thus, identifying how competitive interactions change across decreasing water availability and increasing nutrient availability are critical to maximize native plant recovery in this, and other, wetland systems.

Here, we empirically manipulate native sowing densities, *P. australis* propagule pressure, abiotic conditions, and sowing timing to identify strategies that optimize native wetland plant performance while minimizing the performance of *P. australis* (Figure 2.1). To our knowledge, this is the first study to address the interaction of these components of community assembly in seed-based wetland restoration. Specifically, we ask:

(1) Under ambient abiotic conditions, what native seed density should be sown across increasing *P. australis* seed densities to optimize native plant performance and suppress *P. australis* (**Experiment 1**)? We expect that higher densities of *P. australis* in the seed bank will require higher native sowing densities to achieve

native-dominated communities, but that thresholds will exist beyond which native plant performance is limited.

(2) How does the level of local resources (water and nutrients) influence the outcome of interactions between native and *P. australis* across sowing densities (**Experiment 2**)? We expect that species interactions will vary across water levels and nutrient levels such that native species will more effectively suppress *P. australis* performance at high water and low nutrient levels.

(3) Does early sowing of native species relative to *P. australis* arrival yield a native dominated community via native priority effects (**Experiment 3**)? We expect that, given the high fertility of this system, there will be strong priority effects that shift the community to a native-dominated state.

Methods

Study site and mesocosm preparation

All experiments were conducted in mesocosms outside Utah State University's research greenhouses in Logan, Utah, USA. We divided the mesocosms (children's wading pools; 1.5 m diameter × 29 cm deep) into four equal quarters (surface area of approximately 0.44m^2) using corrugated plastic inserts. We filled mesocosms to a uniform level with 0.16 m^3 of Sunshine #3 propagation mix, which is comprised of *Sphagnum* peat moss, vermiculite, and dolomitic limestone (Sungro Horticulture; Agawam, MA, USA). This propagation mix was chosen over field-collected wetland soils to mimic natural wetland drainage and water retention patterns (low drainage, fine particle size, high water retention) and was devoid of a seed bank. This medium also contains no nutrients, which allowed us to control nutrient additions throughout the study.

We positioned mesocosms in an area that had approximately 15 hours of direct sunlight and was buffered from weather extremes such that microclimatic conditions (temperature and light) were relatively uniform.

Seed mixtures and density treatments

We chose a native seed mix consisting of five native wetland species that are often targeted for restoration based on their ability to provide forage and nesting habitat for bird species (Rohal et al. 2018): *Bolboschoenus maritimus* (L.) Palla (alkali bulrush), *Schoenoplectus acutus* var. *acutus* Muhl. ex Bigelow (hardstem bulrush), *S. americanus* (Pers.) Volkart ex Schinz & R. Keller (threesquare bulrush), *Distichlis spicata* (L.) Greene (saltgrass), and *Juncus arcticus* Willd. (Arctic rush). Although *Typha* species was identified as important in suppressing *P. australis* in other studies (Byun et al. 2015), we chose to exclude *Typha* from our seed mix. Although native, *Typha* species are considered problematic for management and are actively controlled in Great Salt Lake wetlands as they make poor waterfowl habitat, replace open water, and choke out more desirable native species (Kettenring et al. 2020). All seeds, including seeds of *P. australis*, were collected from Great Salt Lake wetlands in 2016 – 2017 and stored in paper bags at room temperature (20–23°C) after collection. Prior to the start of the experiment, we tested viability of our seed lots using a standard tetrazolium analysis following the methods of Miller et al (2010) to estimate pure live seeding rate.

We chose four native sowing densities to manipulate across our experiments based on the current recommended and applied sowing rates on Great Salt Lake wetlands (Tarsa et al. 2022; K. Hambrecht, *personal communication*; Table 2.1): (1) 1× (16.81 kg/ha, equivalent to 1,938 seeds/m^2), (2) 2× the recommended native sowing rate (3,876

seeds/m^2), (3) 3× the recommended native sowing rate (5,814 seeds/m^2), and (4) 5× the recommended native sowing rate (9,688 seeds/m^2; Table 2.2). We chose three *P. australis* sowing densities to manipulate across our experiments: (1) low treatment (10 seeds/m^2), (2) medium treatment (500 seeds/m^2), and (3) high treatment (5,000 seeds/m^2; Table S.2). The high-density sowing treatment of *P. australis* was comparable to average *P. australis* seed densities in Great Salt Lake wetlands (5,800 seeds/m^2; Rohal 2018); with the lower *P. australis* densities treatments chosen as treatments that might elucidate ecological thresholds in this system.

The composition of species in the native seed mix, which represents a commonly applied composition in Great Salt Lake wetlands, was held constant across the study; we only manipulated the total density of the mix to reflect our treatments (i.e., native species composition was scaled proportionally within the seed mix). To assemble our native seed mix, we calculated the PLS seeds/m^2 from the recommended PLS kg/ha (Table 2.1) and adjusted the native PLS seeds/m^2 to the size of our experimental unit (mesocosm quarters: 0.44 m^2). We then weighed and counted 3 replicates of 1-g of seed per species to determine the number of seeds per gram. The average number of seeds per gram was then scaled to the experimental unit size to determine the number of seeds (by weight) per treatment applied to a quarter. After calculating seed numbers for our density treatments, seeds of *S. acutus, S. americanus,* and *D. spicata* were cold stratified at 4°C for 35-days to break physiological seed dormancy, following the methods of Marty and Kettenring (2017). To break physiological dormancy for *B. maritimus,* seeds were placed in a 3% bleach solution for 24 hours, after which they were rinsed thoroughly and

immediately seeded (Marty & Kettenring, 2017). *Juncus arcticus* and *P. australis* were not pre-treated prior to seeding as they exhibit no dormancy.

Experimental design

For Experiment 1, we established 15 mesocosms in a 3 × 4 full factorial split-plot design to test the effects of *P. australis* and native seed mix densities (with three and four seed density levels, respectively; 'Objective 1'); each treatment combination was replicated five times (see Appendix A: Figure S.2.1 for experimental set-up). We seeded each mesocosm with one of three *P. australis* densities (10 seeds/m^2, 500 seeds/m^2, 5000 seeds/m^2), such that all quarters in a pool contained the same density of *P. australis* seeds. In each quarter, we seeded one of four native seed mix densities (1938 seeds/m^2, 3876 seeds/m^2, 5814 seeds/m^2, 9688 seeds/m^2); densities were randomly assigned to quarters, and each mesocosm contained all four densities. We mixed all seeds for a given treatment prior to seeding and evenly applied seeds to the appropriate mesocosm quarter on June 22, 2018. Mesocosms were thoroughly watered to saturate the soil profile prior to seeding, after which they were watered to the appropriate level. Water level was maintained at the soil surface (i.e., saturated soil) throughout the experiment using an automatic irrigation system that sprayed water evenly across the mesocosm multiple times a day, adjusted as needed throughout the growing season to maintain a moist soil profile. We applied Nutricote 18-6-8 Type 100 slow-release fertilizer twice during the growing season at a rate of 21.6 g N/m^2 per pool to ensure nutrient limitation was not impacting plant growth (Appendix A: Table S.2.1).

In Experiment 2, we prepared 40 mesocosms in an incomplete block split-plot design to test the effect of nutrients (two levels), water (two levels), *P. australis* density

(three levels), and native seed mix density (three levels; 'Objective 2'). Each combination of water (high, low) and nutrient (high, low) levels was randomly assigned to mesocosms at the whole-plot level (see Appendix A: Fig. S.2.2 for experimental set-up). Hand-watering of the mesocosms (twice per day) allowed for a high-water level, in which each quarter was soaked for 30 seconds each to maintain water at the soil surface, and a low water level that applied 10 seconds of water to each quarter to maintain water 2 cm below the soil surface. Careful daily observation throughout the experiment ensured that water application was consistently applied and maintained across mesocosms. Nutrients were applied twice during the growing season. The first application occurred on June 12, 2019, using Nutricote 18-6-8 Type 100 slow-release fertilizer applied at a rate of 38.0 g N/m^2 for the high-nutrient mesocosms and 9.5 g N/m^2 for the low-nutrient mesocosms. A second nutrient application (Polyon 16-6-13 slow-release fertilizer) occurred on August 8, 2019 (Appendix A: Table S.2.1). Sowing density treatments were defined as a full 2 (native: 5814 seeds/m^2 [3×] and 9688 seeds/m^2 [5×]) × 3 (*Phragmites:* 0 seeds/m^2, 500 seeds/m^2 [medium], and 5000 seeds/m^2 [high]) factorial plus one (native: 0 seeds/m^2, *Phragmites*: 5000 seeds/m^2 [high]) for a total of seven sowing treatments (Appendix A: Table S.2.2). Four of the seven treatments were randomly assigned to quarters in each mesocosm. Across mesocosms, each sowing treatment was replicated five times, for a total of 140 of the 160 mesocosm quarters filled. We applied nutrients directly to quarters in which seeds were sown and did not apply nutrients in empty quarters. All seeds for a given sowing treatment were mixed prior to seeding and evenly applied to the appropriate mesocosm quarter on June 12, 2019. Mesocosms were thoroughly watered to saturate the soil profile prior to seeding, after which they were watered to the appropriate level.

In Experiment 3, we established 8 mesocosms to evaluate native sowing density (two levels) and native sowing timing (three levels) on *P. australis* and total native cover and biomass (Appendix A: Figure S.2.3 for experimental set-up; 'Objective 3'). *Phragmites australis* seeds were sown at 500 seeds/m^2 within each pool on July 10, 2019. In each quarter, one of two native seed mix densities (5814 seeds/m^2 [3×] and 9688 seeds/m^2 [5×] treatment) was sown at one of three randomly assigned sowing times (4-week native priority [June 12, 2019], 2-week native priority [June 26, 2019], and no native priority in which seeds were sown at the same time as *P. australis* [July 10, 2019]). Across mesocosms, the full 2 (sowing density) × 3 (sowing timing) factorial was replicated six times, filling 30 of the 32 mesocosm quarters. Mesocosms were hand-watered to the high-water level (i.e., soil surface saturation) and nutrients were applied to seeded quarters at the same time and rate as the high-nutrient treatment described in the Experiment 2 study. Mesocosms were thoroughly watered to saturate the soil profile prior to seeding, after which they were watered to the appropriate level.

Data collection

We collected percent cover and aboveground biomass data within each quarter partitioned between *P. australis* and total native species for all experiments. Percent cover data were visually estimated throughout the growing season using a classification system based on Brohman and Bryant's (2005) 10-percent class breaks. We included an additional three classes at the tail ends of the distribution to represent plant cover at 0%, 0–1%, and 99–100% for a total of 13 cover classes (Appendix A: Table S.2.2). Percent cover data were collected by a single observer for each experiment. Aboveground biomass was harvested at the end of each growing season (August 27–31, 2018; August

26–September 1, 2019) and sorted into separate paper bags by species and quarter. Biomass was dried in a forced air oven at 60°C for 48 hours and weighed.

Statistical analysis

Statistical analyses were performed in R version 3.6.3 (R Core Team 2020). We used end-of-season percent cover data converted to midpoint values in the analyses. We summed the percent cover and biomass of all native species to assess total native performance relative to *P. australis* performance. In instances where the summed native cover exceeded 100%, we capped the total cover at 100% for analyses, which was supported by visual estimations of each quarter indicating that no bare ground was present (i.e., the total native cover occupied 100% of the quarter). Percent cover data were analyzed as continuous proportions using a generalized linear mixed model with a beta distribution and logit link in the glmmTMB package for all experiments (v 1.0.2.1; Brooks et al. 2017). Because the beta distribution only allows for [0,1] bounded data, we added or subtracted 0.001 to data on the lower and upper bounds prior to running the cover models (Douma & Weedon, 2019). Biomass was analyzed with a linear mixed model using the lmerTest package for all experiments. (v 3.1.3; Kuznetsova et al. 2017). Model were inspected for over/underdispersion and zero-inflation using the DHARMa package (v 0.4.1; Hartig, 2020). We used the Tukey HSD method at $\alpha = 0.10$ to assess pertinent mean comparisons adjusted as needed for family-wise Type I error rate (Day and Quinn, 1989).

For Experiment 1, we compared the effects of *P. australis* sowing density and native sowing density for the two vegetation components (*P. australis* or pooled native) on biomass or percent using a split-split plot design. Pool was the whole-plot unit, with *P.*

australis sowing density as the whole-plot treatment factor. Quarter nested within pool was the split-plot unit, with native sowing density as the split-plot treatment factor. The vegetation partition nested within quarter within pool was the split-split plot unit, with vegetation component as the split-split plot treatment factor. The vegetation partition was a random effects factor and represents the repeated measurement of cover or biomass that is nested within each quarter and was associated with the two levels of the vegetation component (pooled native or *P. australis*) as a fixed effects factor. Both biomass and percent cover models included pool (15 levels), quarter (60 levels; nested within pool), and vegetation partition (120 levels; nested within quarter) as random effects; *P. australis* sowing density (3 levels), native sowing density (4 levels), vegetation component (2 levels: *P. australis* or pooled native), and all interactions were included as fixed effects. Biomass was square-root transformed to better meet assumptions of normality and homogeneity of variance.

To address the 2 × 3 + 1 factorial treatment structure in Experiment 2, we crafted two sub-designs from the full design, each of which had a full factorial treatment structure (subsequently referred to as design A & B). For design A, we used a split-plot design to assess the effects of water (2 levels), nutrients (2 levels), native sowing density (3 levels), and all interactions on *P. australis* biomass and cover when seeded at high *P. australis* density. Pool was the whole-plot unit, with water × nutrients as the whole-plot treatment factors. Quarter nested within pool was the split-plot unit, with native sowing density as the split-plot treatment factor. Both biomass and percent cover models for data design A included pool (40 levels) and quarter (140 levels; nested within pool) as random effect factors. Data design B used a split-split-plot design to assess the effects of water (2

levels), nutrients (2 levels), native sowing density (2 levels), *P. australis* density (3 levels), vegetation component (2 levels), and all 2^{nd-} and 3rd-order interactions as fixed effects on *P. australis* and total native cover and biomass. Pool was the whole-plot unit, with water × nutrients as the whole-plot treatment factors. Quarter nested within pool was the split-plot unit, with native sowing density and *P. australis* sowing density as the split-plot treatment factors. The vegetation partition nested within quarter within pool was the split-split plot unit, with vegetation component as the split-split plot treatment factor. Random effects included pool (40 levels), quarter (140 levels; nested within pool), and vegetation partition (280 levels; nested within quarter within pool)**.** Biomass data were log-transformed as necessary to meet assumptions of normality and homogeneity of variance.

We analyzed data from Experiment 3 using a split-split-plot design to compare the effects of native sowing density and sowing timing for the two vegetation components on biomass and cover. Pool was the whole-plot unit, with *P. australis* sowing density as the whole-plot treatment factor. Quarter nested within pool was the split-plot unit, with native sowing density × sowing timing as the split-plot treatment factors. The vegetation partition nested within quarter within pool was the split-split plot unit, with vegetation component as the split-split plot treatment factor. Pool (8 levels), quarter (30 levels), and vegetation partition (60 levels) were included as random effects in the model; native density (2 levels), sowing timing (3 levels), vegetation component (2 levels: *P. australis* or pooled native), and all interactions were included as fixed effects.

Results

Plant performance varies across native and P. australis sowing densities (Experiment 1)

Our model results indicated a significant 2-way interaction between *P. australis* density and percent cover (Table 2.3). Increasing densities of *P. australis* yielded a significant increase in *P. australis* cover s and a significant decrease in native cover (Figure 2.2a). At the low and medium *P. australis* densities, there was no statistically significant difference in native cover, but native cover was reduced by 55% at the highest *P. australis* density (Figure 2.2a). We also found a significant 2-way interaction between native density and cover, such that *P. australis* cover decreased with increasing native sowing density (Table 2.3; Figure 2.2b). However, a significant reduction in *P. australis* cover was only observed between the 1× and 2× native sowing treatments; *Phragmites australis* cover reductions at the highest native treatments (3× and 5×) did not significantly differ from each other or from the 2× native sowing density (Figure 2.2b). Similarly, increasing native sowing density beyond the 2× native sowing treatment did not significantly increase native cover (Figure 2.2b).

Our model also identified a significant 2-way interaction between *P. australis* density and biomass (Table 2.3). Increasing *P. australis* seed densities yielded increasing *P. australis* biomass and decreasing native biomass (Figure 2.2c). Native biomass was significantly higher than *P. australis* only at the lowest *P. australis* density; there was no statistical difference between native biomass and *P. australis* biomass at the medium *P. australis* density and the highest *P. australis* density suppressed native biomass by 70% relative to the medium *P. australis* density (Figure 2.2c). There was also a significant 2-way interaction between native density and biomass, which showed a significant

reduction in *P. australis* biomass between the 3× and 5× native sowing densities (Table 2.3; Figure 2.2d). *Phragmites australis* biomass was not statistically distinguishable between the 1× and 3× native sowing densities (Figure 2.2d). Across all models, we found no 3-way interaction. To understand how individual native species in the seed mix were driving plant responses, we determined the relative contribution of each individual native species to total native cover and biomass. Nearly 50% of the final percent cover of native species was contributed by *D. spicata* (range: 42–61%), followed by *B. maritimus* (30–47%), *J. arcticus* (6–11%), *S. acutus* (<10%), and *S. americanus* (<1%; Figure 3a-c). *Distichlis spicata* made up most of the native biomass (35–80%), followed by *B. maritimus* (15–58%), *J. arcticus* (3–13%), *S. acutus* (<5%), and *S. americanus* (<1%; Figure 3d–f). Except for *D. spicata* and *B. maritimus*, all sown native species underperformed relative to their starting density in the seed mix (Figure 2.3).

Water level alters the competitive relationship between native and P. australis performance across sowing densities (Experiment 2)

Effects of water, nutrients, and native sowing density on plant performance at the highest P. australis density (5000 seeds m^{-2}; data design A)

We found a significant 2-way interaction between native density and water level on *P. australis* cover and biomass (Table 2.4). In high-water conditions, there was no significant reduction in *P. australis* cover and biomass with increasing native sowing densities (Figure 2.4a, b). Relative to high-water conditions, *P. australis* cover was reduced by 18% and *P. australis* biomass was reduced by 50% in low-water conditions at the highest native sowing density (5× treatment; Figure 2.4a, b). Across all native sowing densities, including the treatment in which no natives were sown (0×), *P. australis* biomass we reduced in low-water levels relative to high-water levels (Figure 2.4b).

Conversely, *P. australis* cover was only reduced in low-water levels relative to high-water levels when sown with native species, with greater suppression of *P. australis* cover observed as native sowing density increased (Figure 2.4a). Nutrients did not significantly impact *P. australis* cover or biomass (Table 2.4; Appendix A: Figures S.2.4-S.2.7).

Effects of water, nutrients, native sowing density, and P. australis density on plant performance (data design B)

We found a significant 3-way interaction between water level, *P. australis* density, and the vegetation component (Table 2.5). Native cover and biomass decreased with increasing *P. australis* density, but the magnitude of the decrease in native cover depended on water level (Figure 2.5a). At the highest *P. australis* density, native cover was reduced by 29% in the high-water condition relative to the low-water condition (Figure 2.5a), but there was no change in native biomass across water levels as *P. australis* density increased (Figure 2.5c). Conversely, *P. australis* cover and biomass increased with increasing *P. australis* density, but the magnitude of that increase depended on water level (Figure 2.5b, d). There was a 10% reduction in *P. australis* cover in the low-water condition relative to the high-water condition at the highest *P. australis* density (Figure 2.5b). *Phragmites australis* biomass was suppressed in the low-water condition relative to the high-water condition at the medium (22% reduction) and high (48% reduction) *P. australis* densities (Figure 2.5d).

Our model also indicated a significant 3-way interaction between *P. australis* density, native density, and the vegetation cover component (Table 2.5). Native cover and biomass decreased with increasing *P. australis* density, but the magnitude of the decrease

depended on native sowing density (Figure 2.6a, c). At the highest *P. australis* density, native cover was 40% higher when sown at the 5× rate relative to the 3× rate (Figure 2.6a). The 5× native sowing rate also resulted in 73% and 79% higher native biomass relative to the 3× sowing rate at the medium and high *P.* australis densities, respectively (Figure 2.6c). *Phragmites australis* cover and biomass increased with increasing *P. australis* density regardless of native sowing density (Figure 2.6b, d).

Early sowing provides priority effect for native species relative to P. australis (Experiment 3)

Native species cover and biomass were significantly higher than *P. australis* cover and biomass when sown 4- or 2-weeks prior to *P. australis* sowing, regardless of native sowing density (Table 2.6; Figure 2.7a, b). A 4-week native priority resulted in a 41% increase in native cover and a modest and non-significant 9% reduction in *P. australis* cover relative to no native priority (Figure 2.7a). *Phragmites australis* biomass experienced significant biomass suppression (97%) and native biomass increased by 282% when natives were sown 4-weeks earlier than *P. australis* (Figure 2.7b). A 2-week native priority increased native cover (19%) and native biomass (118%) relative to no native priority, with modest and insignificant reductions in *P. australis* cover and biomass (Figure 2.7a, b). Approximately 75% of the native response was driven by *D. spicata* with other native species playing a moderate (*B. maritimus*) or minor role (all other species; Appendix A: Figure S8).

Discussion

Reassembling plant communities that favor native species over invaders requires an understanding of the interaction between biotic and abiotic drivers of vegetation

dynamics (Hobbs & Norton, 2004; Bradley et al. 2010; Yannelli 2021). Here, we manipulated invader propagule pressure, abiotic conditions, and timing of species arrival across native sowing densities in experimental wetland communities to identify restoration manipulations to enhance native plants relative to the aggressive invader, *P. australis*. We predicted that higher densities of *P. australis* in the seed bank would require higher native sowing densities to achieve native-dominated communities. Surprisingly, our findings did not fully support this prediction; rather, propagule pressure and native density acted independently and increasing native sowing densities only increased native performance with a modest negative impact on *P. australis*. *Phragmites australis* propagule pressure was the predominant driving factor: increasing invader propagule pressure resulted in a more substantial reduction in native cover and biomass than the native performance gains associated with increasing native sowing density. Native-invader interactions varied across abiotic conditions, although not in ways that we predicted. Low-water levels were more effective at suppressing *P. australis* relative to high-water levels. To our surprise and contrary to the rich literature linking *P. australis* success to nutrient enrichment (e.g., Saltonstall & Stevenson, 2007; Holdredge et al. 2010; Kettenring et al. 2011), we found that nutrient levels did not affect *P. australis* or native performance. We also predicted that this wetland system would be sensitive to species introduction such that native priority effects would result in native-dominated communities. Our findings supported this prediction; native species performance was significantly greater than *P. australis* performance when natives were sown 2- and 4-weeks earlier than *P. australis*. Given the urgent wetland restoration need combined with the limited studies on seed-based wetland restoration, these findings provide guidance on

restoration manipulations that are grounded in ecological theory to improve seed-based wetland restoration outcomes.

The interplay between native seed density and invader propagule pressure on wetland plant communities

Increasing native sowing density is a common restoration manipulation to increase native establishment and suppress invasive plant species (Nemec et al. 2013; Barr et al. 2017; Yannelli et al. 2018). However, many studies suggest that above a certain density, there will be little to no benefit of increasing the native sowing rate (Burton et al. 2006; Wilkerson et al. 2014). In the present study, increasing native sowing density provided some benefit to native performance and a statistically significant, but modest, suppression of *P. australis* performance in some conditions. This *P. australis* suppression was not observed consistently across experiments, indicating that native sowing rates in this study may be below the ecological threshold needed to yield a significant and consistent suppression of *P. australis*. Further, we did not find evidence of density-dependent mortality at higher native sowing rates, indicating that higher sowing rates (as others have used; see below) could be applied to enhance *P. australis* suppression, which may have resulted in a more consistent suppression of *P. australis* across our experiments. For comparison, Byun et al. (2015) saw a 93% reduction in *P. australis* shoots when natives were sown at a rate of ~25,000 seeds/m^2, 12× the commonly applied seeding rate in Great Salt Lake wetlands. Adams and Galatowitsch (2008) sowed a native mix at 15,000 seeds/m^2 and saw a 50% biomass reduction in another wetland grass invader, *Phalaris arundinacea*. While high native sowing densities can offer significant suppression of wetland invaders, these densities may be financially

infeasible for practitioners. From a management perspective, gains in native plant responses and suppressive effects on invaders should provide significant ecological benefits to justify the (oftentimes large) increase in expense and labor. Our results suggest there may be justification for increasing native sowing densities to increase native cover and biomass, particularly at 5× the recommended rate (9,688 seeds/m^2), but that higher native sowing densities must be applied in conjunction with (or secondary to) decreasing invader propagule pressure.

Invasive propagule pressure is a strong predictor of invasion success (Lockwood et al. 2005; Holle and Simberloff, 2005; Simberloff, 2009). Here, native recovery was more dependent on *P. australis* propagule pressure than on native sowing density, supporting the idea that invader propagule pressure can overwhelm community assembly (Lockwood et al. 2005; Lockwood et al. 2009). We identified propagule pressure thresholds that are critical in guiding seed-based wetland restoration efforts; *Phragmites. australis* seed bank densities should be ≤ 500 seeds/m^2 to maintain high native cover and biomass. When *P. australis* densities increased from 500 to 5,000 seeds/m^2 there was a large and significant reduction in native cover and biomass. Studies on seed bank dynamics indicate that *P. australis* abundance in the seed bank can range from low (e.g., 10 seeds/m^2; Baldwin et al. 2010) to high abundance (27,000 seeds/m^2; Elsey-Quirk & Leck, 2021). This variation does not always correlate to standing *P. australis* vegetation (Wilson et al. 1993) but can be partially attributed to propagule movement across the landscape (e.g., via tidal action or wind; Galatowitsch & Biederman, 1998; Baldwin et al. 2010). Given the importance of propagule pressure in driving community assembly, propagule pressure mitigation techniques and strategies need to be widely adopted in

management and restoration plans (Stringham & Lockwood, 2021). More research is warranted to identify factors that predict *P. australis* seed bank abundance and on functional traits that shed light on *P. australis* seed behavior in the seed bank (e.g., longevity/persistence traits; Larson & Funk, 2016).

The effect of abiotic conditions on native – invasive plant interactions

Biotic factors interact with an array of abiotic conditions at a site to influence community assembly trajectories (Byun et al. 2015). In this study, we found that hydrology was the primary driver of community outcomes. Hydrology is known to have a strong influence on *P. australis* growth across life stages with deeply flooded conditions (> 5 cm above soil surface) limiting germination and emergence at early regenerative stages (Elhaak et al. 1993; Alvarez et al. 2005; Li et al. 2013) and flooded to moist soils promoting growth in adult plants (Packer et al. 2017). When grown in the absence of native species in this study, there was a significant reduction in *P. australis* biomass (but not cover) between the high- (saturated) and low-water level (dry) treatments. These findings are in line with the expected physiological and morphological response of *P. australis* to decreased water availability—in low to moderate drought stress, *P. australis* employs a tolerance strategy by reducing the production of new leaves, increasing leaf shedding, and reducing overall leaf size (Pagter et al. 2005).In the presence of the native seed mix, there were significant reductions in *P. australis* cover and biomass in the low- relative to the high-water levels. Furthermore, *P. australis* growing in high-water conditions did not experience any suppression regardless of native sowing density. These findings suggest that low-water levels increase the susceptibility of *P. australis* to suppression by native species, particularly when grown with the drought-tolerant *D.*

spicata (Ungar, 1974), and manipulating water levels could be an effective strategy to enhance *P. australis* suppression in wetland restoration in wetlands (such as the Great Salt Lake wetlands) that have the infrastructure to do so.

The statistical non-significance of nutrients in driving community outcomes in this study was unexpected, though not necessarily surprising in retrospect. Nutrient enrichment is widely recognized as a driver of invasion (Davis et al. 2000), particularly for *P. australis* that exploits high nutrient conditions across juvenile and adult life stages (Saltonstall & Stevenson, 2007; King et al. 2007; Uddin & Robinson, 2018). The nutrient levels tested in this study were in line with other *P. australis* nutrient studies (Minchinton & Bertness, 2003; Kettenring & Whigham, 2018), although our application of a 100-day slow-release fertilizer as opposed to liquid fertilizer, in which nutrients are readily available, could have resulted in a more muted effect across the duration of the study. Further, the invasive lineage of *P. australis* is known to exhibit a high degree of phenotypic plasticity (e.g., Mozder & Megonigal, 2012), which could partially explain the lack of response across nutrient levels tested in this experiment. Our study does not diminish the importance of nutrient enrichment, but it does highlight a strong influence of hydrology in *P. australis* growth. Conveniently, manipulating water levels to reduce *P. australis* performance may be a more tractable management tool at a restoration site (especially in this study region where impoundments and headgates for managing water are common; Downard et al. 2014) relative to reducing nutrient enrichment at the watershed scale.

Native priority effects can benefit native communities given appropriate species selection and site conditions

Although priority effects have become a recent topic of interest in restoring invasion resistant communities (e.g., Hess et al. 2019; Hess et al. 2020; Byun, 2022), they have yet to be studied in wetland systems (Weidlich et al. 2020). Furthermore, studies conducted to investigate the interaction between priority effects and other restoration manipulations, such as sowing density, are relatively scarce in the literature. We found evidence that priority effects provided an advantage to native species performance when sown 2- and 4-weeks prior to *P. australis* sowing. This was particularly true for species biomass; a 4-week native sowing advantage profoundly tipped the balance towards a native-dominated plant community relative to no native priority advantage. Interestingly, native species had a strong priority effect regardless of the density sown, which is in line with other studies (von Gillhaussen et al. 2014; Hess et al. 2020). While increasing native sowing density can yield higher initial performance of sown species (this study; Yannelli et al. 2017; Byun et al. 2020), the native cover and biomass differences between the 5× native sowing rate relative to the 3× rate stabilized, as would be expected based on the law of constant yield (Drew & Flewelling, 1979). Thus, providing a priority advantage by sowing natives earlier in the season may be a feasible alternative when financial constraints limit increasing native sowing densities.

Many wetlands are highly productive (Zedler and Kercher, 2004), thus light is considered the primary limiting resource (Perry & Galatowitsch, 2004*b*; 2006). *Distichlis spicata*, which germinates rapidly following dormancy release (E. Tarsa, *unpublished data*) and has a dense growth form (Ungar, 1974), was able to rapidly occupy the available above-ground space in this study relative to the other study species and limit

light necessary for *P. australis* germination and establishment, thus preempting niche space and modifying subsequent niches to make them less suitable for invader establishment (Vannette & Fukami, 2014; Fukami, 2015). Native species that have similar functional traits (e.g., rapid germination, fast relative growth rate) to preempt above-ground resources may compete well with *P. australis* (Byun et al. 2013; Byun et al. 2015), but the germination requirements of native species should be considered to ensure that those requirements line up with early-season abiotic conditions in the field. This point is particularly important when applying our findings in a field restoration context. In restoration scenarios where *P. australis* seeds are already present in the seed bank, it is critical to identify and sow native species that can withstand early-season germination conditions, exhibit rapid early growth, and have a light-inhibiting growth form to effectively create a priority effect that suppresses *P. australis* germination and growth (Byun et al. 2013; Byun et al. 2015). Furthermore, species that exhibit dormancy should undergo dormancy breaking treatments prior to sowing to ensure seeds are able to germinate rapidly after sowing (Kettenring & Tarsa, 2020).

Experimental challenges and opportunities for future research

No experiment is perfect in replicating real-world ecological systems and there are always opportunities for improvement of experimental design, experimental realism, and the temporal effects of experimental treatments. In the present study, we saw *P. australis* contamination in quarters that were not seeded with *P. australis*, resulting in some *P. australis* cover and biomass in those quarters. This contamination was not significant across water or nutrients levels but was slightly higher in the 5× relative to the 3× native sowing density for *P. australis* cover. This pattern is opposite of what we

would have expected based on experimental results indicating the 5× native sowing density was superior in *P. australis* suppression relative to the 3× sowing density. In other words, the *P. australis* contamination was likely dampening treatment effects rather than contributing to the patterns we observed in the data. While the contamination of *P. australis* could have been related to imperfect methodology, it may also be related to *P. australis* seeds being wind dispersed onto the plots from sources in the landscape or rhizome expansion between quarters. Regardless, this background *P. australis* movement does reflect more realistic field conditions—the likelihood of *P. australis* rhizome expansion and seed dispersal in previously invaded wetlands is high. Because we did not see significant differences in native performance across native sowing densities in quarters where *P. australis* seeds were not sown but where quarters were contaminated, we deduce that background *P. australis* movement had little impact on the findings of this study.

More research is needed to investigate long-term impacts of seeding in wetlands to determine if the initial first-year plant community can persist in subsequent years. Some evidence suggests that the initial native priority advantage is not maintained in the plant community many years after seeding (Young et al. 2017). Additional experimentation on priority effects in wetlands is recommended to identify which species have germination requirements that align with early-season field conditions and how native priority effects change over *P. australis* propagule pressure (here only 500 seeds/m^2 *P. australis* density was tested). Moreover, more research is needed to identify specific strategies that can enhance native priority in a field setting where *P. australis* is likely already present in the soil (e.g., winter vs. spring sowing, sowing species with

functional regeneration traits conducive to rapid colonization, ameliorating ecological filters limiting native species germination). Additional factors that influence the importance of priority effects (e.g., disturbance, fertility, species pools) and native-invader species interactions can vary substantially in the field, emphasizing the importance of scaling up this experiment to a wetland field setting.

Conclusions & recommendations

Limited seed supplies at a global scale, in addition to limited funding for restoration, underscore the importance of identifying seed-based wetland restoration techniques that maximize native plant recovery (Merritt and Dixon, 2011; Harrison et al. 2020). Based on our experimental results, we recommend the following practices for seed-based wetland restoration:

1. **Prioritize restoration sites that have low *P. australis* propagule pressure and work to mitigate *P. australis* propagules at the landscape-scale.** Once existing stands of *Phragmites* are sufficiently controlled with herbicide treatments, maximum native plant recovery is likely to be achieved in sites with ≤ 500 seeds/m^2 *P. australis* seeds in the seedbank. Our findings, in combination with others, suggest that: 1) at the site level, areas with low invader propagule pressure should be chosen for restoration, and 2) at the landscape level, collaboration between landowners and agencies should focus on systematically mitigating *P. australis* propagule movement across the landscape (e.g., Kettenring et al. 2011; Hazelton et al. 2014). Incorporating propagule pressure mitigation techniques should be adopted widely into management and restoration plans.

2. **Increase native sowing density to promote higher native cover and biomass.** Native densities sown at 5× the recommended sowing rate (9,688 seeds/m^2) yield significantly higher native cover and biomass relative to the 3× sowing rate (5,813 seeds/m^2) and offer modest suppression of *P. australis*. In combination with reducing invader propagule pressure, this is likely to yield a native-dominated plant community.
3. **Where possible, reduce water levels at the restoration site to suppress *P. australis* growth.** We found significant suppression of *P. australis* by native species in low-water levels (water table >2 cm below soil surface), but this suppression was largely driven by *D. spicata*, a drought-tolerant native grass that flourished under these conditions. This finding is consistent with field observations of many Great Salt Lake wetland managers who now intentionally reduce water levels to suppress *P. australis* germination (Kettenring et al. 2020). Including *D. spicata* or a similar drought-tolerant native in the seed mix can maximize *P. australis* suppression at low-water levels. Future research should be conducted in a field setting to determine how native priority effects influence plant community assembly in the field across heterogenous abiotic conditions and disturbance levels.
4. **Sow native species early in the season before *P. australis* has emerged.** This approach will allow native plants to get a 'head-start' on acquiring resources, making *P. australis* germination more difficult. Sowing early can benefit natives regardless of sowing density, making it an attractive option when budgets limit high native sowing density. However, this approach must be applied when 1) native species can effectively acquire early-season resources (i.e., fast-growing *D. spicata*

in this study), and 2) when the germination requirements of native species align with the early-season conditions at the site.

5. **Maintaining the newly restored wetland is critical for long-term success.** Regular monitoring and maintenance of the site will ensure that any subsequent *P. australis* invasion, either via seedling establishment or clonal expansion from nearby patches, can be addressed through spot-spraying or manual removal (Kettenring et al. 2020). Prioritizing areas directly around the restoration site for *P. australis* herbicide control can help buffer the restoration site from reinvasion via clonal expansion (Long et al. 2017).

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Tables and Figures

TABLE 2.1. Seeding rate in PLS (pure live seed) kg/ha and seeds/m^2 for target species included in native seed mix.

Species name	**Common name**	**PLS kg/ha**	**Seeds/m^2**	**% PLS in mix**
Schoenoplectus americanus	Threesquare bulrush	4.48	183	9.5
Schoenoplectus acutus	Hardstem bulrush	2.24	183	9.5
Bolboschoenus maritimus	Alkali bulrush	4.48	161	8.3
Distichlis spicata	Saltgrass	5.27	603	31.1
Juncus arcticus	Arctic rush	0.34	807	41.6
	TOTAL:	16.81	1938	100.0

TABLE 2.2. Seed sowing treatments for Experiment 1 (top), Experiment 2 (middle), and Experiment 3 (bottom).

Experiment 1	
Native treatment	**Seeds/m^2**
1× recommended rate	1938
2× recommended rate	3876
3× recommended rate	5814
5× recommended rate	9688
***P. australis* treatment**	**Seeds/m^2**
Low	10
Medium	500
High	5000

Experiment 2	
Native treatment	**Seeds/m^2**
0× recommended rate	0
3× recommended rate	5814
5× recommended rate	9688
***P. australis* treatment**	**Seeds/m^2**
None	0
Medium	500
High	5000

Experiment 3	
Native treatment	**Seeds/m^2**
3× recommended rate	5814
5× recommended rate	9688
***P. australis* treatment**	**Seeds/m^2**
Medium	500

TABLE 2.3. Analysis of deviance results from mixed effects model analyzing the effects of *P. australis* density, native density, the vegetation component, and their interactions on (A) biomass and (B) cover (Experiment 1). Also reported are the variance estimates for the model random effects; estimates are on the square root scale (biomass) and logit scale (cover). Type III significance tests at $P < 0.10$ are shown in bold.

(A) Model Predictors for Biomass	**Chi-sq**	**Df**	***P* value**
(Intercept)	**2115.810**	**1**	**< 0.001**
***P. australis* density**	**30.094**	**2**	**< 0.001**
Native density	1.464	3	0.691
Vegetation component	**8.287**	**1**	**0.004**
P. australis density × native density	7.248	6	0.300
***P. australis* density × vegetation component**	**556.859**	**2**	**< 0.001**
Native density × vegetation component	**28.500**	**3**	**< 0.001**
P. australis density × native density × vegetation component	4.272	6	0.640

Variance Estimates of Random Effects	**Variance (σ^2)**	**Std. Dev. (σ)**
Quarter: Pool	0.000	0.000
Pool	0.230	0.480
Residual	3.195	1.788

(B) Model Predictors for Cover	**Chi-sq**	**Df**	***P* value**
(Intercept)	**157.892**	**1**	**< 0.001**
P. australis density	**22.771**	**2**	**< 0.001**
Native density	0.062	3	0.996
Vegetation component	**68.097**	**1**	**< 0.001**
P. australis density × native density	9.132	6	0.166
***P. australis* density × vegetation component**	**238.982**	**2**	**< 0.001**
Native density × vegetation component	**19.055**	**3**	**< 0.001**
P. australis density × native density × vegetation component	3.010	6	0.796

Variance Estimates of Random Effects	**Variance (σ^2)**	**Std. Dev. (σ)**
Pool	0.011	0.104
Quarter: Pool	0.000	0.000

TABLE 2.4. Analysis of deviance results from mixed effects models analyzing the effects of water, nutrients, native density, and their interactions on *P. australis* (A) biomass and (B) cover when *P. australis* density is 5,000 seeds m^{-2} (Experiment 2; data design A). Also reported are the variance estimates for the model random effects; estimates are on the log scale (biomass) and logit scale (cover). Type III significance tests at $P < 0.10$ are shown in bold.

(A) Model Predictors for Biomass	**Chi-sq**	**Df**	***P* value**
(Intercept)	**15417.299**	**1**	**< 0.001**
Water	**36.081**	**1**	**< 0.001**
Nutrients	0.186	1	0.667
Native density	**18.572**	**2**	**< 0.001**
Water × nutrients	0.085	1	0.770
Water × native density	**5.283**	**2**	**0.071**
Nutrients × native density	0.769	2	0.681
Water × nutrients × native density	3.085	2	0.214
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Pool		0.015	0.123
Residual		0.070	0.265

(B) Model Predictors for Cover	**Chi-sq**	**Df**	***P* value**
(Intercept)	**284.041**	**1**	**< 0.001**
Water	**19.169**	**1**	**< 0.001**
Nutrients	0.002	1	0.969
Native density	**22.555**	**2**	**< 0.001**
Water × nutrients	0.444	1	0.505
Water × native density	**14.702**	**2**	**< 0.001**
Nutrients × native density	0.821	2	0.663
Water × nutrients × native density	2.924	2	0.232
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Pool		0.183	0.428

TABLE 2.5. Analysis of deviance results from mixed effects models assessing the effects of water, nutrients, native density, *P. australis* density, vegetation component, and their interactions on native and *P. australis* (A) biomass and (B) cover (Experiment 2; data design B). Also reported are the variance estimates for the model random effects; estimates are on the square root scale (biomass) and logit scale (cover). Type III significance tests at $P < 0.10$ are shown in bold.

(A) Model Predictors for Biomass	**Chi-sq**	**Df**	***P* value**
(Intercept)	**3113.962**	**1**	**< 0.001**
Water	**9.383**	**1**	**0.002**
Nutrients	**13.757**	**1**	**< 0.001**
Native density	1.161	1	0.281
***P. australis* density**	**46.752**	**2**	**< 0.001**
Vegetation component	0.114	1	0.736
Water × nutrients	0.008	1	0.929
Water × native density	0.091	1	0.763
Water × *P. australis* density	1.988	2	0.370
Water × vegetation component	**9.165**	**1**	**0.002**
Nutrients × native density	0.879	1	0.349
Nutrients × *P. australis* density	3.399	2	0.183
Nutrients × vegetation component	1.074	1	0.300
Native density × *P. australis* density	2.989	2	0.224
Native density × vegetation component	**6.789**	**1**	**0.009**
***P. australis* density × vegetation component**	**343.500**	**2**	**< 0.001**
Water × nutrients × native density	1.618	1	0.203
Water × nutrients × *P. australis* density	1.847	2	0.397
Water × nutrients × vegetation component	0.511	1	0.475
Water × native density × *P. australis* density	0.958	2	0.619
Water × native density × vegetation component	0.686	1	0.408
Water × *P. australis* density × vegetation component	**9.081**	**2**	**0.012**
Nutrients × native density × *P. australis* density	0.727	2	0.695
Nutrients × native density × vegetation component	0.588	1	0.443
Nutrients × *P. australis* density × vegetation component	1.020	2	0.601
Native density × *P. australis* density × vegetation component	**8.325**	**2**	**0.016**

Variance Estimates of Random Effects	**Variance (σ^2)**	**Std. Dev. (σ)**
Quarter: Pool	0.000	0.000
Pool	0.000	0.000
Residual	6.018	2.453

TABLE 2.5 (cont.)

(B) Model Predictors for Cover	**Chi-sq**	**Df**	***P* value**
(Intercept)	**339.364**	**1**	**< 0.001**
Water	0.566	1	0.452
Nutrients	1.815	1	0.178
Native density	**6.839**	**1**	**0.009**
***P. australis* density**	**22.869**	**2**	**< 0.001**
Vegetation component	**144.386**	**1**	**< 0.001**
Water × nutrients	0.155	1	0.694
Water × native density	0.338	1	0.561
Water × *P. australis* density	**5.857**	**2**	**0.053**
Water × vegetation component	**9.785**	**1**	**0.002**
Nutrients × native density	0.667	1	0.414
Nutrients × *P. australis* density	2.712	2	0.258
Nutrients × vegetation component	0.496	1	0.481
Native density × *P. australis* density	**4.695**	**2**	**0.096**
Native density × vegetation component	**10.269**	**1**	**0.001**
***P. australis* density × vegetation component**	**312.266**	**2**	**< 0.001**
Water × nutrients × native density	0.218	1	0.641
Water × nutrients × *P. australis* density	1.544	2	0.462
Water × nutrients × vegetation component	0.136	1	0.713
Water × native density × *P. australis* density	0.394	2	0.821
Water × native density × vegetation component	1.364	1	0.243
Water × *P. australis* density × vegetation component	**27.946**	**2**	**< 0.001**
Nutrients × native density × *P. australis* density	0.288	2	0.866
Nutrients × native density × vegetation component	0.076	1	0.783
Nutrients × *P. australis* density × vegetation component	0.312	2	0.830
Native density × *P. australis* density × vegetation component	**22.356**	**2**	**< 0.001**

Variance Estimates of Random Effects	**Variance (σ^2)**	**Std. Dev. (σ)**
Pool	0.000	0.000
Quarter: Pool	0.000	0.000

TABLE 2.6. Analysis of deviance results from mixed effects models analyzing the effects of native density, sowing time, vegetation component, and their interactions on native and *P. australis* (A) biomass and (B) cover (Experiment 3). Also reported are the variance estimates for the model random effects; estimates are on the square-root scale (biomass) and logit scale (cover). Type III significance tests at $P < 0.10$ are shown in bold.

(A) Model Predictors for Biomass	**Chi-sq**	**Df**	***P* value**
(Intercept)	**758.221**	**1**	**< 0.001**
Native density	0.145	1	0.704
Sowing time	2.439	2	0.295
Vegetation component	**91.387**	**1**	**< 0.001**
Native density × sowing time	0.220	2	0.896
Native density × vegetation component	1.081	1	0.299
Sowing time × vegetation component	**90.628**	**2**	**< 0.001**
Native density × sowing time × vegetation component	0.440	2	0.803
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Quarter: Pool		0.000	0.000
Pool		0.000	0.000
Residual		6.260	2.502

(B) Model Predictors for Cover	**Chi-sq**	**Df**	***P* value**
(Intercept)	2.522	**1**	0.112
Native density	2.370	1	0.123
Sowing time	14.008	2	**< 0.001**
Vegetation component	**148.438**	**1**	**< 0.001**
Native density × sowing time	0.175	2	0.916
Native density × vegetation component	5.506	1	0.019
Sowing time × vegetation component	**37.928**	**2**	**< 0.001**
Native density × sowing time × vegetation component	1.428	2	0.490
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Pool		0.000	0.000
Quarter: Pool		0.000	0.000

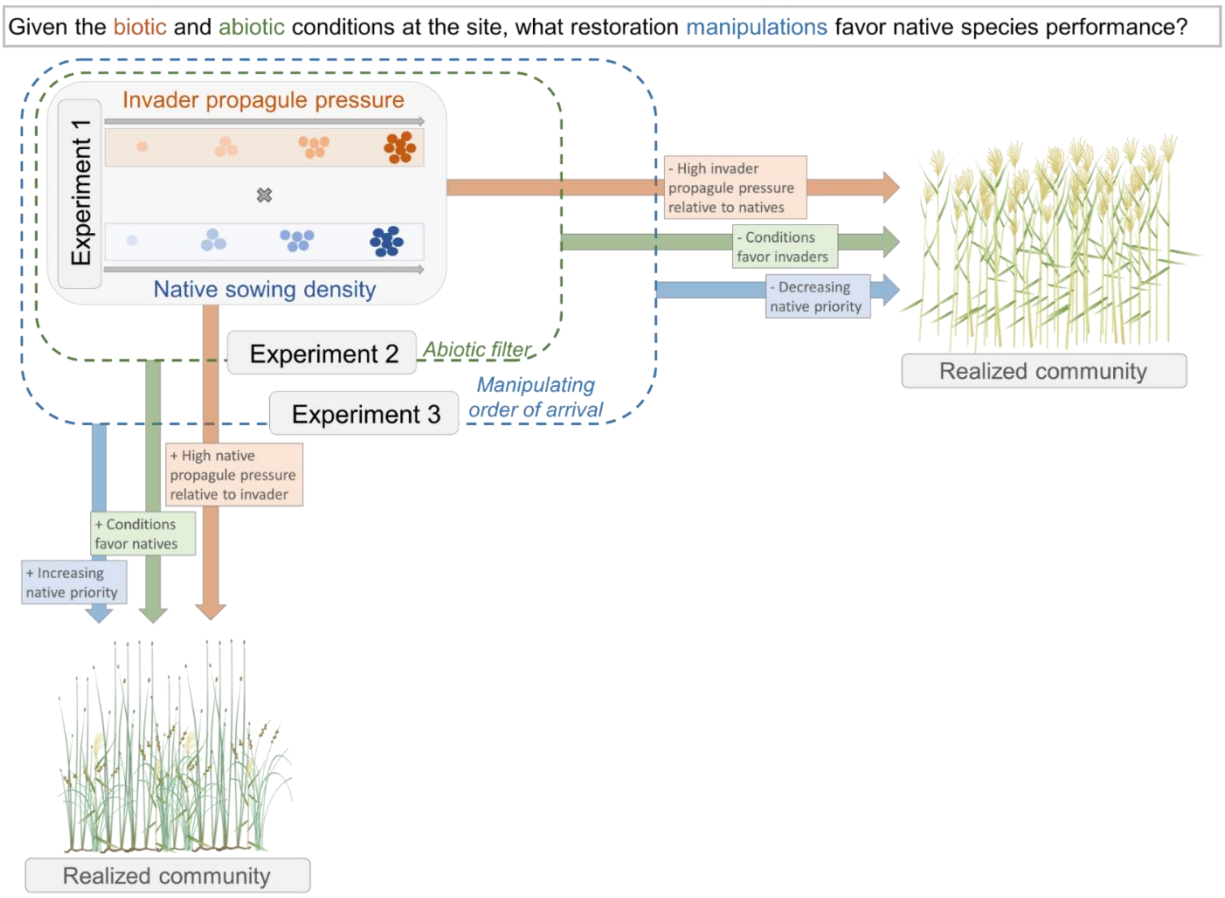

FIG 2.1. Conceptual model outlining seed-based wetland restoration manipulations applied in the study. Restoring native plant communities via seed-based wetland restoration requires implementing restoration manipulations (shown in blue; e.g., altering native sowing density, sowing seeds earlier in the season) that favor native recruitment. Additionally, biotic conditions at the site (orange; e.g., invader propagule pressure) and abiotic site conditions (green; e.g. water & nutrient availability) must be accounted for when developing seed-based wetland restoration plans. At the seed level and in the absence of limiting abiotic conditions, invasive and native seeds directly compete and influence community outcomes—high invader propagule pressure relative to native sowing density can yield a realized community composed primarily of invasive plants; and vice versa (**Experiment 1**). Spatially, these seed level dynamics shift as site level abiotic conditions vary—abiotic conditions that favor native species (or suppress invaders) can yield a realized community primarily composed on sown native species (**Experiment 2**). Temporally manipulating the order of species arrival by sowing native seeds earlier in the season (i.e., 'priority effects') can also benefit native plant establishment (**Experiment 3**). Plant images: ian.umces.edu.

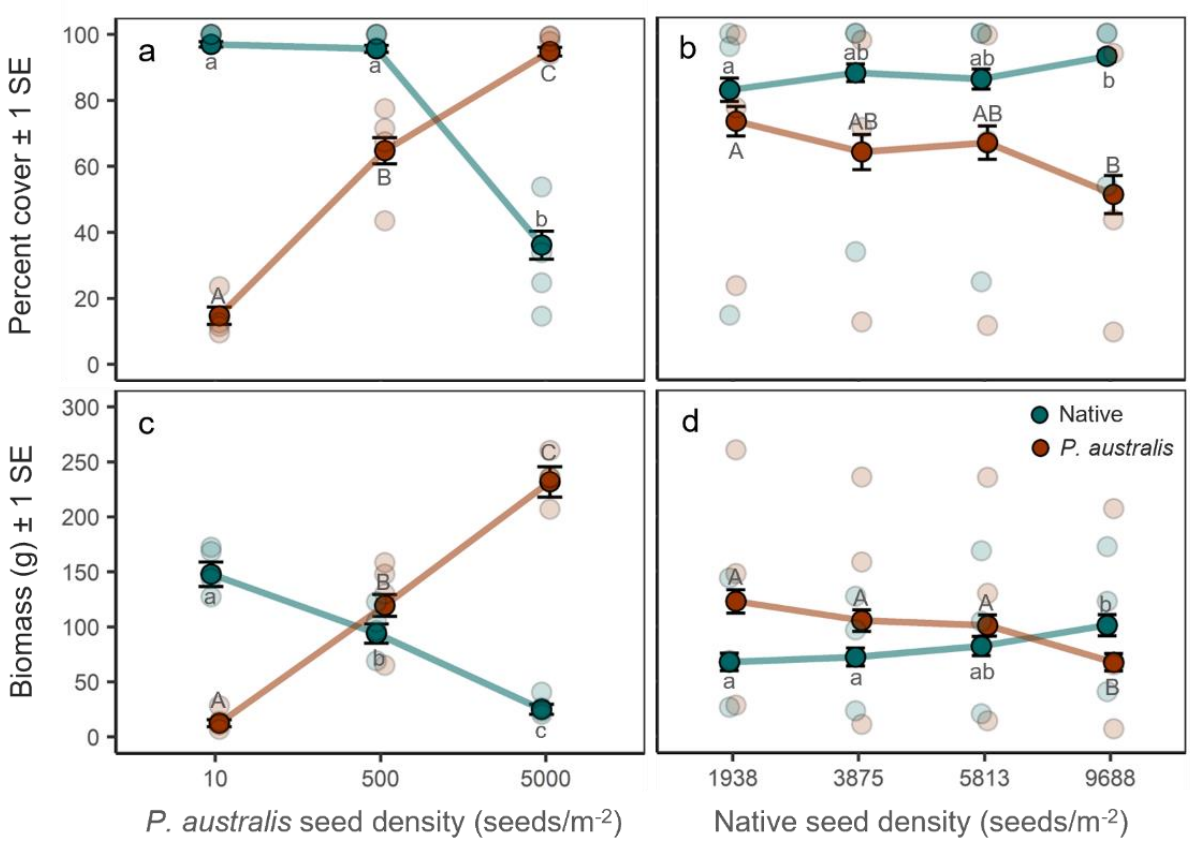

FIG 2.2. (a, b) Percent cover and (c, d) biomass of *P. australis* (orange) and native species (blue) across (a, c) *P. australis* seed densities and (b, d) native sowing densities. Solid lines represent modeled data; circles represent observed data. Tukey post hoc significant values at an alpha level of 0.10 are shown in capital letters for *P. australis* comparisons and lowercase letters for native comparisons.

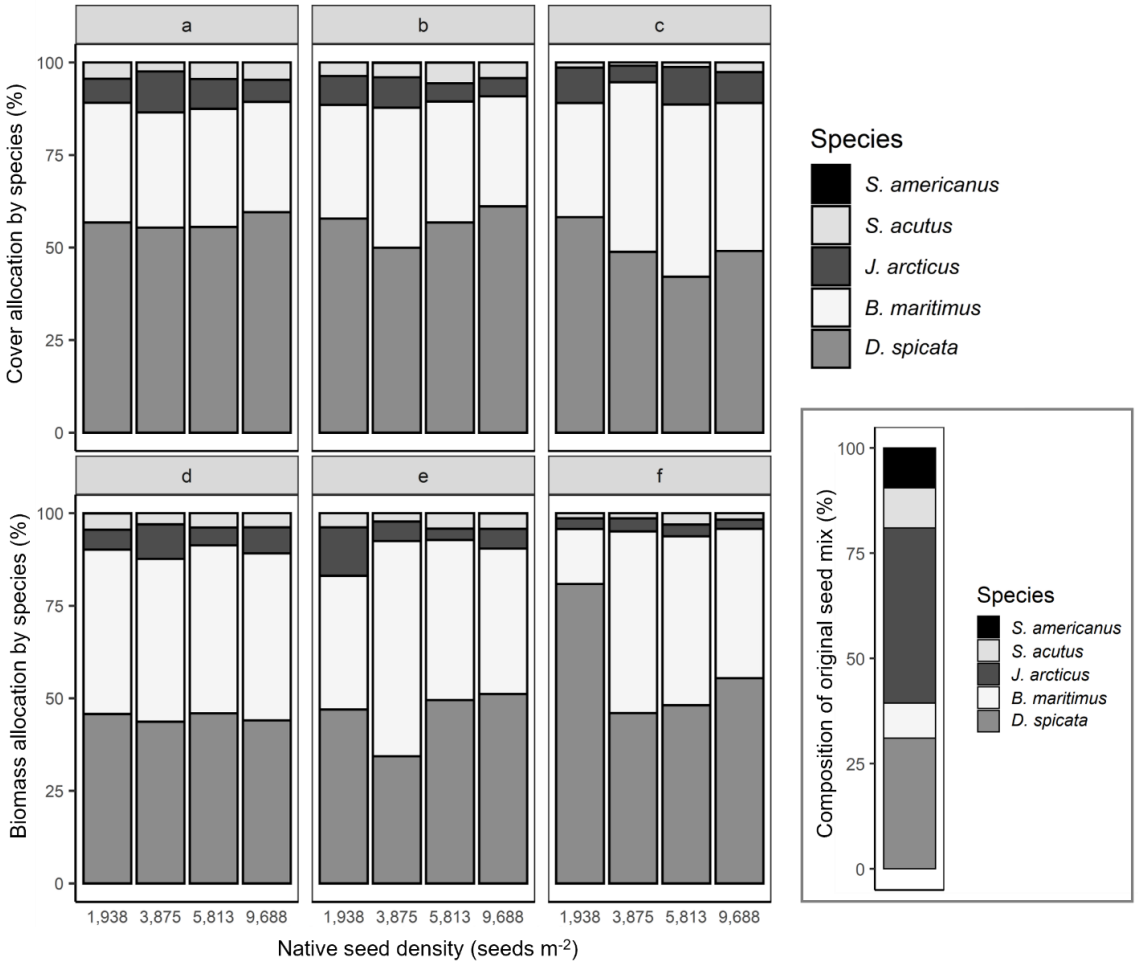

FIG 2.3. Percent cover (top row) and biomass (bottom row) allocation by native species across native sowing densities at (a, d) 10 *P. australis* seeds/m^2, (b, e) 500 *P. australis* seeds/m^2, and (c, f) 5,000 *P. australis* seeds/m^2, scaled to 100% of the total native cover/biomass. The relative abundance, expressed as a percent, of the species composition in the original seed mix is shown on the right.

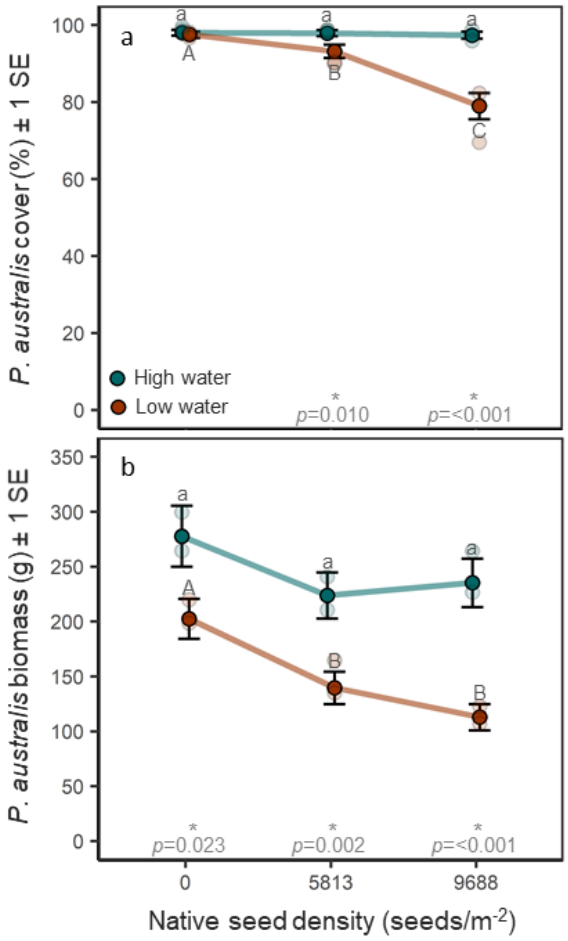

FIG 2.4. (a) Percent cover and (b) biomass of the high-density *P. australis* treatment (5000 seeds m^{-2}) at high-water (blue) and low-water (orange) levels. Solid lines represent modeled data; circles represent observed data. Significant pairwise comparisons between water levels for each native sowing density are indicated by an asterisk with corresponding *p*-value. Upper-case letters indicate Tukey post-hoc comparisons (α=0.10) of *P. australis* cover and biomass across native sowing densities for the low-water treatment; lower-case letters indicate Tukey post-hoc comparisons (α=0.10) of *P. australis* cover and biomass across native sowing densities for the high-water treatment.

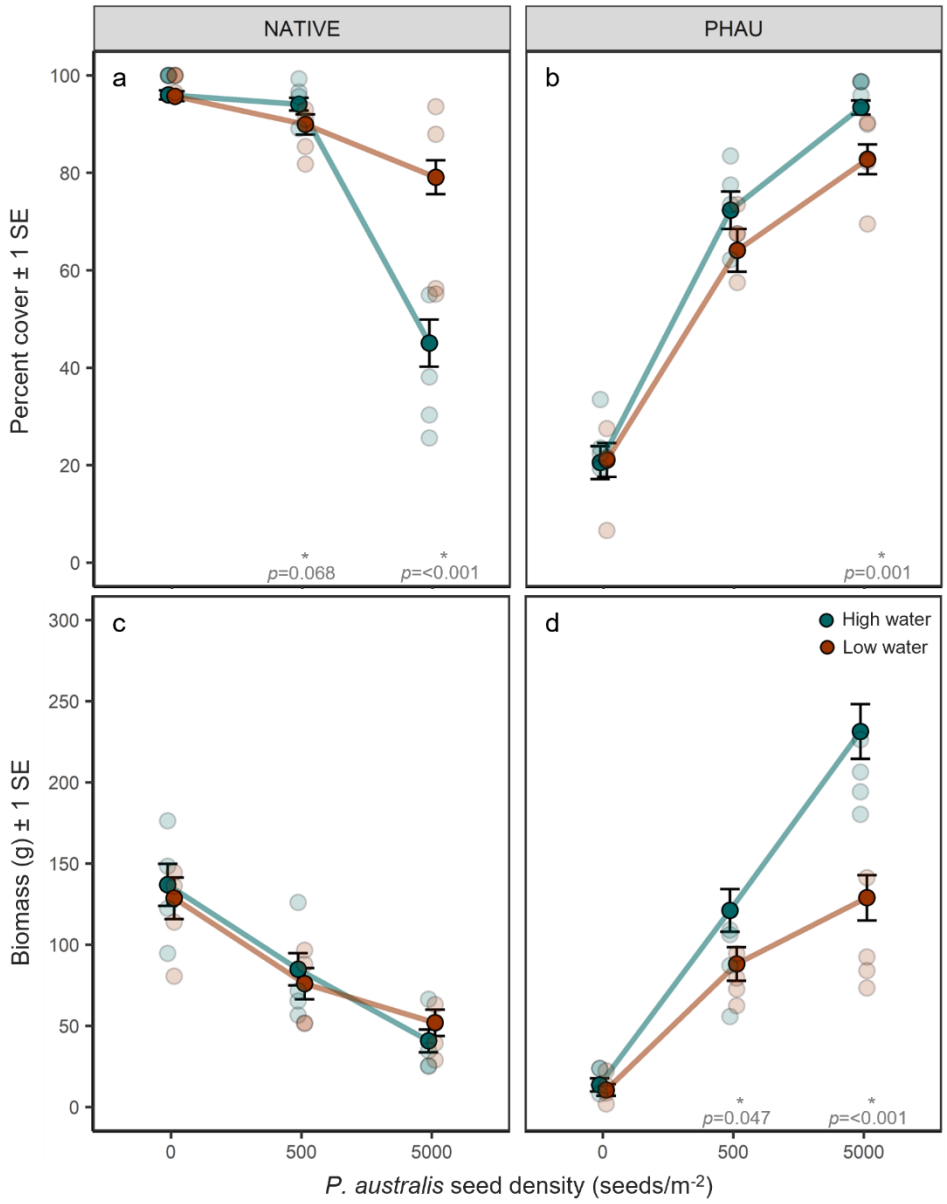

FIG 2.5. (a, b) Percent cover and (c, d) biomass of (a, c) native species and (b, d) *P. australis* across *P. australis* seed densities at high-water levels (blue) and low-water levels (orange). Solid lines represent modeled data; circles represent observed data. Significant pairwise comparisons (Tukey HSD, α=0.10) between high- and low-water conditions at each *P. australis* seed density for total native and *P. australis* cover and biomass are indicated by an asterisk with corresponding *p*-value.

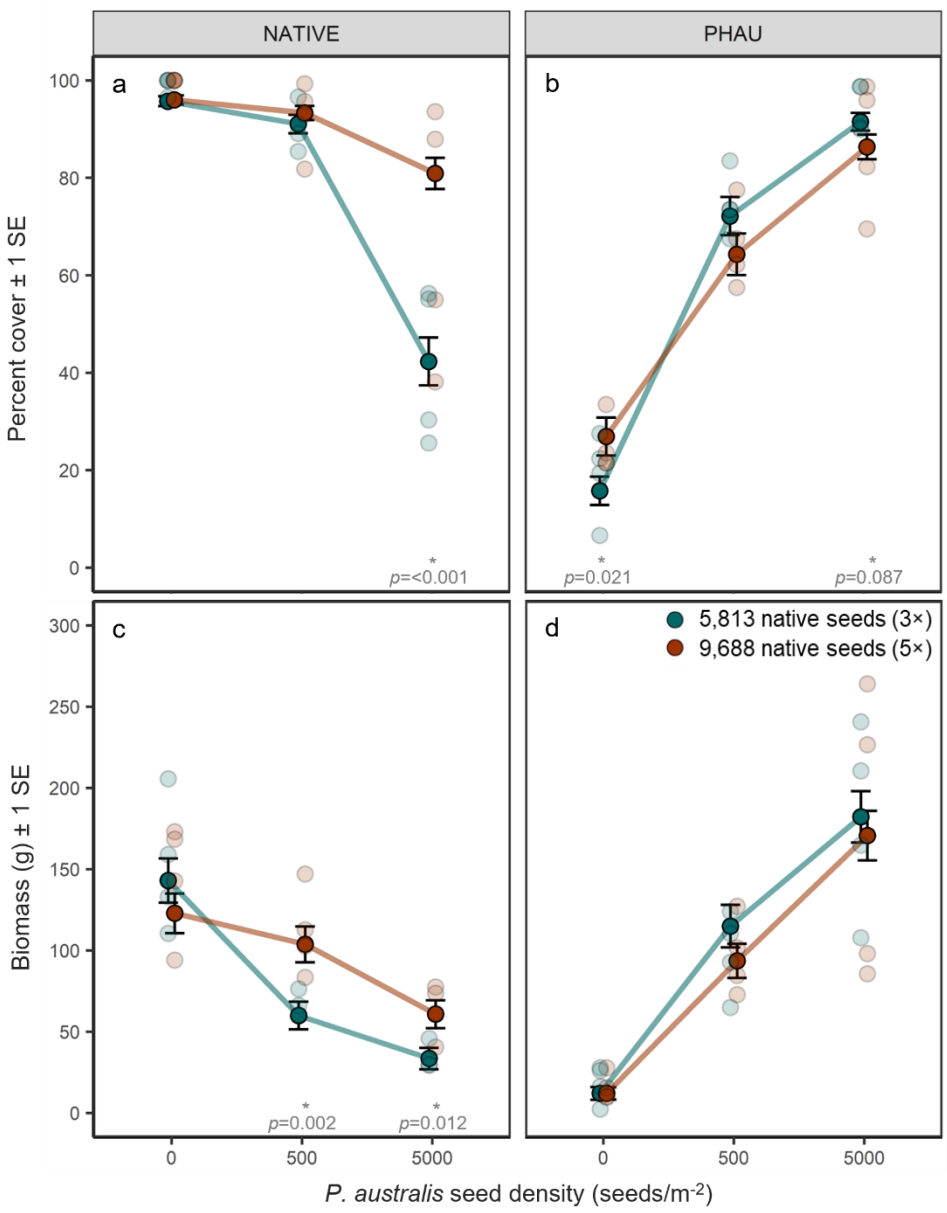

FIG 2.6. (a, b) Percent cover and (c, d) biomass of (a, c) native species and (b, d) *P. australis* across *P. australis* seed densities at native sowing densities of 5,813 seeds/m^2 (3× the recommended rate; blue) and 9,688 seeds/m^2 (5× the recommended rate; orange). Solid lines represent modeled data; circles represent observed data. Significant pairwise comparisons (Tukey HSD, α=0.10) between the 3× and 5× native sowing density at each *P. australis* seed density for total native and *P. australis* cover and biomass are indicated by an asterisk with corresponding *p*-value.

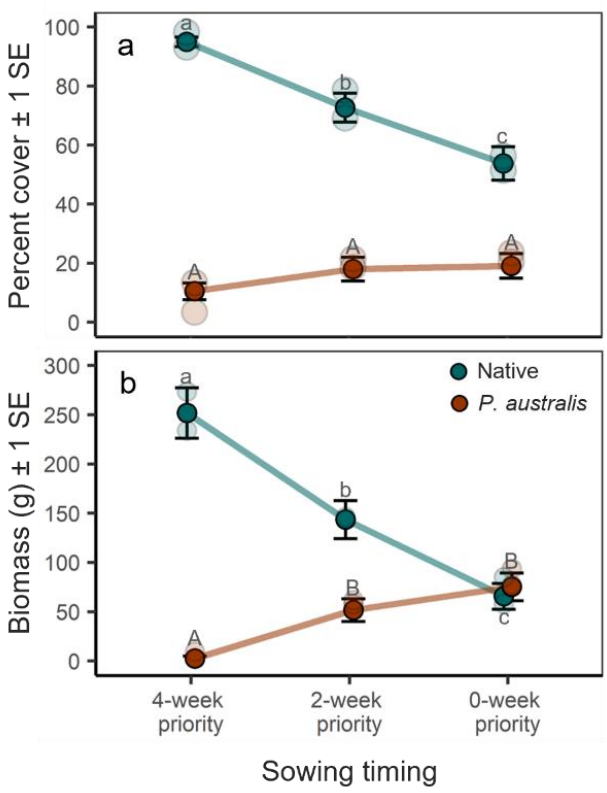

FIG 2.7. (a) Percent cover and (b) biomass of native species (blue) and *P. australis* (orange) across priority timing treatments. '4-week priority' = natives sown 4 weeks prior to *P. australis*; '2-week priority' = natives sown 2 weeks prior to *P. australis*; '0-week priority' = natives and *P. australis* sown together. Results are averaged across native sowing densities, which were not significant. Solid lines represent modeled data; circles represent observed data. Upper-case letters indicate Tukey post-hoc comparisons (α=0.10) across sowing timing for *P. australis* cover and biomass; lower-case letters indicate Tukey post-hoc comparisons (α=0.10) across sowing timing for total native cover and biomass.

CHAPTER 3

INTER- AND INTRASPECIFIC REGENERATION TRAITS OF WETLAND PLANTS: EMERGING PATTERNS AND UNEXPECTED TRADE-OFFS[1]

Abstract

Plant regeneration is a critical driver of plant community assembly and community dynamics but is often overlooked in trait-based research, particularly for wetland ecosystems. Wetlands are among the most biologically productive ecosystems and are degrading at an unprecedented rate. Understanding the mechanisms driving seed dispersal, persistence, germination, and seedling growth for wetland plants across species and populations can enhance predictions of community assembly and improve seed-based wetland restoration outcomes. Here, we collected seeds from 7 wetland species and a total of 36 populations across the Intermountain West, USA. A suite of seed traits was measured in the lab, and each species × population was grown in growth chambers at three temperature and two water potential regimes. Seedlings were harvested at two points during development and seedling traits were calculated from measurements taken via WinRHIZO images and plant weights. We also quantified abiotic conditions at the collection site to assess the influence of maternal effects on seed traits. We found substantial variation among seed traits that appeared to provide adaptive value for plants relative to their habitat preferences. Maternal effects were not detected for seed mass or three other seed traits, but decreasing temperatures and increasing elevation led to deeper seed dormancy for *Bolboschoenus maritimus* and *Schoenoplectus acutus*, respectively. We also identified unexpected trade-offs between seedling growth traits and tissue construction traits that went against traditional plant economic spectrum predictions.

[1]Co-authored with Margaret Hallerud, Stephen Hovick, and Karin Kettenring

Rather, slow-growing wetland species exhibited a flooding tolerance strategy that involved high specific leaf area and specific root length, presumably to support aerenchyma development. Surprisingly, the abiotic conditions we tested did not have a strong or consistent effect on seedling trait expression across species and populations, which could partly be explained by high phenotypic plasticity across populations or trait-environment relationships that are less relevant to wetland species than what is observed for terrestrial species. Our findings suggest that seed and seedling traits can be an important tool for predicting plant community assembly, but that current regeneration research should expand to include the constraints and patterns unique to wetland plants.

Key words

abiotic gradients, functional traits, interspecific variation, intraspecific variation, plant economics, seeds, seedlings, trait spectrum, wetland restoration

Introduction

Predicting plant distribution and community composition in response to abiotic change has been a decades-long goal in ecology (Raunkiaer, 1937; Grime, 1979; Díaz & Cabido, 1997; Lavorel et al. 1997; Chapin et al. 2000). To meet this goal, extensive research has focused on adult plant functional traits to predict how species respond to abiotic conditions and affect subsequent ecosystem processes (e.g., Lavorel & Garnier, 2002). Significant strides have been made in trait-based ecological research, such as the development of the leaf economic spectrum (‘LES’; Wright et al. 2004) and the larger plant economic spectrum (‘PES’; Reich, 2014), which identify relationships among key traits that link to ecological processes (e.g., specific leaf area and growth rate; Wright et

al. 2004). However, trait-based approaches have lagged in their incorporation of regeneration traits (i.e., functional traits driving seed and seedling dynamics and growth; Larson & Funk, 2016). Incorporating regeneration traits into a trait-based framework is a critical endeavor given the high mortality during early life stages (James et al. 2011; Barrett-Lennard et al. 2016) and the contribution of regeneration traits to a diversity of ecological and evolutionary processes (Larson & Funk, 2016). For example, incorporating regeneration traits into trait-based ecological frameworks can enhance predictions of when and where seeds will germinate (Donohue et al. 2010; Fraaije et al. 2015; Huang et al. 2016), identify tradeoffs and strategies exhibited by seedlings that contribute to their establishment success (or lack thereof; Fraaije et al. 2015; Larson et al. 2020; Larson et al. 2021), and predict population maintenance of species' across space (i.e., via seed dispersal; Freestone & Inouye, 2006; Harsch et al. 2014) and time (i.e., via seed persistence; Thompson et al. 2003; Gardarin et al. 2010; Ooi 2012; Cochrane et al. 2015). Because seeds and seedlings are subject to strong filtering at small spatiotemporal scales relative to mature plants (e.g., Keddy, 1992; Leck et al. 2008), incorporating regeneration traits into trait-based frameworks and plant community assembly models can provide additional dimension(s) of functional or adaptive plant strategies.

There is ample empirical support for a strongly limited set of functional trait combinations associated with adult plant leaves and roots separately, and together as a whole-plant economic spectrum (Reich et al. 1997; Wright et al. 2004; Pierce et al. 2013; Reich, 2014; Diaz et al. 2014). These trait combinations identify multidimensional tradeoffs that constrain the development of plant organs along resource gradients and is often observed as an economic continuum with resource acquisitive strategies on one end

(i.e., ‘fast’ traits facilitating thin tissues and rapid growth; e.g., high elongation rate, high specific leaf area; Ruberti et al. 2012; Ballaré & Pierik, 2017) and a resource conservation strategy on the other end (i.e., ‘slow’ traits facilitating thick tissues and slow growth; e.g., high biomass allocation; Markesteijn & Poorter, 2009; Reich, 2014). This economic spectrum has been well-documented for aboveground plant growth (i.e., ‘leaf economic spectrum’; Wright et al. 2004), and some indication (though contradictory) of a similar economic spectrum driving root trait variation (Roumet et al. 2006; Mommer & Weemstra, 2012; Reich, 2014; Zhou et al. 2018). To date, however, the development of a plant economic spectrum has been largely focused on adult plant strategies (e.g., Diaz et al. 2014). Less is known about whether a similar spectrum applies at the seed and seedling stage or if there are additional dimensions of variation in seed and seedling traits that could increase the explanatory power of plant community assembly models by bridging adult and regenerative plant stages (Larson & Funk, 2016).

The idea of a similarly structured ‘seed economic spectrum’ (*sensu* Saatkamp et al. 2019) could identify multivariate ecological strategies at the seed level that impact plant performance and community dynamics across ecological situations. Much of what we currently know about regeneration traits is largely based on a small subset of seed traits studied in isolation to map seed traits to regenerative processes (e.g., dispersal, persistence, dormancy, germination; Poschold 2013; Saatkamp et al. 2019; but see Phartyal et al. 2020; Rosbakh et al. 2020). For example, studies have identified traits related to seed persistence (e.g., seed coat thickness; Gardarin et al. 2010; Hamilton et al. 2013), traits related to dispersal of propagules across the landscape (e.g., seed buoyancy; van Den Broek et al. 2005; Soons et al. 2008), and traits related to germination speed

across abiotic conditions (e.g., time to germination; Ordoñez-Salanueva et al. 2015; Gioria & Pyšek, 2017). Yet, focusing on just a few seed traits and related ecological function in isolation masks larger patterns about plant trade-offs related to regeneration (e.g., seed size—number trade-off; Moles & Westoby, 2006) and plant trade-offs that unite seed, seedling, and adult life stages (e.g., higher seed mass linked to higher seedling survival due to greater internal seed reserves; Westoby et al. 2002; Moles & Westoby, 2004; Lebrija-Trejos et al. 2016). Examining a comprehensive suite of morphological and physiological seed traits can identify major axes of variation and covariation among seed traits that may explain how plants adapt to and perform at the seed level (Jiménez-Alfaro et al. 2016; Liu et al. 2017; Tudela-Isanta et al. 2018).

Following germination, regeneration traits that drive early plant growth can have long-lasting ecological consequences for plant community assembly (e.g., Larson et al. 2015; Leger et al. 2019). These functional regeneration traits, such as root elongation rate (RER) and specific leaf area (SLA), provide insight into plant strategies that allow seedlings to acclimate to abiotic conditions or compete with neighboring recruits (Rowe & Leger, 2011; Zangaro et al. 2016; Larson et al. 2020). There is some evidence that the 'PES' associated with mature plants may align with seedling strategies, even at just a few days post-germination (Larson et al. 2021), suggesting that strategies of mature plants can be used to infer ecological processes at the seedling stage (Larson & Funk, 2016). However, longitudinal assessments of plant economic trait relationships over ontogenetic development have identified substantial variation in plant strategies with developmental stage (Mason et al. 2013; Garbowski et al. 2021; Havrilla et al. 2021). Thus, additional

studies are needed to advance understanding of strategies and trade-offs that might constrain development in a predictable way at the seedling stage.

To date, research exploring regenerative plant strategies has been largely biased towards terrestrial, upland species, which limits the generalizability of seed and seedling strategies across ecosystems (de Bello et al. 2010; Moor et al. 2017). Fewer studies have focused on multivariate assessments of wetland seeds and seedlings, despite the disproportionate importance of wetland ecosystem functions and services relative to their global surface area (<10%; Zedler, 2000). Further, the rapid degradation of wetland ecosystems (>70%; Kingsford et al. 2016), combined with an increasingly limited passive recolonization potential due to dispersal limitations and depleted native seed banks (Seabloom & van der Valk, 2003; Kettenring & Galatowitsch, 2011; Soomers et al. 2013), necessitates a more advanced understanding of the mechanisms driving seed and seedling dynamics in wetlands (Seabloom & van der Valk, 2003; Carlson et al. 2009; Rohal et al. 2019; Kettenring & Tarsa, 2020).

Extensive research has identified morphological and physiological wetland plant responses to water stress, such as aerenchyma development, radial oxygen loss to the rhizosphere, and shifts in plant metabolic pathways (Armstrong et al. 1994; Cronk & Fennessy, 2016; Fukao et al. 2019), though plant trait responses to hydrological gradients have been inconsistent. For example, SLA has been found to increase along a flooding gradient (Mommer et al. 2007; Jung et al. 2010; Tanentzap & Lee, 2017), whereas other studies have demonstrated a decrease in SLA with flooding (Howison et al. 2015; Purcell et al. 2019). Further, the few multidimensional studies of mature wetland plant traits suggest that trade-offs observed in terrestrial systems do not play out in wetlands (Wright

& Sutton-Grier, 2012; reviewed in Moor et al. 2017). In addition to limited studies on multivariate trait-trait relationships in wetland species, particularly for seeds and seedlings, comparatively less attention has been paid to how plant functional traits respond to the hydrologic reality of many wetlands that experience early-onset drought due to increased upstream water use and climate change (Downard et al. 2014; Maleki et al. 2018), and how these multidimensional trait-water relations interact with increasing temperatures at the seedling stage.

A common assumption in trait-based ecological research is that there is more trait variation between rather than within a species, which has been evidenced in many studies (e.g., Hulshof & Swenson, 2010; Kichenin et al. 2013). However, intraspecific variation can be substantial (Siefert et al. 2015) and can have important consequences ecologically (e.g., Bolnick et al. 2011; Enquist et al. 2015) and evolutionarily (e.g., Etterson & Shaw, 2011). Intraspecific trait variation may be particularly important in wetland systems that typically have relatively few abundant plant species which occupy large geographic distributions (Bruno & Bertness, 2001). However, wetland plants often exhibit high phenotypic plasticity due to dynamic conditions over a relatively small spatiotemporal scale (Rea & Ganf, 1994; Shipley et al. 1989; Weiher & Keddy, 1995; Dorken & Barrett, 2004); thus, intraspecific trait correlations may either be more fluid (i.e., less prominent than what would be observed in less plastic species; Jacob et al. 2021) or could be more prominent if plasticity allowed for an enhanced evolutionary response (Futuyma, 2021). From a restoration perspective, intraspecific variation in seed and seedling traits is important in applying regeneration trait concepts to restoration (Pywell et al. 2003; Clark et al. 2012; Leger et al. 2019). For example, Leger et al. (2019) found that intraspecific

variation in root length, seed mass, and emergence timing were related to the likelihood of first-season survival among 34 populations of *Elymus elymoides*. This intraspecific variation was partially linked to maternal-environment effects, which have been well documented to influence early plant stages (i.e., at the seed stage) and decline with increasing plant age (Roach & Wulff, 1987; Bischoff & Müller-Schärer, 2010). Specifically, maternal-environment effects have been found to influence seed mass (Liebman & Davis 2000; Sultan et al. 2009; Dyer et al. 2010), germination (Luzuriaga et al. 2006; Donohue, 2009), and dormancy (Fernández Farnocchia et al. 2019). However, the influence of maternal effects on other seed traits is less clear. Understanding how maternal-environment effects influence seed trait variation would allow for more targeted predictions about when and where we might expect to find seed trait values that yield enhanced restoration outcomes (Bischoff et al. 2006; Espeland & Hammon, 2013).

Broadly, the purpose of this study was to explore inter- and intraspecific multivariate functional trait relationships separately among seeds and seedlings. To do this, we performed several principal components analyses for each stage and quantified seedling trait variation across species, populations, and abiotic conditions in multivariate trait space. In addition to a multivariate approach, we were interested in quantifying bivariate trait-trait relationships to clarify patterns observed in multivariate ordinations, particularly for the seed trait analysis (i.e., seed trait-seed trait relationships). Further, we viewed two of our calculated and measured traits—depth of seed dormancy and time to germination—as ‘transition stages’ between inherent seed traits (e.g., seed mass, seed dimensions) and subsequent seedling growth and allocation traits (e.g., specific leaf area, root dry matter content). Thus, we focused bivariate analyses on the relationship between

these transition traits and individual seed and seedling traits to explore two biologically-based questions— (1) are morphological seed traits related to our two transition stages such that seed traits could predict initiation of dormancy break and germination? and (2) do these two transition stages influence seedling trait expression?

In this study, we assessed inter- and intraspecific variation in morphological seed traits ('seed traits'), physiological seed traits related to dormancy and germination ('transition traits'), and seedling growth and biomass allocation traits ('seedling traits') across seven focal species sourced from wetlands across the Intermountain West, USA (see Table 3.1 for measured traits; Figure 3.1 for population map). We focused on six native wetland species that are often targeted for seed-based wetland restoration, and one prolific wetland invasive species. Our focus was on identifying trait-trait relationships at the species and population level, and the trait-environment relationships that predominate wetlands in the Western US (i.e., decreasing water availability and increasing temperature; Downard et al. 2014; Maleki et al. 2018), with the goal of identifying how species selection and source population might influence seed-based wetland restoration outcomes. Our objectives were as follows:

Identifying intra- and interspecific variation in morphological and physiological seed traits across species, populations, and multivariate trait space

(1) Identify variation in morphological and physiological seed traits in multivariate trait space across both populations and species. We expected to see significant variation in measured seed traits that, when mapped in multivariate trait space, were consistent with plant adaptations necessary for dispersal, persistence, and germination in unique wetland habitats.

(2) Identify abiotic conditions at the seed collection site (i.e., maternal-environment effects) that partially explain the observed intraspecific variation in seed traits (see 'seed traits' in Table 3.1) for *Bolboschoenus maritimus* and *Schoenoplectus acutus*. Based on the literature, we expected to see maternal-environment influences on seed mass and depth of dormancy, but less influence on other measured seed traits.

Determine if and how potential restoration-site conditions influence inter- and intraspecific multivariate tradeoffs in germination and seedling traits

(3) Determine if and how potential abiotic conditions at the restoration site (i.e., temperature and water availability) influence multivariate tradeoffs in time to germination and seedling traits across species and populations. We expected to find variation in phenotypic seedling traits across species and populations that, across abiotic gradients, demonstrated a similar 'fast-slow' strategy that is observed in terrestrial adult plants.

Determine how time to germination and dormancy depth align with seed and seedling traits

(4) Determine how time to germination and depth of dormancy (i.e., 'transition traits') align with seed and seedling traits across species and populations. We also expected to observe a 'fast-slow' strategy that spanned stages such that species and populations exhibiting slower germination and deeper dormancy would also exhibit conservative seedling traits (e.g., higher biomass allocation relative to growth rates) and seed traits related to higher persistence (e.g., thicker seed coats).

Methods

Population sampling

Seeds were collected between August and October 2018 from wild populations of *Bolboschoenus maritimus* (12 populations), *Schoenoplectus acutus* (14 populations), *Schoenoplectus americanus* (5 populations), *Phragmites australis* (3 populations), *Distichlis spicata* (1 population; composite seed mix comprised of multiple nearby patches), and *Eleocharis palustris* (1 population; composite seed mix comprised of multiple nearby patches). Sites for collection were chosen to span a range of elevations and climate conditions across the Intermountain West in the USA, yet still represent the geographic distribution of natural dispersal pathways (Figure 3.1; Appendix B: Table S.3.1; Kettenring et al. 2019). At each collection site, seeds were harvested broadly from 50–200 individual plants at three distinct patches within a site (> 100 m apart) to ensure that we captured an adequate representation of site-level genetic diversity (Kettenring et al. 2019). Commercially available *D. spicata* and *E. palustris* were included from a local seed distributor that captured a composite of patches for each species within Great Salt Lake wetlands. After collection, viability tests were performed, and seeds were stored in paper bags at room temperature prior to seed trait measurements and the germination and seedling experiment.

Abiotic conditions from seed source populations

Abiotic condition data at the collection site for each species × population were gathered using the software package Climate NA (v 7.10; Wang et al. 2016; Daly et al. 2008). We extracted data only from the preceding and current year in which seeds were collected (2017-2018) to account for maternal conditions influencing seed traits. In

addition to topographic variables collected at each site (i.e., latitude, longitude, elevation), we included seasonal abiotic variables that likely impact seed development (e.g., maximum temperature, minimum temperature, precipitation) from autumn (Sept – Nov 2017), winter (Dec 2017 – Feb 2018), spring (Mar – May 2018), and summer (Jun – Aug 2018). We also included annual variables for 2017 and 2018 that characterized site differences likely to impact plant growth and seed characteristics, such as number of frost-free days, mean annual temperature, and mean annual precipitation (Appendix B: Table S.3.2).

Measurement of seed traits

Following seed collection, we measured a suite of morphological and physiological seed traits for each species and population that are hypothesized to have implications for germination success (Table 3.1; Jiménez-Alfaro et al. 2016). We measured seed mass as the average per seed dry weight estimated from five replicates of 25 seeds for each species × population after being dried for 96 hours at 60 ℃ in a forced air-drying oven. Then, we captured images of 25 seeds per species × population using a 2×–225× zoom stereomicroscope (ZM-1TW3-FOD-10M; AmScope) equipped with a 10 MP digital camera (MU1000; AmScope) in two views: 1) top-down view of seed to calculate seed dimensions and 2) cross-section of seed after cutting it in half to view the seed coat (Appendix B: Figure S.3.1). From the cross-section images, we measured seed coat thickness at six equidistant points along the periphery of the seed on each replicate using AmScope MU series digital camera solution software (version 3.7) and averaged these values for a single seed coat thickness measurement (Appendix B: Figure S.3.1). From the top-down images, we measured seed dimensions as the length and width of the

longest point on each vertically aligned seed and measured height from seed cross-sections using the same software as above (Appendix B: Figure S.3.1). From the seed dimension measurements, we computed a seed shape index to capture the variance of the relative seed dimensions for each species × population, as described in Gardarin et al. (2010) and Thompson et al. (1993). This 'dimension index' ranges from zero (round seeds) to one (elongated seeds) and provides a straightforward method to compare seed shape across species (Gardarin et al. 2010).

To measure seed buoyancy, we placed 3 replicates of 25 seeds for each species × population into separate 60 mL plastic cup filled with tap water. Cups were labeled and randomly placed on a countertop in a dark room set at room temperature (18-21 ℃). During each data collection, we opened each cup and gently stirred the water three times to break surface tension in the cup. Then, we counted the number of seeds that had sunk to the bottom of the cup. Cups were counted every day from March 26th – April 16th 2019, every other day from April 16th – June 1st 2019, every week from June 1st, – July 24th 2019, every month from July to October 2019, and then every three months from October 2019 to June 2020. The experiment concluded on June 3rd, 2020, for a total of 463 days. We then calculated the 'Floating Percentage' (FP) to indicate the number of days in which 10% (FP_10), 25% (FP_25), 50% (FP_50), 75% (FP_75), and 90% (FP_90) of the seeds for each species × population had sunk, as described in van den Broek et al. (2005). We used FP_50 in subsequent analyses to represent the variation in seed buoyancy across species and populations.

To capture depth of dormancy, we placed three replicates of all species × population that exhibited dormancy (*B. maritimus, S. acutus, S. americanus, D. spicata,*

E. palustris) in one of seven cold stratification treatments: one untreated control (0 days of cold stratification) and six cold stratification treatments at 30-day intervals (30-, 60-, 90-, 120-, 150-, 180-days of cold stratification). For each species × population, 3 replicates of 100 seeds were counted out for each cold stratification treatment and wrapped in mesh. The mesh bags of seed were tied with color-coded ribbon specific to each species, source, and cold stratification treatment. This experiment began on June 19th, 2019 (first day of untreated control treatment), approximately 8 months past seed collection. The experiment ended on January 14th, 2020 (last day of 180-day treatment).

Three 20-gallon totes with holes drilled at the bottom were used as cold stratification containers and labeled by species (BOMA, SCAC, OTHER [ELPA, DISP, SCAM]). Each container was layered with a 4:1 mix of silica sand and peat per layer. Between every 2-inch layer of substrate, a layer of mesh bags of seeds was randomly placed in the container. The ribbons signifying the cold stratification treatments were cut to a length so that they were long enough to protrude out of the top of the container to remove the designated bags more easily on each specific cold stratification treatment date. The layering of seeds and substrate was repeated until all seed bags were sufficiently buried in the sand: peat substrate. Containers were filled with water until they started draining and were placed in cold rooms set between 2-4 ℃ for 180 days. Containers were re-watered every 15 days to maintain adequate moisture. All seed bags were buried on the same day and pulled out every 30 days for germination testing. For germination testing, seeds were placed in germination boxes (dimensions: 11 x 11 x 4 cm) filled with 100 mL of distilled water. Germination was conducted in Conviron growth chambers at one temperature regime (32/15℃; day/night) and germinated seeds

were counted and removed every other day for 30 days. The dormancy index ranges from 0 to 1, where populations with deeper dormancy have values closer to 0 and populations with less deep dormancy have values closer to 1. Methods to develop the depth of dormancy index are detailed in Appendix C.

Trait sampling across abiotic conditions

To explore the effect of potential restoration site abiotic conditions on time to germination and early seedling traits, we conducted a growth chamber experiment to track germination and seedling growth for each species × population across three temperature regimes (28/10 ℃, 32/15 ℃, 36/20 ℃) and two water potentials (0 MPa, -0.6 MPa). Current-day and future predicted temperatures were chosen to represent present day May temperatures (28/10 ℃), present July (and June 2070) temperatures (32/15 ℃), and July 2070 temperatures (36/20 ℃) in Great Salt Lake wetlands, computed from the maximum and minimum monthly average temperatures from a CMIP5 global climate model (Worldclim; Hijmans et al. 2005). Water potentials were manipulated using polyethylene glycol (PEG) MW 8000 and chosen to represent non-limiting water availability (0 MPa) and a low water-availability condition (-0.6 MPa) that noticeably impacted germination for our study species in pilot studies.

Prior to the experiment, dormancy was broken for *S. acutus*, *S. americanus*, and *D. spicata* with a 40-day cold stratification as described above. For each germination trial, seed lots of *B. maritimus* and *E. palustris* were divided in half and soaked in a 3% bleach solution for 24-hour or 48-hours to account for variation in depth of dormancy (Kettenring, 2016; Marty & Kettenring, 2017; Rosbakh et al. 2019), after which they were thoroughly rinsed and immediately sown. Three germination trials were conducted

between December 2019 and April 2020. Each trial was a replicate for which every combination of (species × population [37 total]) × temperature (3) × water potential (2) was represented (see Appendix B: Table S1 for species × population combinations). Temperature treatments were rotated across growth chambers for each consecutive trial to minimize any chamber effect.

Growing containers ("cups") were constructed from a 946 mL clear cup reservoir base, a plastic net pot wrapped in mesh placed inside the base, and a 710 mL clear cup lid to minimize evaporation (Appendix B: Figure S.3.2). In each reservoir base, a solution of water, nutrients (Peter's Professional Hydroponic Fertilizer, 5-11-26; applied at a rate of 3 grams nutrients to 1 L water), and calcium nitrate (1.5 g to 1 L water) was added. For low water potential treatments, PEG was added to the reservoir solution at a separate rate for each temperature according to Michel (1983). Plastic net pots were filled with a uniform amount of profile ceramic clay as a growing media (Profile Products LLC; Buffalo Grove, IL), which was thoroughly pre-rinsed to remove excess labile ions (Adams et al. 2014). Plastic net pots were placed in reservoir bases and the appropriate solution was added to the reservoirs such that the solution was level with the surface of the growing media.

A known number of seeds (~15 PLS) for each species × population were evenly gridded over the surface of the growing medium and the top lid was placed on, wrapped in parafilm to minimize evaporative loss, and randomized within the appropriate growth chamber. Throughout the experiment, DI water was added as needed to maintain the target water potential treatment. Germination censusing was done every other day and each new germinant was marked with a uniquely numbered toothpick on which the date

of germination was recorded. Seedlings were harvested 7- or 21-days post-germination (randomly assigned within each cup) and three seedling subsamples per harvest day per cup were collected. After harvest, seedling roots and shoots were scanned to measure root and shoot length and surface area (WinRHIZO, Regent Instruments Inc., Sainte-Foy, Canada). Fresh weights were collected immediately after scanning and seedlings were dried at 60℃ for 24 hours in a forced-air drying oven.

Time to germination and seedling trait calculations

From data gathered during the growth chamber experiment, we focused on one germination metric to capture the speed of germination, which would allow us to explore if rapid germination led to early seedling traits associated with rapid growth. To capture the speed of germination, we calculated the time to 50% germination ('t_{50}') using the equation

$$T_{50} = t_i + \frac{(N/2 - n_i)(t_j - t_i)}{(n_i - n_j)}$$

where N is the total number of seeds germinated in each replicate, n_i and n_j are the number of seeds germinated at adjacent time t_i and t_j when $n_i < N/2 < n_j$ (Farooq et al. 2005). Because of the low germination observed in several species and treatments (common for native species germination studies relative to crop germination studies), time to 50% germination in this analysis represents the time to reach 50% of the maximum germination reached for each of the three species × population × temperature × water potential replicates (i.e., 50% germination relative to maximum observed germination vs. 50% germination of an assumed 100% germination). Time to 50%

germination was averaged across three trials for species × population × temperature × water potential treatment.

We were interested in eight seedling traits related to biomass allocation, seedling growth, and tissue construction, all of which were measured on individual seedling subsamples at each of the two harvest days. Root mass ratio (RMR), calculated as the ratio of dry root mass to total dry plant mass, was included as a biomass allocation trait. Seedling growth traits included: root elongation rate (RER) and shoot elongation rate (SER), calculated using the relative growth rate formula (Pérez-Harguindeguy et al. 2013): $\ln (X_2 - X_1) / (t_2 - t_1)$ where X_2 is the length at the 21-day harvest (t_2) and X_1 is the length at the 7-day harvest (t_1). Tissue construction traits included: specific root length (SRL), calculated as root length divided by root dry mass, specific leaf area (SLA), calculated as above ground area divided by the above ground dry mass, and root dry matter content (RDMC) and shoot dry matter content (SDMC), calculated by dividing the dry root or shoot biomass by the total fresh biomass. For the SLA calculations, we calculated whole-plant aboveground specific area rather than first leaf specific area due to the presence of rudimentary basal leaves for many of these wetland species (Blaser, 1944; Gunn et al. 1999). All seed, germination, and seedling traits are described in Table 3.1.

Data analysis

Objective 1: Identify intra- and interspecific variation in morphological and physiological seed traits across species, populations, and multivariate trait space

We used a series of linear models to investigate the role of population on seed traits as the response variable ('seed mass', 'seed coat thickness', 'seed dimension index',

'seed buoyancy') using the *lme4* package in R 4.0.2 (Bates et al. 2015). Intraspecific models included 'population' as the independent variable and was only conducted for species in which we had a large enough population sample size to make robust estimations (*B. maritimus, S. acutus, S. americanus*). Interspecific models (averaged over populations) included 'species' as the independent variable. Residuals were inspected in the *DHARMa* package and response variables were transformed as needed to meet the assumptions of normality and homogeneity of variance (Hartig, 2020). Tukey HSD tests were performed to test the significance ($\alpha = 0.05$) of the differences in mean trait values across populations and species. To identify tradeoffs and axes of covariation among morphological and physiological seed traits, we conducted a principal component analysis for measured seed traits (centered and scaled) across species and populations using the '*prcomp*' function in R 4.0.2 (R Core Team, 2020). To visualize intraspecific seed trait tradeoffs, we performed two additional principal component analyses on data from *B. maritimus* and *S. acutus* populations.

Objective 2: Identify collection-site abiotic conditions that contribute to intraspecific variation in physiological and morphological seed traits

To understand how seed traits were influenced by specific collection-site abiotic conditions, we scaled abiotic variables to a mean of zero and standard deviation of one and conducted a principal component analysis to reduce dimensionality in the dataset using the '*prcomp*' function in R 4.0.2 (R Core Team, 2020). Two abiotic variables with zero variance (summer degree-days below 0°C (DD_0_sm) and winter degree-days above 18°C (DD18_wt) were removed prior to running the PCA. We selected a single abiotic variable that was most strongly associated with each of the first three principal

components and inspected Pearson's correlation coefficients to ensure that the three variables we selected were not correlated. We used a series of robust linear regressions to individually examine the influence of the top three abiotic variables as predictor variables ('2018 mean annual temperature', '2017 mean annual precipitation', and 'elevation') on individual seed traits for *B. maritimus* and *S.* acutus with the *robustbase* package in R 4.0.2 (Maechler et al. 2022). Robust regressions were chosen over ordinary least squares (OLS) linear regression methods to dampen the influence of outliers and provide a better fit to most of the data, rather than explicitly removing valid outlying cases from the dataset (Yu & Yao, 2017).

Objective 3: Determine if and how potential restoration-site conditions influence inter- and intraspecific multivariate tradeoffs in germination and seedling traits

To detect overall differences in time to germination and seedling traits across species, populations, and potential restoration site conditions (temperature and water potential), we performed three principal components analyses (PCA) using the '*prcomp*' function in R 4.0.2: (1) assessing interspecific differences in seedling traits using one Great Salt Lake population per species, (2) assessing intraspecific differences in seedling traits among populations for *B. maritimus*, and (3) assessing intraspecific differences in seedling traits among populations for *S. acutus*. We chose PCA over other ordination methods because we were interested in describing overall (multivariate) patterns among the most important dimensions of trait variation, rather than the response of individual traits themselves. Prior to running the PCAs, the variables 'SDMC', 'RDMC', 'SLA', 'SRL', and 't50' were $\log_{10}$-transformed to improve skew and then all trait values were centered and standardized. After running each PCA, we compared species and population

scores along the first two principal components, treating these scores as representative of trait differences among our samples. To test the for differences among species and abiotic conditions, we used a three-way analysis of variance, with temperature regime ('28/10', '32/15', or '36/20'), water potential ('0' or '-0.6' MPa), and species (and all interactions) as factors in our model and PC1, PC2, and PC3 as response variables (3 separate models). To test for intraspecific variation, we ran separate three-way ANOVA models for *B. maritimus* and *S. acutus* data with temperature regime ('28/10', '32/15', or '36/20'), water potential ('0' or '-0.6' MPa), and population (and all interactions) as factors in our model and PC1, PC2, and PC3 as response variables (3 models per species with PC1, PC2, or PC3 as the response; temperature, water potential, population, and interactions as fixed effects). Prior to running our models, we compared the log-likelihood of an ANOVA model without the random effects of trial, chamber (nested within trial), and cup (nested within chamber within trail) and a mixed effects model that included our random effect structure. Incorporating random effects did not improve our model fit (based on AIC values and non-significant log-likelihood ratio tests), thus we dropped random effects from our models to reduce complexity. For significant effects identified by our ANOVA model, we used Tukey HSD at α=0.05 to make *post-hoc* inferences about between-site, between-treatment, and between-population differences.

Objective 4: Determine how time to germination and dormancy depth align with seed and seedling traits

To achieve this objective, we used standard major axis (SMA) regression to evaluate the interspecific relationships between seeds traits, time to germination, depth of dormancy, and seedling traits using the '*smatr*' package in R (Warton et al. 2012). We

chose standard major axis regression to account for the independence and natural variability in both the *x* and *y* variables. Separate regressions were run for (1) time to germination and each individual seed and seedling trait, and (2) depth of dormancy and each seed and seedling trait. We were also interested in the relationship between morphological seed traits themselves, and thus ran additional individual regressions comparing seeds traits with one another.

Results

Variation in morphological and physiological seed traits across species, populations, and trait space (Objective 1)

We found significant intraspecific variation in seed traits across species and populations. Seed mass was particularly variable among populations and these population differences appeared to follow latitudinal trends (Appendix B: Table S.3.3)—*B. maritimus* seed mass increased significantly with increasing latitudes, while *S. americanus* seed mass decreased significantly with increasing latitude (Figure 3.2; Appendix B: Table S.3.4; $p = <0.001$). *Schoenoplectus acutus* seed mass variability was not consistent across latitude; rather, *S. acutus* seed mass exhibited within-region structuring in which seed mass significantly increased or decreased within the populations' region (Figure 3.2; Appendix B: Table S.3.4; $p = <0.001$). Seed coat thickness and seed dimension index exhibited less variability among populations for all species relative to seed mass but was still significantly different across populations (Figure 3.2; Appendix B: Tables S.3.5-S.3.8; $p = <0.001$). There was no significant difference in seed buoyancy across populations for *S. americanus* and *S. acutus* (Figure 3.2; Appendix B: Tables S.3.9-S.3.10; $p = 0.3202$ and $p = 0.4162$, respectively), while *B.*

maritimus experienced significantly higher seed buoyancy in the 'FISP' population relative to other tested populations (Figure 3.2; Appendix B: Figure S.3.3; Appendix B: Tables S.3.9-S.3.10; $p = 0.008$). Across species, *B. maritimus* has significantly larger seeds, thicker seed coats, and more buoyant seeds relative to other tested species (Figure 3.2; Tables S.3.3-S.3.10). Dormancy depth, which was calculated as a single averaged value for each species and population, exhibited substantial variation across species and populations—in general, *B. maritimus* and *E. palustris* were more deeply dormant relative to most populations of *S. acutus* and *D. spicata* (Figure 3.3).

In the interspecific seed trait principal component analyses, we captured most of the variation with two principal components (85.23%; Figure 3.4, Appendix B: Table S.3.11). The first axes of variation (63.37%) represented a 'size-persistence' relationship that captured variation in seed mass and depth of dormancy such that heavier seeds were more deeply dormant relative to lighter, less dormant seeds (Figure 3.4; Appendix B: Table S.3.11). There was also a strong correlation between seed mass and seed coat thickness identified on the first axis of variation (Figure 3.4; Appendix B: Table S.3.11). PC2 (21.86%) was characterized by a tradeoff between seed dimensions and seed coat thickness, with elongated seeds demonstrating thinner seed coats relative to rounder seeds with thick seed coats (Figure 3.4; Appendix B: Table S.3.11).

Intraspecific principal component analyses performed across *B. maritimus* populations revealed a similar tradeoff between seed mass (which was strongly correlated with seed dimension) and depth of dormancy on PC1 (38.4%), with heavier (and rounder) seeds more deeply dormant than lighter (more elongated) seeds (Appendix B: Table S.3.12; Appendix B: Figure S.3.4). Interestingly, a similar tradeoff was not observed for

S. acutus on PC1 (35.32%)—rather, seed mass and depth of dormancy acted independently, and the axes of variation on the first PC represented a morphological seed tradeoff between seed mass and seed buoyancy such that lighter seeds were more buoyant than heavier seeds (Appendix B: Table S.3.12; Appendix B: Figure S.3.4). For *B. maritimus* PC2 (23.14%), a correlation was observed between seed buoyancy and seed coat thickness, but these traits acted independently from seed mass, seed dimensions, and depth of dormancy (Appendix B: Table S.3.12; Appendix B: Figure S.3.4). For *S. acutus* (PC2: 22.78%) captured a persistence tradeoff between seed coat thickness and depth of dormancy such that seeds with thicker coats had deeper dormancy (Appendix B: Table S.3.12; Appendix B: Figure S.3.4).

Relating variation in seed traits to collection-site abiotic conditions (Objective 2)

A principal component analysis intended to reduce the dimensionality of our collection-site abiotic conditions identified three principal components that explained 94.99% of the variation in the data set (Appendix B: Table S.3.13). The top three abiotic conditions that loaded onto each axis of variation were the mean annual temperature in 2018 (PC1), mean annual precipitation in 2017 (PC2), and elevation (PC3). These three variables had low correlation among them (Appendix B: Table S.3.14) and high correlation among the next four highest loaded variables for the first two principal components (Appendix B: Table S.3.15), indicating that these top three abiotic conditions were sufficient in representing the general temperature, precipitation, and elevation gradients of variation in the data set. Robust linear models investigating the influence of the top three collection-site abiotic conditions on intraspecific seed traits of *B. maritimus* and *S. acutus* showed no significant effect of 2017 mean annual precipitation, 2018 mean

annual temperature, or elevation on seed mass, seed coat thickness, seed dimensions, or seed buoyancy for either species (Appendix B: Tables S.3.16-S.3.25). Mean annual temperature in 2018 did have a moderately significant effect on depth of dormancy across *B. maritimus* populations such that increasing temperatures yielded shallower dormancy (i.e., dormancy index closer to 1; (p = 0.056; Figure 3.5A; Appendix B: Table S.3.20). For *S. acutus*, there was a significant effect of elevation on depth of dormancy with seeds collected from higher elevations exhibiting a deeper dormancy (p = 0.005; Figure 5B; Appendix B: Table S.3.25).

Assessing the variation in seedling trait responses to temperature and water potential across species and populations (Objective 3)

The interspecific principal component analysis reduced seven seedling traits down to three components that captured much of the variation (75.31% total; PC1: 31.3%, PC2: 25.1%, PC3: 17.94%; Table 3.2a; Figure 3.6a). PC1 largely represented variation in belowground and aboveground allocation and growth strategies, reflecting a tradeoff between belowground biomass allocation (high RMR, RDMC) and acquisitive aboveground growth traits (high SER). Interestingly, we saw a strong positive correlation between time to 50% germination and belowground biomass allocation traits (RMR, RDMC) along PC1 – species that invested more biomass in root growth germinated more slowly relative to species that had higher SER (Table 3.2a; Figure 3.6a). PC2 captured variation in tissue construction and growth traits of both above and belowground parts, with an observed tradeoff between specific root and shoot length per unit biomass (SRL/SLA) and root and shoot elongation rate (RER/SER). PC3 captured a tradeoff between root elongation rate (RER)/shoot elongation rate (RER) and

belowground/aboveground biomass allocation (RDMC/SDMC), indicating that greater elongation per unit area/length comes at a cost of overall biomass allocated to those tissues.

PC1 scores varied significantly by species ($p < 0.001$; Table 3.3), with *E. palustris* consistently allocating more to belowground biomass allocation (high root mass ratio) and *D. spicata* and *P. australis* exhibiting high shoot elongation rates (Figure 3.7). Temperature also had a significant effect on PC1 across all species ($p = 0.002$; Table 3.3), such that higher temperatures yielded higher shoot elongation rates (i.e., more negative PC1 values; Figure 3.7). PC2 scores varied significantly by species only ($p = 0.002$; Table 3.3), with *B. maritimus* displaying higher specific root length (SRL) relative to *D. spicata*, *P. australis*, and *E. palustris* that had a higher rate of root elongation (high RER, Figure 3.7). We did not observe any significant difference in PC2 scores across temperatures ($p = 0.725$; Table 3.3). We found a significant temperature × species interaction on PC3 ($p = 0.044$; Table 3.3). This interaction was presumably driven by the growth response of *S. acutus*—a shift to the highest temperature regime yielded an increase in aboveground biomass allocation (SDMC) and decrease in root elongation rate (i.e., more negative PC3 scores; Appendix B: Figure S.3.5). No PC scores varied significantly in response to water potential (Table 3.3).

The intraspecific principal component analysis for *B. maritimus* reduced much of the variation in seedling traits down to three principal components (70.75% total; PC1: 34.68%, PC2: 21.23%, PC3: 14.84%; Table 2b; Figure 3.6b). PC1 largely represented a separation between biomass allocation to belowground parts in some populations (high RDMC, RMR) versus acquisitive belowground strategies due to longer, thinner roots in

others (high SRL; Table 3.2b; Figure 3.6b). There was a significant difference in PC1 scores across populations (p = 0.001; Table 3.3; Figure 3.8), with the 'PAHR' population (Pahranagat, NV) exhibiting greater belowground biomass allocation (RDMC) relative to the 'CLLA1', 'WASPUT', 'ALK2', or 'FABA1' populations. There were no significant effects of temperature (p = 0.072; Table 3.4) or water potential (p = 0.944; Table 3.4) on PC1. PC2 was characterized by conservative vs. acquisitive aboveground plant strategies with higher PC2 values representing greater allocation to aboveground biomass (high SDMC) and lower PC2 values representing higher above- and belowground elongation rates (SER/RER, Table 3.1b; Figure 3.6b). There weresignificant temperature (p = 0.009; Table 3.4; Figure 3.8) and water potential (p 0.001; Table 3.4; Figure 3.8) effects on PC2—the lowest temperature regime ('28-10') yielded higher shoot and root elongation rates, as did the drier treatment ('-0.6 MPa' [WP2]), though there was significant variation, and the overall effect was small (Appendix B: Figure S.3.5). PC3 represented a trade-off between aboveground biomass allocation (high SDMC) and time to germination (Table 3.2b), for which there was a significant temperature effect (p = < 0.001; Table 3.4)—the highest temperature treatment ('36-20') yielded significantly lower PC3 scores, indicating quicker germination and higher biomass allocation to shoots (i.e. high SDMC; Table 3.2b; Appendix B: Figure S.3.5).

The intraspecific PCA for *S. acutus* populations reduced seven seedling traits down to three components that captured much of the variation (72.79% total; PC1: 28.02%, PC2: 26.98%, PC3: 17.78%; Table 3.2c; Figure 3.6c). PC1 represented a tradeoff between belowground biomass allocation (high RDMC) and above- and belowground elongation rates (SER/RER; Table 3.1c), but there was no population effect

(p = 0.848; Table 3.5; Figure 3.9), temperature (p = 0.542; Table 3.5; Figure 3.9), or water potential (p = 0.491; Table 3.5; Figure 3.9). PC2 was characterized by belowground strategies related to tissue construction with higher values of PC2 representing high root elongation rates (RER) and lower values of PC2 representing higher specific root lengths (SRL; Table 3.2c; Figure 3.6c). There was a significant temperature (p = <0.001; Table 3.5) and water potential (p = <0.001; Table 3.5) effect on PC2, such that higher temperatures and wetter conditions yielded higher specific root lengths and lower root elongation rates (i.e., more negative PC2 scores) relative to colder or drier conditions (Figure 3.9). PC3 represented a tradeoff between aboveground biomass allocation and specific leaf area, with higher PC3 values indicating higher aboveground allocation (high SDMC) and lower PC3 values indicating high SLA (Table 3.2c). There was a significant effect of temperature (p = 0.003; Table 3.5), water potential (p = 0.003; Table 3.5), and population (p = 0.003; Table 3.5; Figure 3.9).

Charactertize how time to germination and dormancy depth align with seed and seedling traits (Objective 4)

Results of the standard major axis regression suggested that heavier seeds and seeds with thicker seed coats are slower to germinate, and rapid germination occurs in elongated seeds with shallow dormancy. This was evidenced by a significant positive relationship between time to 50% germination and: (1) seed mass (p = <0.001, R^2 = 0.30; Figure 3.10) and (2) seed coat thickness (p = <0.001, R^2 = 0.49; Figure 3.10). There was also a significant negative relationship between time to 50% germination and: (1) depth of seed dormancy (p = 0.003, R^2 = 0.21; Figure 3.10) and (2) seed dimensions (p =

<0.001, R^2 = 0.33; Figure 3.10). There was no significant relationship between seed buoyancy and time to 50% germination (p = 0.122, R^2 = 0.03; Figure 3.10).

Standard major axis regression also suggested that species and populations that are slower to germinate (greater time to 50% germination) with deeper dormancy invest more in belowground biomass allocation, whereas rapidly germinating seeds that have shallow dormancy favor rapid shoot elongation rate and above ground biomass investment (Figure 3.12). This was evidenced by a significant positive relationship between time to 50% germination and: (1) root dry matter content (p = 0.020, R^2 = 0.08; Figure 3.11), (2) root mass ratio (p = < 0.001, R^2 = 0.26; Figure 3.11), and (3) specific leaf area (p = 0.001, R^2 = 0.15; Figure 3.11). There was also a significant negative relationship between time to 50% germination and: (1) shoot dry matter content (p = 0.002, R^2 = 0.14; Figure 3.11) and (2) shoot elongation rate (p = 0.003, R^2 = 0.13; Figure 3.11). There was nosignificant relationship between time to 50% germination and: (1) root elongation rate (p = 0.398, R^2 = 0.01; Figure 3.11) and (2) specific root length (p = 0.760, R^2 = 0.00; Figure 3.11). We also found a significant positive relationship between depth of dormancy and shoot elongation rate (p = 0.008, R^2 = 0.12; Figure 3.12), and a significant negative relationship between depth of dormancy and: (1) root dry matter content (p = < 0.001, R^2 = 0.20; Figure 3.12), and (2) root mass ratio (p = < 0.001, R^2 = 0.24; Figure 3.12).

Regarding seed trait relationships, we found a significant positive relationship between seed buoyancy and: (1) seed coat thickness (p = < 0.001, R^2 = 0.33; Figure 3.13) and (2) seed mass (p = < 0.001, R^2 = 0.60; Figure 3.13), and a negative relationship between seed buoyancy and depth of dormancy (p = < 0.001, R^2 = 0.34; Figure 3.13).

There was a significant positive relationship (but weak explanatory power) between seed dimension index and dormancy depth (p = < 0.001, R^2 = 0.07; Figure 3.13). We also observed a negative relationship between seed mass and depth of dormancy (p = < 0.001, R^2 = 0.53; Figure 3.13) and a positive relationship between seed mass and seed coat thickness (p = < 0.001, R^2 = 0.59; Figure 3.13). These patterns suggest that heavier seeds have thicker seed coats, are more buoyant, are rounder, and have deeper dormancy.

Discussion

Here, we investigated inter- and intraspecific variation in seed, germination, and seedling traits with the goal of identifying ecological strategies at early life stages to make inferences about how wetland species persist, diserperse, and grow following seed-based wetland restoration. Our first objective was to identify variation in seed traits across species, populations, and in multivariate trait space. As expected, we found substantial inter- and intraspecific variation in seed traits, particularly for seed mass and dormancy depth. The seed mass/seed dimension and depth of dormancy relationship characterized a primary seed trait tradeoff across species such that heavier, rounder seeds were more deeply dormant, but the morphological mechanism driving dormancy depth was not coordinated at the intraspecific level between species—deeper dormancy was linked to heavier, rounder seeds for *B. maritimus*, but was linked to thicker seed coats for *S. acutus*. Our second objective was to identify abiotic conditions at the seed collection site that contribute to intraspecific variation in seed traits for *B. maritimus* and *S. acutus*. Contrary to our predictions, the intraspecific variation we observed in seed mass was not linked to abiotic conditions at the collection-site. We did, however, find evidence of collection-site influences on depth of dormancy such that dormancy depth increased

(deeper dormancy) with decreasing mean annual temperatures for *B. maritimus* and with increasing elevation for *S. acutus*. Our third objective was to determine if and how potential restoration site conditions influence multivariate tradeoffs in time to germination and seedling traits across species and populations. In line with our predictions, inter- and intraspecific assessments of seedling traits in multidimensional trait space revealed a general tradeoff among the first axis of variation between conservative and acquisitive ('fast-slow') plant growth strategies typically associated with the larger, adult plant economic spectrum ('PES'; Wright et al. 2004; Diaz et al. 2016). However, to our surprise and contrary to 'PES' predictions, the second PC axis revealed a tradeoff between specific root length and root elongation rate at the species level and, even more surprisingly, orthogonality of these root traits at the population level for both *B. maritimus* and *S. acutus*. As expected, there were clear differences in seedling functional traits among species, but less apparent variation among populations. We were surprised to find that, in general, there were not consistent or strong effects of temperature and water potential on seedling trait expression, perhaps due to large variation in these traits among species and populations. Our fourth objective was to determine how germination speed and dormancy depth relate to seed and seedling traits, and how seed and seedling traits relate to one another. At the seed level, regression results suggested that, across species, seed buoyancy was higher for heavier seeds with deeper dormancy, and that seed buoyancy was partially explained by variation in seed coat thickness. Time to 50% germination and depth of dormancy were critical links between seed and seedling traits—light seeds with thin seed coats and shallow dormancy had faster germination and favored acquisitive aboveground strategies (high shoot

elongation rate), whereas heavy seeded species with thick seed coats, deep dormancy, and slower germination favored conservative belowground strategies (high root dry matter content and root mass ratio).

Seed dispersal and persistence traits contributed to species adaptability in unique wetland environments

We identified several important seed trait relationships that may have functional implications for dispersal, persistence, and germination at population- and community-levels (Jiménez-Alfaro et al. 2016; Beckman et al. 2020). Seed coat thickness, which has been hypothesized to aid in endozoochorous dispersal for some wetland species (Soons et al. 2008; Reynolds & Cumming, 2016; Kettenring et al. 2019), was positively correlated to seed buoyancy in this study. This relationship aligns with an evolutionary adaptation to endozoochorous dispersal via waterfowl ingestion in some wetland species—seeds that are more buoyant are generally more likely to be ingested by waterfowl such as dabbling ducks, and thicker seed coats allow for the seed to: (1) withstand hydrochloric stomach acids, and (2) pass through the gut with an increased germination ability following degradation of the hard seed coat (Kleyheeg et al. 2018; Costea et al. 2019; Kettenring et al. 2019; Lovas-Kiss et al. 2020). Further, we found that more buoyant seeds also had deeper dormancy, which could indicate an adaptation of delaying germination to account for long-distance water or endozoochorous dispersal away from the parent plant. Deep dormancy can also facilitate spatiotemporal bet-hedging, which can be adaptive in unpredictable, heterogenous environments (Evans & Dennehy, 2005). The findings from this study supported the idea that these seed traits may be highly adaptive to the unique microenvironment in which these species typically reside—obligate wetland species

('BOMA, 'SCAC', 'SCAM', 'ELPA') that grow in and around water tended to have higher seed buoyancy, seed mass, seed coat thickness, and deeper dormancy, while facultative wetland species ('DISP', 'PHAU') had lighter seeds, were less buoyant, and had shallower dormancy. Our findings are consistent with other studies on multidimensional wetland seed traits by Phartyal et al. (2020) and Rosbach et al. (2020), who found support for the adaptive value of seed traits relative to specific habitat niches in wetland environments.

Seed persistence—defined as the ability of a seed to survive after maturity—has important implications for the maintenance of plant abundance and community composition over time (Long et al. 2015). Thompson et al. (1993) proposed that smaller seeds were more likely to persist in the seed bank due to increased likelihood of seed burial, which has been supported by numerous studies across hundreds of floras around the world (e.g., Funes et al. 1999, Thompson et al. 2001, Cerabolini et al. 2003), but not supported by others (e.g., Leishman & Westboy, 1998; Moles et al. 2000). The findings from our study did not support this idea—we found that larger seeds had deeper dormancy, which implies that they persist for longer periods of time in the seed bank. Part of this divergence could be related to a distinction (and possible misconception) that increased depth of dormancy is equivalent to increased soil persistence (Thompson et al. 2003), which is not something we measured directly in this study. This divergence could also be explained by seed coat thickness, which was correlated with seed mass in this study, and has been linked to decreased mortality in soil seed banks (Gardarin et al. 2010). Thus, our findings that seed persistence (i.e., deep dormancy) increased with increasing seed mass could be explained, at least in part, by increasing seed coat

thickness and not seed mass, *per se*. Ultimately, patterns between seed size and seed persistence do not appear to be universal and are likely driven by specific ecological and evolutionary forces, like water level or predation, for a given species and site.

Maternal environment effects influenced dormancy depth, but had little effect on other measured seed traits

Despite empirical studies highlighting the relationship between the maternal environment and seed mass development, collection-site abiotic conditions in the year leading up to seed harvest did not explain any of the seed mass variation we observed in the intraspecific analyses across populations. This finding may be attributed to the spatial scale of the abiotic conditions used in the analysis—it is likely that heterogenous abiotic variation, which is typical of wetlands on a small spatiotemporal scale (Euliss et al. 2004; Jackson, 2006), was occurring at a much finer resolution than the abiotic data gathered from the Climate NA dataset. Further, the abiotic conditions gathered from the Climate NA dataset may not be a good representation of the unique abiotic conditions that control wetland plant communities (e.g., inter-annual water table fluctuations, prolonged flooding, elevated nutrient inputs from upstream sources; Cronk & Fennessy, 2016). While collection-site level abiotic conditions did not explain seed mass variation, we did find evidence for increasing dormancy depth in areas with low temperatures and high elevation, which is in line with numerous other studies that have reported on the importance of local climate in regulating seed dormancy (Fenner, 1991; Huang et al. 2014; Donohue, 2014; Springthorpe & Penfield, 2015, Carta et al. 2016). These climatic patterns were observed in the population-level PCA of seed traits—*Bolboschoenus maritimus* populations with the highest annual temperature exhibited the shallowest

dormancy (e.g., ‘PAHR’, Appendix B: Figure S3) while northernmost populations with low annual temperatures had the deepest dormancy (e.g., ‘BLHO’, Appendix B: Figure S3). As temperatures continue to rise in the context of global climate change, particularly in the American West, this finding implies that seeds that are typically deeply dormant may experience a reduction in dormancy depth with rising temperatures. This phenomenon has important population-level implications (e.g., reduction in spatial or temporal bet-hedging; Evans & Dennehy, 2005) as well as restoration implications (e.g., more logistically feasible to induce germination prior to or during restoration). Interestingly, elevation, but not temperature, was responsible for dormancy differences among *S. acutus* populations, which suggests that other factors correlated with elevation drive differences in dormancy depth for *S. acutus* (e.g., photoperiod; Cavieres & Arroyo, 2001; Huang et al. 2018; Fernández Farnocchia et al. 2021).

Some indication of a seed economic fast-slow spectrum for functional seed traits

In this study, inter-species analyses revealed that rapidly germinating species had thin seed coats, shallow dormancy, and high shoot elongation rates. Conversely, species that had a slower rate of germination tended to have thick seed coats, deep dormancy, and greater biomass allocation to belowground structures. These findings suggest that a similar economic (i.e., ‘fast-slow’) spectrum that operates in mature plants could also operate at the seed-seedling scale, which has been observed in at least one other study (Larson et al. 2021). Larson et al. (2021) hypothesized that this relationship could be an indicator of drought escape strategies beginning in early regenerative stages, which could very well hold true for regeneration processes of terrestrial species. This mechanism may be less relevant in wetland systems where species have adapted and evolved strategies to

withstand periodic flooding (Cronk & Fennessy, 2016). At the wetland seed-seedling scale, rapid germination and shoot elongation could be a flooding avoidance strategy for flooding-intolerant species during early establishment. *Distichlis spicata* and *P. australis* both exhibited this strategy in our study, which may be related to flooding intolerance for these species in early life stages (Elhaak et al. 1993). Both species germinate early in the season, when moisture and flooding is generally more prevalent (Downard et al. 2014), relative to the other focal species in this study. The other end of this spectrum represented species that may adopt a flooding tolerance strategy, which, in this study, was composed of obligate wetland species that have demonstrated tolerance to periods of flooding during germination (Clevering, 1995; Jutila, 2001; Kettenring, 2016). We did not observe a similar 'avoidance-tolerance' spectrum in the intraspecific analysis, which further supports that this pattern is observable only across wetland species with different habitat preferences. Rather than a tradeoff, intraspecific analyses identified a positive correlation between time to germination and shoot elongation rate for both *B. maritimus* and *S. acutus*. In other words, populations that were slower to germinate had more rapid shoot elongation rates, which could allow for those seedlings to "catch up" to more rapidly germinating populations.

Emerging patterns and unexpected tradeoffs among wetland seedling traits

One particularly intriguing finding in this study was the observed tradeoffs between growth traits and root/shoot tissue constructions traits (Figure 6). These patterns run contrary to the plant economic spectrum which predicts that thin leaves and roots (high SLA/SRL) indicate rapid growth rates in plants operating on the 'fast' end of the growth spectrum (Wright et al. 2004; Reich, 2014). The positive association between

SLA and relative growth rate characterizes the 'leaf economic spectrum' and has been well-documented across species and systems (Grime et al. 1997; Wright et al. 2004; Reich et al. 2003; Freschet et al. 2010), though a large majority of these assessments have focused on terrestrial vascular plants in grasslands (de Bello et al. 2010). In a meta-analysis of 103 plant trait studies among tree species, Gibert et al. (2016) found the association between specific leaf area and relative growth rate to be even stronger at the seedling stage relative to the adult stage due to an increase in non-photosynthetic tissue development with increasing size. Here, we find an important distinction in wetland species demonstrating that functional traits in wetland plants, even at the seedling stage, may not conform to expectations for grassland or forest plant species (Moor et al. 2017).

High water tables and soil saturation are a defining feature of wetlands, and these conditions shape plant community assembly following disturbance (Keddy, 1992). Obligate wetland species that tolerate periodic flooding events and soil saturation have a higher volume of aerenchyma in both root and shoot structures relative to non-flood tolerant species (McCoy-Sulentic et al. 2017), which allows for the maintenance of gas exchange and plant functioning during periods of high water (Jackson & Armstrong, 1999; Pezeshki, 2001; Cronk & Fennessey, 2016). Studies assessing leaf morphology of plants in response to flooding have found that, in general, SLA increases to optimize gas-exchange capacity along a gradient of growth in 'less to more frequently flooded' conditions (Mommer & Visser, 2005; Winkler et al. 2016). High SLA was found to have a positive correlation with leaf longevity underwater and was associated with greater recovery times after flooding (Mommer et al. 2006; Wright et al. 2017), which suggests that high SLA is an important 'flood tolerance' adaptation for wetland species. In this

study, obligate wetland species tended to have higher SLA and lower shoot elongation rates relative to facultative wetland species, demonstrating that higher SLA values were associated with flood-tolerant wetland plants, and is likely related to aerenchyma volume (Mommer & Visser, 2005; Colmer & Voesenek, 2009). This pattern still maintains an 'acquisitive vs. conservative' dimension, albeit with high SLA operating on the conservative end of the spectrum to allow for plants to tolerate flooding events and high SER operating on the acquisitive end to escape potential floods during early life stages. To our knowledge, this is the first study demonstrating functional trait tradeoffs of wetland seedlings and our results suggest there is some cohesiveness in these tradeoffs between seedling and adult wetland plant stages, but that they occupy markedly different patterns than that of the traditional 'PES' framework.

The tradeoff we observed between root elongation rate (RER) and specific root length (SRL) at the interspecies level also contrasts with a similar 'fast-slow' growth strategy hypothesized as the 'root economic spectrum' ('RES', Reich, 2014; Roumet et al. 2006). Functional tradeoffs among root traits are less clear than that of leaf tradeoffs, and several studies have identified the presence of multidimensional root responses throughout development and across abiotic gradients (Kramer-Walter et al. 2016; Zhou et al. 2017; Kong et al. 2019; Shen et al. 2022). These multidimensional responses suggest that root development and subsequent function are not constrained in the same way as leaf traits. Kramer-Walter et al. (2016) identified SRL specifically as being independent of the plant economic spectrum. Similarly, in this study we found that SRL was orthogonal to (i.e., developed independent from) root elongation rate among our populations (but not among species), supporting the idea that the 'RES' operates among

multiple dimensions that are not yet fully understood. In the interspecies analysis, the SRL and root elongation rate tradeoff appeared to be coordinated with the aboveground SLA and shoot elongation rate tradeoff. This belowground tradeoff may be explained by differences in life-history of the species we worked with relative to the species for which many of these principles were tested and developed (terrestrial, annual grassland species; de Bello et al. 2010). The focal species in this study were all perennial, clonal species that tend to invest more energy in belowground biomass acquisition to develop clonal structures relative to non-clonal plants (e.g., bud bank, Martínková et al. 2020). In a system where clonality is the common plant syndrome, it is possible that clonal species adapted to wet environments develop thicker roots (i.e., lower SRL, presumably due to higher root aerenchyma volume; Tanentzap & Lee, 2017) that can withstand and elongate more rapidly under waterlogged conditions. However, there was not a clear distinction between wetland plant indicator status (i.e., obligate vs. facultative wetland species) along this spectrum, which suggests some other evolutionary or ecological (beyond temperature and water potential, for which there was no significant effect) driver of this pattern. Overall, an important takeaway here is that there are large gaps in our knowledge related to the intersection of root functional trait tradeoffs and early seedling growth, and the high plasticity of root traits make these patterns less distinguishable than that of aboveground leaf traits (Valverde-Barrantes et al. 2013). Further, root functional trait strategies in wetland plants likely exhibit patterns that are not observed in upland species due to strong ecological and evolutionary factors, like water levels and subsequent anoxia, driving root development.

Abiotic treatments did not markedly influence the expression of seedling functional traits in multivariate trait space

We did not find strong or consistent patterns of the tested abiotic treatments on inter- or intraspecific seedling traits. The lack of trait-environment relationships, particularly for root traits, may be the consequence of differences in root morphology (i.e., aerenchyma) that are unique to wetland species. Supporting this theory, Laughlin et al. (2021) found that root traits (and particularly, SRL) were not related to climatic gradients or probability of occurrence for wetland species, although they were for forest and upland species. Thus, the development of aerenchyma confounds the expected root trait-climate relationships based on observations in non-wetland species (Laughlin et al. 2021; Ye & Ryser, 2022). The lack of any strong aboveground trait-environment relationships could be the result of high phenotypic plasticity of wetland species, which exist in highly heterogenous environments, where species must adapt to a wide range of conditions (Baythavong, 2011). High plasticity in these species, particularly across populations for *B. maritimus* and *S. acutus*, would dampen any discernable patterns of phenotypic trait differentiation across abiotic conditions (Nicotra et al. 2010). From a restoration context, these findings suggest that sourcing seeds to optimize growth in future site conditions (i.e., 'pre-restoration' *sensu* Butterfield et al. 2017) may be less important in wetlands species that have high phenotypic plasticity to grow and adapt to a wide range of conditions relative to non-wetland species. Furthermore, it is possible that other mechanisms, such as light-competition induced by neighboring plants, would be a stronger driver of aboveground trait differences, which was not something we measured here.

Conclusions

Given the importance of regeneration to plant community assembly and community dynamics, identifying patterns and consequences of functional trait variation across species and populations is critical, particularly for species in the many ecosystems that have been generally underrepresented (i.e., not grasslands) in trait-based ecological research. Without such broad assessments of functional regeneration traits, emerging principles will be limited in scope and potentially erroneous. Furthermore, such research is especially pertinent for wetland species given the unique abiotic conditions that may result in unexpected trait characteristics and tradeoffs, as well as the growing need for seed-based wetland restoration solutions. Our study demonstrates that seed traits provide adaptive value for the specific habitat in which a wetland plant resides and can provide insights into how seedlings will later perform (e.g., fast time to germination = prioritizes elongation relative to biomass allocation). Further, we highlight important distinctions between the traditional 'PES' and the strategies driving wetland plant variation, particularly at the seedling stage. Given the relatively scarce research on wetland plant regeneration traits, more studies are needed across a wider range of species and populations to confirm and determine the extent of these patterns. We found a great deal of variation among *B. maritimus* and *S. acutus* populations that may partially explain the lack of strong trait differences across abiotic conditions at the seedling stage. Field studies testing intraspecific functional traits and plant performance across a wider range of abiotic conditions common in wetlands could help elucidate the importance (or lack thereof) of trait-environment relationships relative to trait plasticity in wetland plants. Ultimately, understanding how, why, and when wetland plants persist, disperse, and grow

will enhance predictions of community dynamics, assembly, and seed-based restoration outcomes in wetland ecosystems.

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Tables and Figures

TABLE 3.1. Seed, germination, and seedling functional traits measured in Chapter 3.

Category	Trait	Unit	Functional significance/type
Seed	Seed mass	mg	Seedling survival, drought tolerance, dispersal capacity, predation
Seed	Seed coat thickness	µg	Seed persistence, time to germination
Seed	Seed dimension index	-	Seed persistence, burial
Seed	Seed buoyancy	days	Hydrochoric dispersal capacity
Transition	Depth of dormancy index	-	
Transition	Time to 50% germination (t50)	days	Competitive ability
Seedling	Root mass ratio (RMR)	$mg \cdot mg^{-1}$	Biomass allocation between above- and belowground parts
Seedling	Root elongation rate (RER)	$cm \cdot days^{-1}$	Growth trait, rate of belowground resource capture
Seedling	Shoot elongation rate (SER)	$cm \cdot days^{-1}$	Growth trait, rate of aboveground resource capture
Seedling	Specific root length (SRL)	$cm \cdot mg^{-1}$	Tissue construction, related to thickness and longevity
Seedling	Specific leaf area (SLA)	$cm^2 \cdot mg^{-1}$	Tissue construction, related to thickness and longevity
Seedling	Root dry matter content (RDMC)	$mg \cdot mg^{-1}$	Biomass allocation
Seedling	Shoot dry matter content (SDMC)	$mg \cdot mg^{-1}$	Biomass allocation

TABLE 3.2. Variable loadings on the first three principal components for the seedling trait analysis. Tables display a) interspecific seedling trait variables for all species combined, b) intraspecific seedling trait variables for *B. maritimus* (BOMA), and c) intraspecific seedling trait variables for *S. acutus* (SCAC). The strongest positive loading and the strongest negative loading are bolded to aid in interpretation of the tradeoffs represented among each axis. *Variable abbreviations: RMR (root mass ratio), RDMC (root dry matter content), SDMC (shoot dry matter content), SLA (specific leaf area), SRL (specific root length), RER (root elongation rate), SER (shoot elongation rate), t50 (time to 50% germination).*

(a) All species			
Variable	PC Axis 1	PC Axis 2	PC Axis 3
RMR	**0.571**	-0.208	0.023
RDMC	0.450	-0.392	-0.287
SDMC	-0.121	-0.335	**-0.588**
SLA	0.371	0.342	0.132
SRL	-0.118	**0.441**	0.058
RER	0.045	**-0.430**	**0.550**
SER	**-0.309**	-0.411	0.434
t50	0.457	0.158	0.246
Variance explained (%)	32.10	25.28	17.94
Cumulative variance (%)	-	57.37	75.31
(b) BOMA			
Variable	PC Axis 1	PC Axis 2	PC Axis 3
RMR	0.481	-0.001	0.413
RDMC	**0.539**	0.245	0.002
SDMC	0.210	**0.414**	**-0.502**
SLA	-0.319	0.060	0.439
SRL	**-0.440**	-0.060	0.043
RER	0.288	-0.557	-0.168
SER	0.075	**-0.668**	-0.193
t50	0.226	-0.068	**0.563**
Variance explained (%)	34.68	21.23	14.84
Cumulative variance (%)	-	55.91	70.75
(c) SCAC			
Variable	PC Axis 1	PC Axis 2	PC Axis 3
RMR	-0.388	0.338	-0.492
RDMC	**-0.593**	0.247	-0.024
SDMC	-0.395	-0.089	**0.564**
SLA	0.046	-0.241	**-0.650**
SRL	0.279	**-0.380**	0.016
RER	0.325	**0.528**	-0.004
SER	**0.395**	0.475	0.112
t50	0.002	0.331	0.063
Variance explained (%)	28.02	26.98	17.78
Cumulative variance (%)	-	55.01	72.79

TABLE 3.3. Results of three-way ANOVAs testing the effects of temperature regime ('Temp'), water potential ('WP'), and all species combined, and their interactions, on PCA axes 1-3. Significant *p* values ($p < 0.05$) are shown in bold; marginally significant *p* values ($0.05 < p < 0.1$) are indicated by an asterisk. *Species included: Distichlis spicata (DISP), Phragmites australis (PHAU), Bolboschoenus maritimus (BOMA), Schoenoplectus acutus (SCAC), S. americanus (SCAM), Eleocharis palustris (ELPA).*

	Sum sq	Df	F value	Pr(>F)
PC axis 1, all species				
Temp	14.11	2	7.623	**0.002**
WP	0.07	1	0.073	0.789
Species	103.57	5	22.378	**< 0.001**
Temp × WP	2.79	2	1.509	0.236
Temp × Species	5.44	10	0.588	0.813
WP × Species	6.54	5	1.413	0.244
Temp × WP × Species	8.04	8	1.086	0.396
Residuals	31.47	34		
PC axis 2, all species				
Temp	1.11	2	0.325	0.725
WP	2.81	1	1.643	0.209
Species	40.86	5	4.778	**0.002**
Temp × WP	1.75	2	0.512	0.604
Temp × Species	17.47	10	1.022	0.446
WP × Species	4.87	5	0.569	0.723
Temp × WP × Species	8.46	8	0.618	0.756
Residuals	58.15	34		
PC axis 3, all species				
Temp	8.18	2	4.090	**0.027**
WP	0.00	1	0.004	0.953
Species	10.51	5	2.102	0.095*
Temp × WP	1.87	2	0.933	0.410
Temp × Species	22.24	10	2.224	**0.044**
WP × Species	4.83	5	0.965	0.464
Temp × WP × Species	13.85	8	1.731	0.135
Residuals	34.68	34	1.020	

TABLE 3.4. Results of three-way ANOVAs testing the effects of temperature regime ('Temp'), water potential ('WP'), and *B. maritimus* (BOMA) population, and their interactions, on PCA axes 1-3. Significant *p* values ($p < 0.05$) are shown in bold; marginally significant *p* values ($0.05 < p < 0.1$) are indicated by an asterisk.

	Sum sq	Df	F value	Pr(>F)
PC axis 1, BOMA				
Temp	13.83	2	2.823	0.072*
WP	0.01	1	0.005	0.944
Population	104.05	11	3.863	**0.001**
Temp × WP	10.73	2	2.191	0.125
Temp × Population	33.32	22	0.618	0.884
WP × Population	11.92	11	0.443	0.926
Temp × WP × Population	13.61	14	0.397	0.967
Residuals	95.49	39		
PC axis 2, BOMA				
Temp	14.70	2	5.303	**0.009**
WP	17.66	1	12.741	**0.001**
Population	17.38	11	1.140	0.359
Temp × WP	1.15	2	0.414	0.664
Temp × Population	24.85	22	0.815	0.691
WP × Population	24.71	11	1.621	0.131
Temp × WP × Population	18.74	14	0.966	0.503
Residuals	54.06	39		
PC axis 3, BOMA				
Temp	30.42	2	15.700	< **0.001**
WP	0.25	1	0.259	0.614
Population	17.04	11	1.599	0.137
Temp × WP	3.50	2	1.808	0.177
Temp × Population	21.48	22	1.008	0.478
WP × Population	2.48	11	0.233	0.994
Temp × WP × Population	8.12	14	0.599	0.849
Residuals	37.78	39		

TABLE 3.5. Results of three-way ANOVAs testing the effects of temperature regime ('Temp'), water potential ('WP'), and *S. acutus* (SCAC) population, and their interactions, on PCA axes 1-3. Significant *p* values ($p < 0.05$) are shown in bold; marginally significant *p* values ($0.05 < p < 0.1$) are indicated by an asterisk.

	Sum sq	Df	F value	Pr(>F)
PC axis 1, SCAC				
Temp	2.91	2	0.616	0.542
WP	1.13	1	0.477	0.491
Population	20.31	14	0.614	0.848
Temp × WP	3.23	2	0.684	0.507
Temp × Population	52.43	28	0.793	0.755
WP × Population	31.34	14	0.948	0.511
Temp × WP × Population	75.58	28	1.143	0.306
Residuals	250.23	106		
PC axis 2, SCAC				
Temp	82.30	2	26.617	**< 0.001**
WP	24.49	1	15.839	**< 0.001**
Population	24.65	14	1.139	0.334
Temp × WP	0.94	2	0.303	0.739
Temp × Population	40.36	28	0.932	0.568
WP × Population	28.00	14	1.294	0.224
Temp × WP × Population	56.35	28	1.302	0.170
Residuals	163.88	106		
PC axis 3, SCAC				
Temp	11.91	2	5.097	**0.008**
WP	5.35	1	4.585	**0.035**
Population	41.79	14	2.556	**0.003**
Temp × WP	5.65	2	2.421	0.094*
Temp × Population	36.49	28	1.116	0.335
WP × Population	21.48	14	1.314	0.211
Temp × WP × Population	30.88	28	0.944	0.552
Residuals	123.80	106		

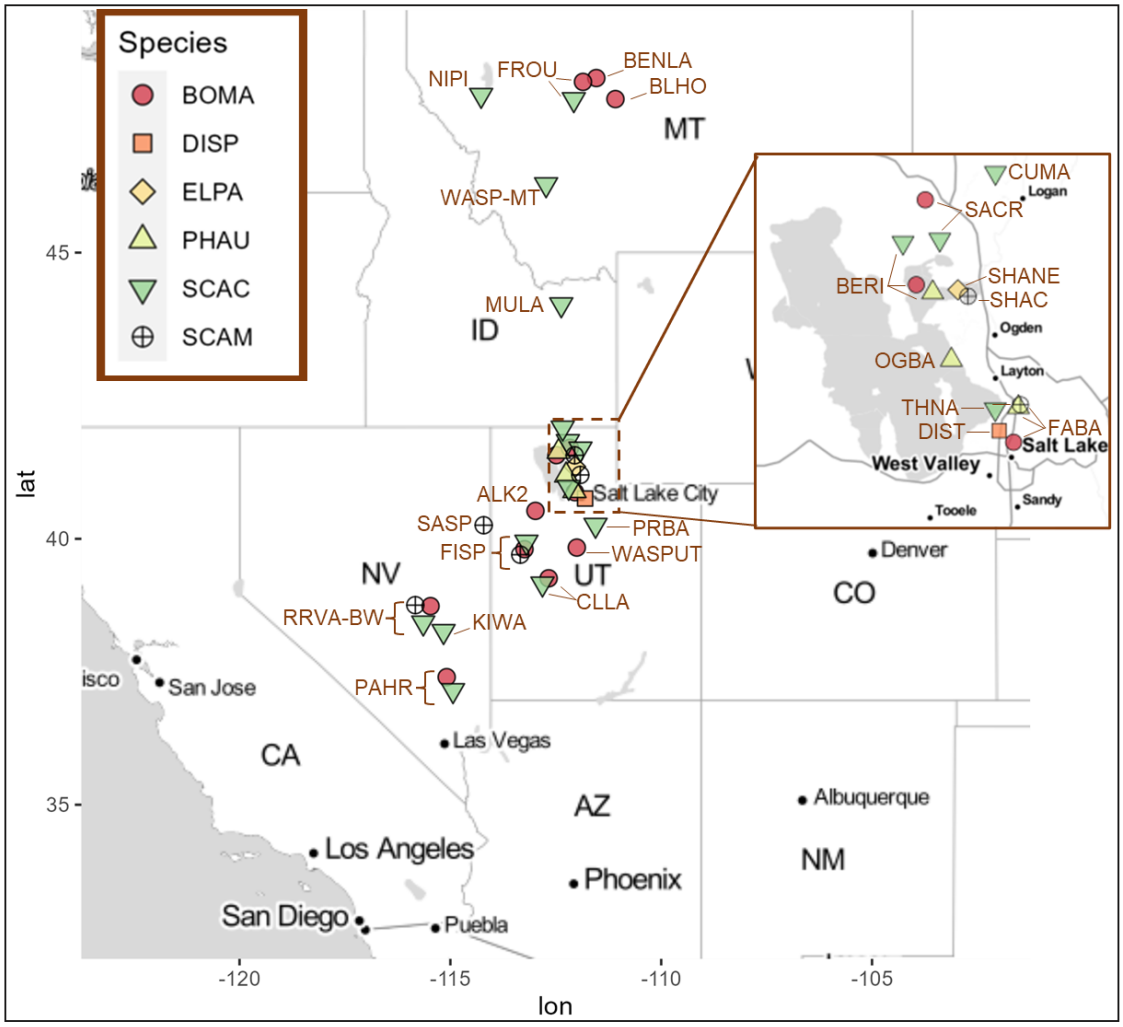


FIG. 3.1. Map of collection sites for each species and population. *Population abbreviations: PAHR = Pahranagat National Wildlife Refuge (NWR); RRVA-BW = Railroad Valley at Big Wells Wildlife Management Area (WMA); KIWA = Kirch WMA; SASP = Salt Springs WMA; FISP = Fish Springs WMA; CLLA = Clear Lake WMA; WASP-UT = Warm Springs WMA (Utah); PRBA = Provo Bay WMA; ALK2 = Tooele county collection (Granite Seed collection); FABA = Farmington Bay WMA; DIST = Great Salt Lake (GSL) collection (Granite Seed collection); THNA = The Nature Conservancy Shorelands Preserve; OGBA = Ogden Bay WMA; SHAC = GSL collection (Granite Seed collection); SHANE = GSL collection from Shane Sterner; BERI = Bear River NWR; SACR = Salt Creek WMA; CUMA = Cutler Marsh; MULA = Mud Lake WMA; WASP-MT = Warm Springs WMA (Montana); BLHO = Black Horse Lake; BENLA = Benton Lake NWR; FROU = Freezeout WMA; NIPI = Ninepine WMA.*

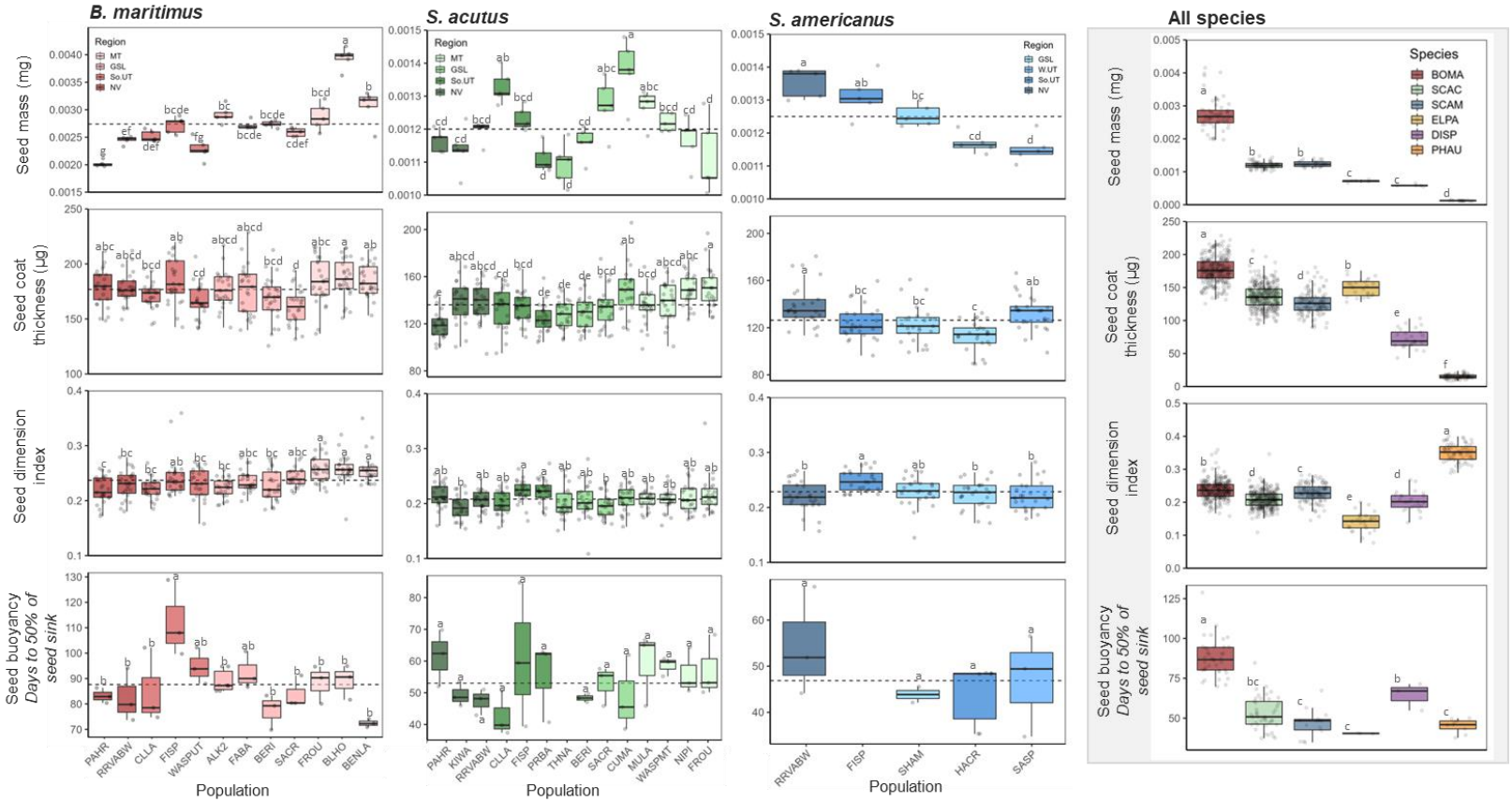


FIG. 3.2. Seed mass, seed coat thickness, seed dimension index, and seed buoyancy for *B. maritimus*, *S. acutus*, *S. americanus*, and all tested species across population and species. Lower-case letters indicate Tukey post-hoc comparisons (α=0.05) across population and species for each. Within each species, color gradients represent seed collection regions. All populations are sorted by latitude, with southernmost latitudes far left and northernmost latitudes far right. *Region abbreviations: MT = Montana; GSL = Great Salt Lake; So.UT = Southern Utah; NV = Nevada; W.UT = Western Utah. Species abbreviations: BOMA = Bolboschoenus maritimus; SCAC = Schoenoplectus acutus; SCAM = Schoenoplectus americanus; ELPA = Eleocharis palustris; DISP = Distichlis spicata; PHAU = Phragmites australis.*

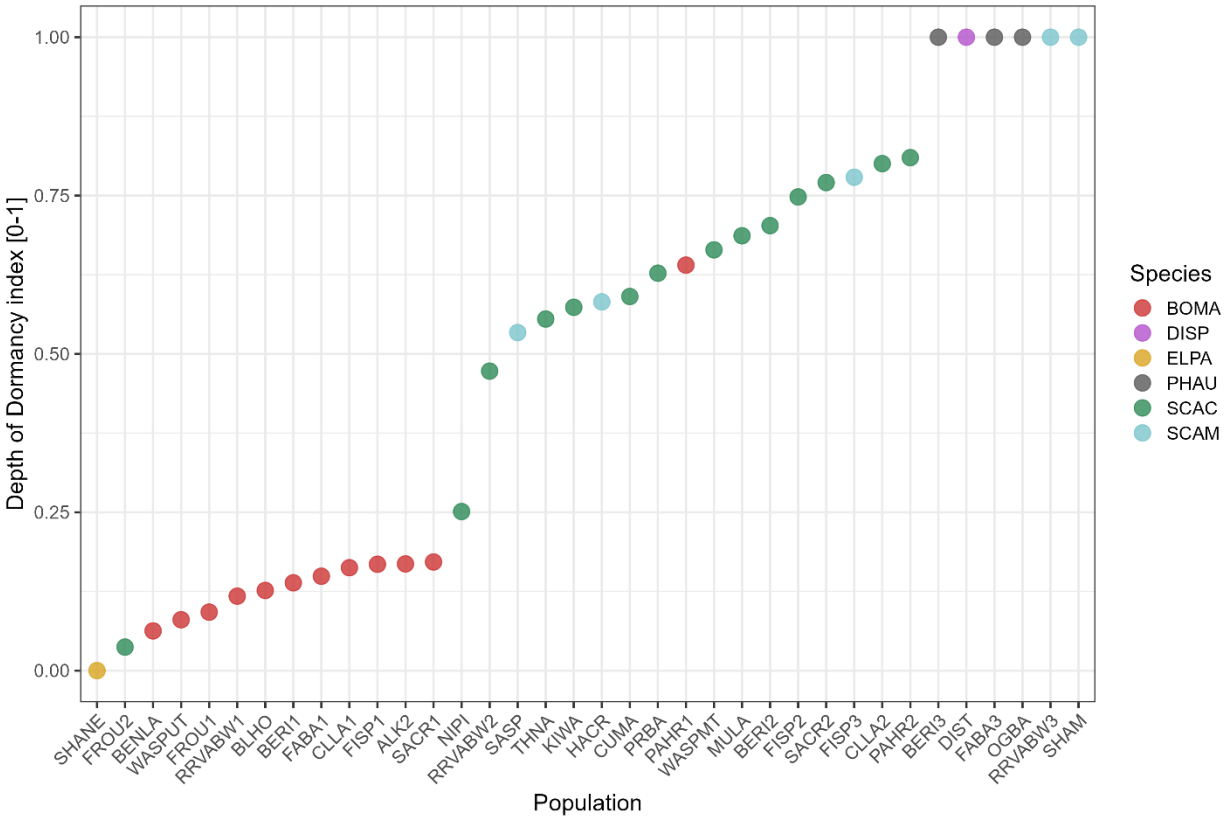


FIG. 3.3. Depth of dormancy index across species × population. A value closer to 0 represents populations that were more deeply dormant; a value closer to 1 represents populations with shallow or no dormancy.

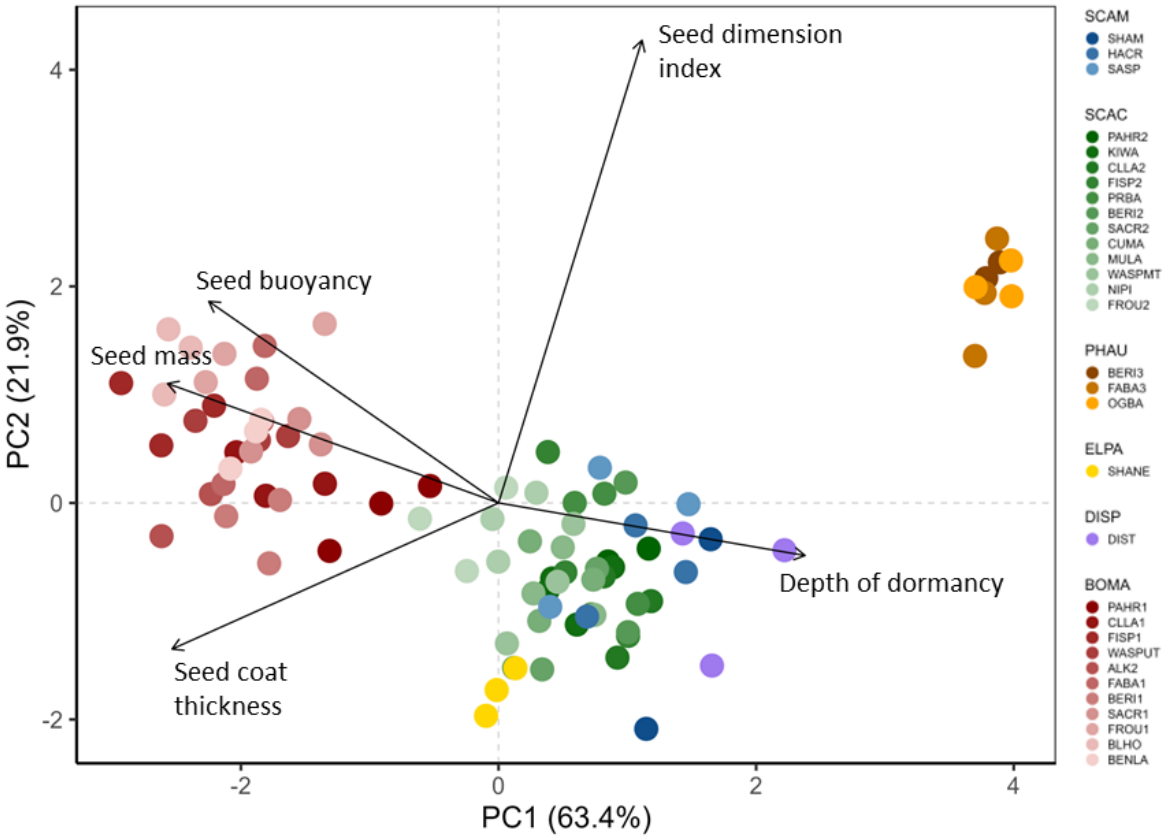


FIG. 3.4. Principal component analysis of seed traits for all species × population.

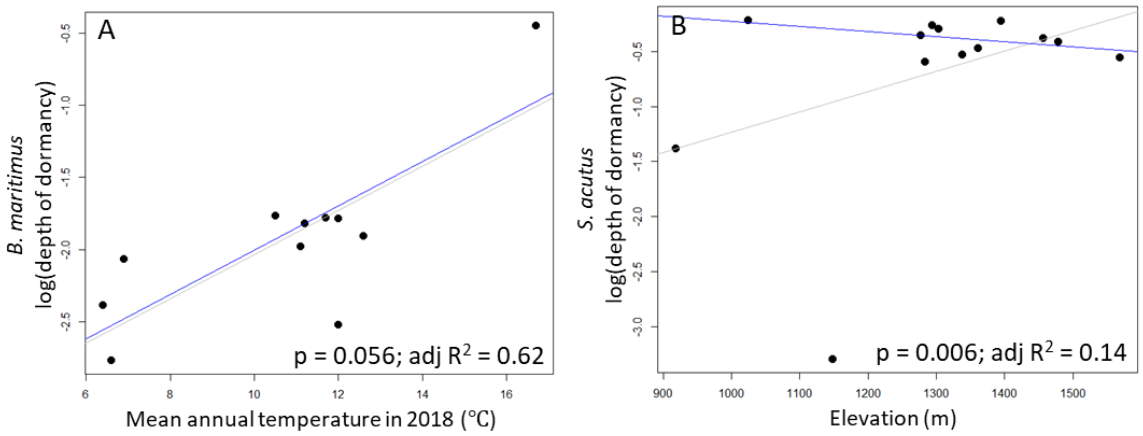


FIG. 3.5. Relationship between (A) *B. maritimus* depth of dormancy index (log-scale) and 2018 mean annual temperature, and (B) *S. acutus* depth of dormancy index (log-scale) and elevation. Modeled results are shown in blue for the robust linear regression and compared with a standard ordinary least squares regression in gray.

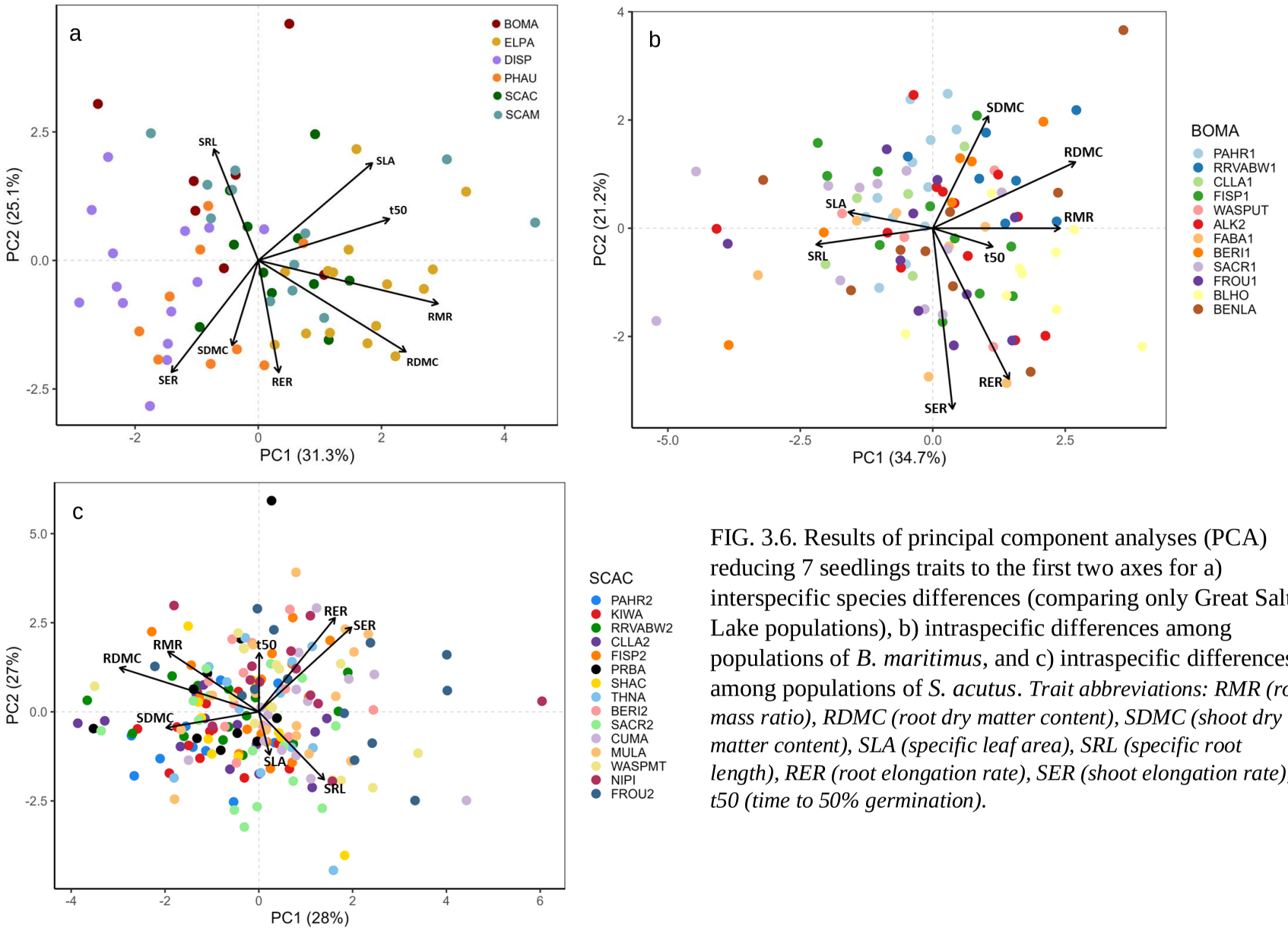
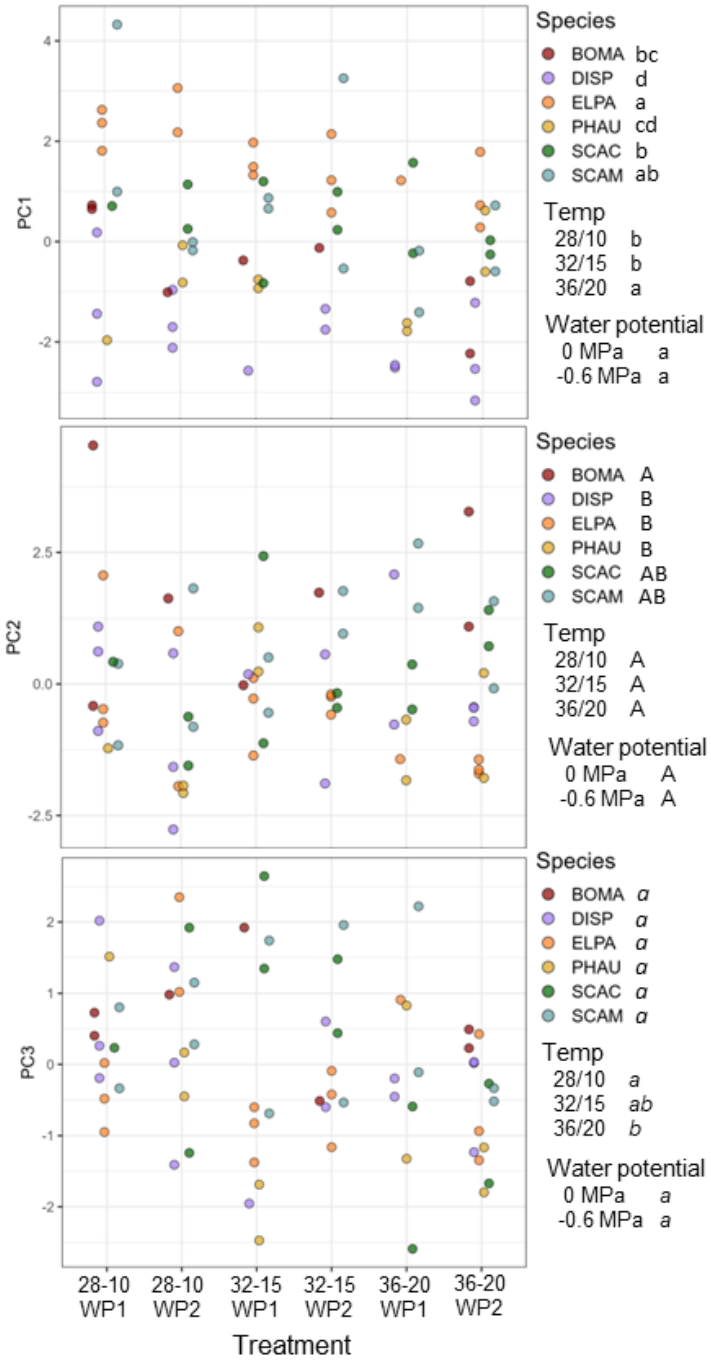


FIG. 3.6. Results of principal component analyses (PCA) reducing 7 seedlings traits to the first two axes for a) interspecific species differences (comparing only Great Salt Lake populations), b) intraspecific differences among populations of *B. maritimus*, and c) intraspecific differences among populations of *S. acutus*. *Trait abbreviations: RMR (root mass ratio), RDMC (root dry matter content), SDMC (shoot dry matter content), SLA (specific leaf area), SRL (specific root length), RER (root elongation rate), SER (shoot elongation rate), t50 (time to 50% germination).*



3.7. Between-species differences in PCA scores across temperature and water potential treatments. Individual species are denoted by color. Tukey HSD significance tests were performed for each PC axis comparing mean differences 1) between species, 2) between temperature regimes, and 3) between water potentials following the three-way ANOVA models. Lower-case letters indicate Tukey HSD results for PC1, upper-case letters indicate Tukey HSD results for PC2, and lower-case italicized letters indicate Tukey HSD results for PC3.

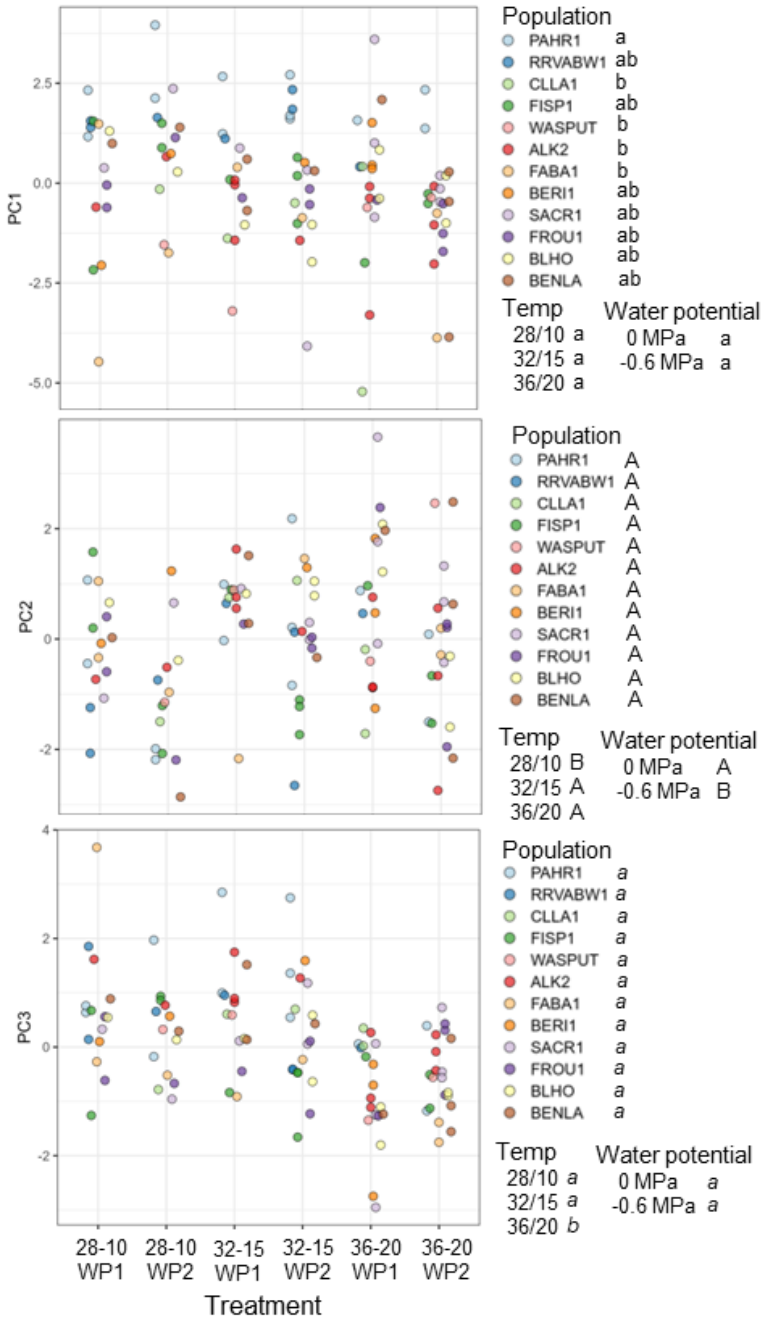


FIG. 3.8. Between-population differences in PCA scores across temperature and water potential treatments for *B. maritimus*. Individual populations are denoted by color. Tukey HSD significance tests were performed for each PC axis comparing mean differences 1) between populations, 2) between temperature regimes, and 3) between water potentials following the three-way ANOVA models. Lower-case letters indicate Tukey HSD results for PC1, upper-case letters indicate Tukey HSD results for PC2, and lower-case italicized letters indicate Tukey HSD results for PC3.

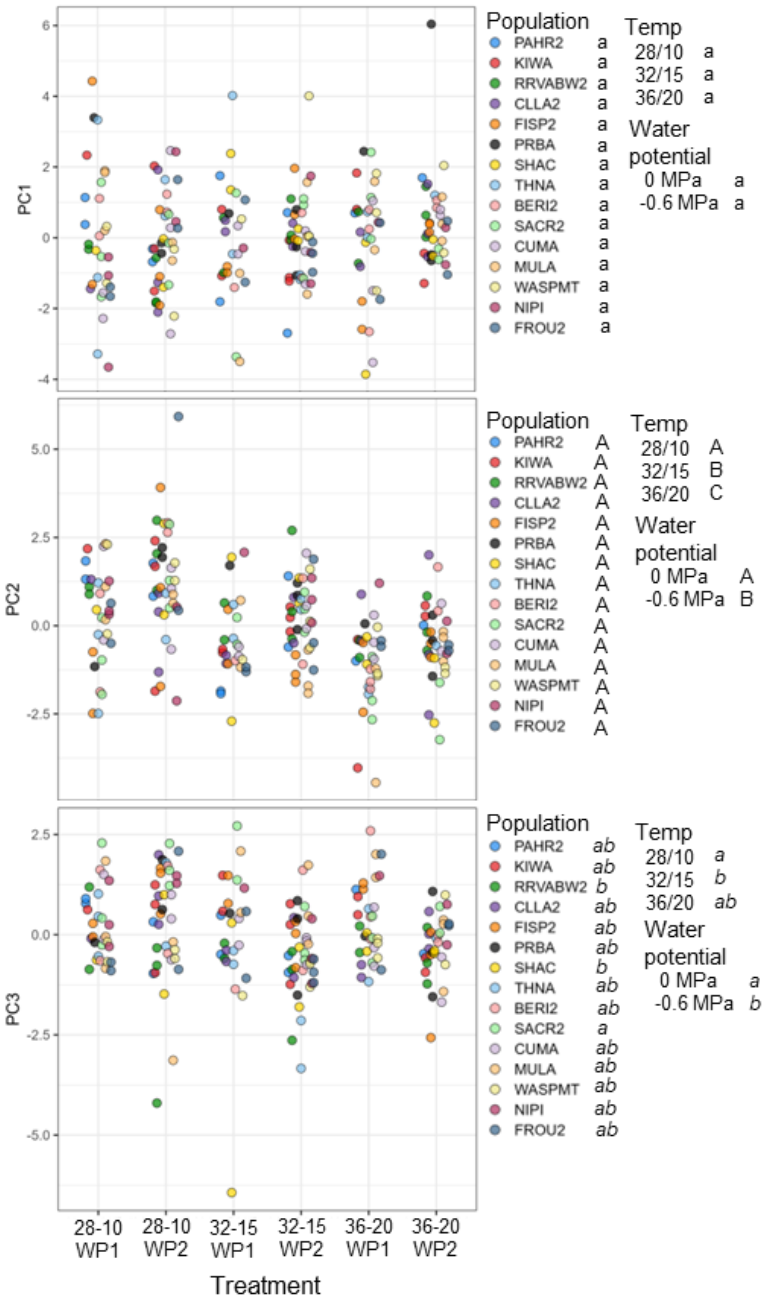


FIG. 3.9. Between-population differences in PCA scores across temperature and water potential treatments for *S. acutus*. Individual species are denoted by color. Tukey HSD significance tests were performed for each PC axis comparing mean differences 1) between populations, 2) between temperature regimes, and 3) between water potentials following the three-way ANOVA models. Lower-case letters indicate Tukey HSD results for PC1, upper-case letters indicate Tukey HSD results for PC2, and lower-case italicized letters indicate Tukey HSD results for PC3

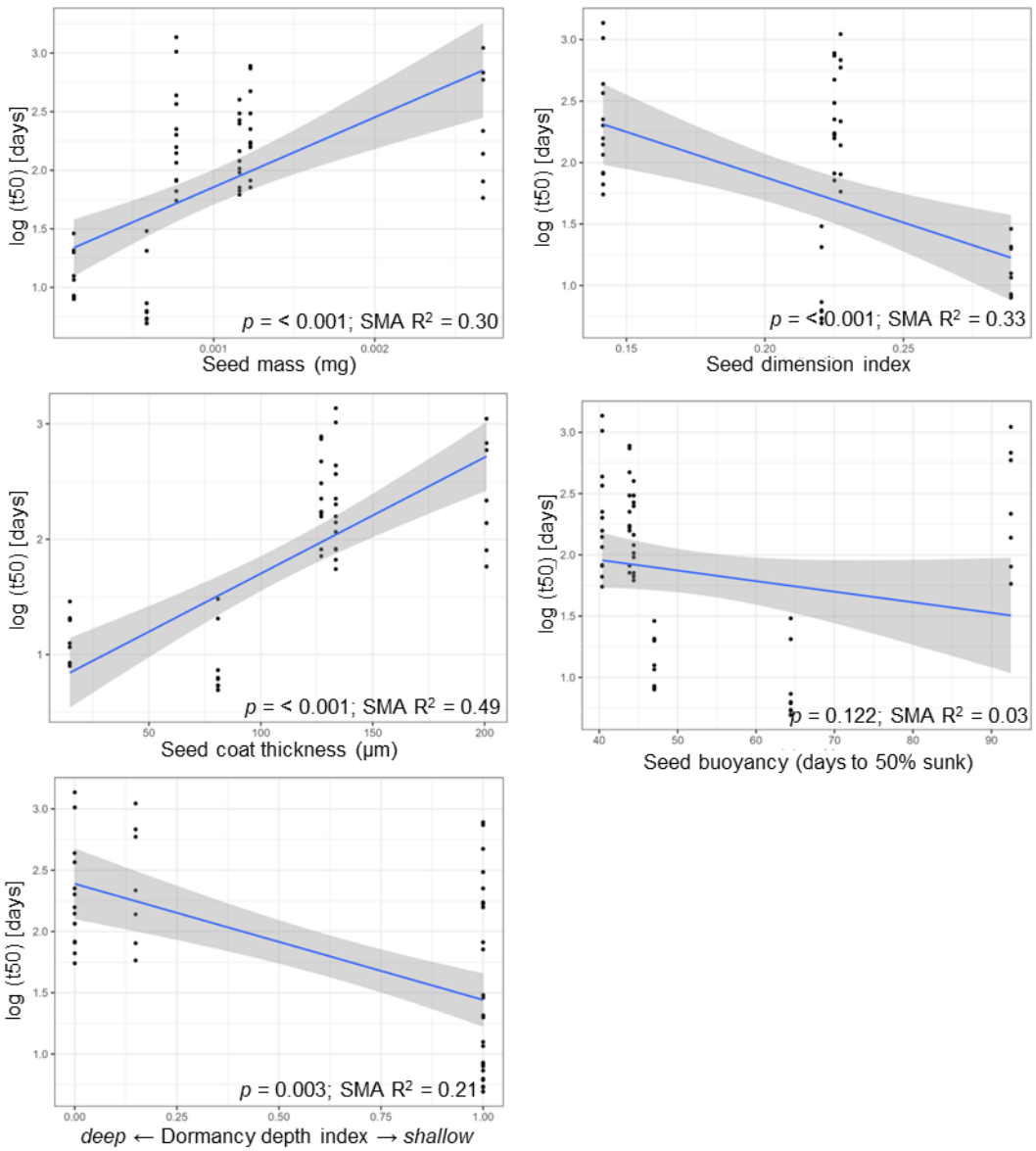


FIG. 3.10. Bivariate relationships between time to 50% germination (log-transformed) and measured seed functional traits with linear regression lines. Coefficients of determination (R^2) and *p*-values from the standard major axis regression are shown on each plot.

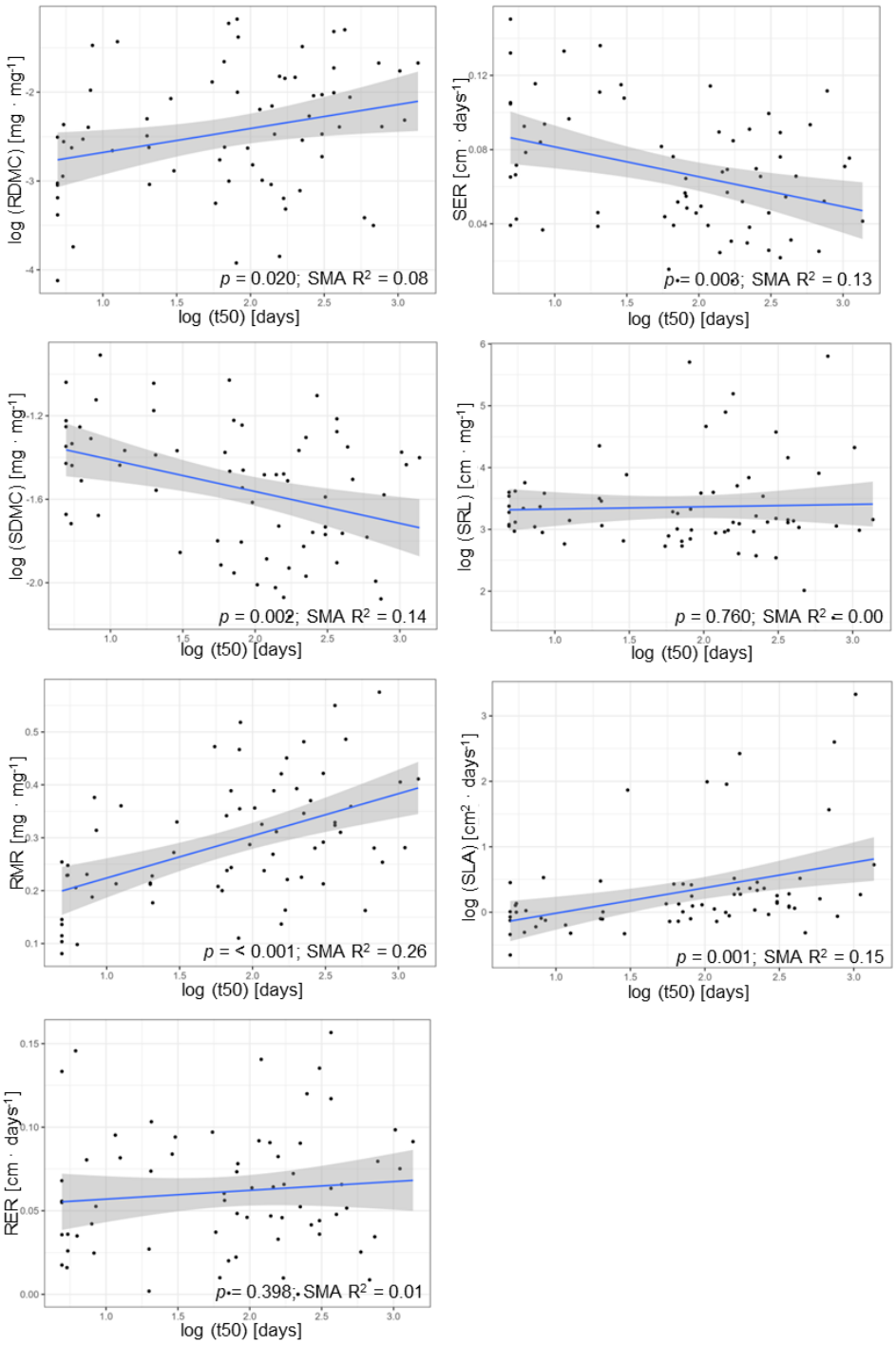


FIG. 3.11. Bivariate relationships between time to 50% germination (log-transformed) and measured seedling functional traits with linear regression lines. Coefficients of determination (R^2) and *p*-values from the standard major axis regression are shown on each plot. *Trait abbreviations: RMR (root mass ratio), RDMC (root dry matter content), SDMC (shoot dry matter content), SLA (specific leaf area), SRL (specific root length), RER (root elongation rate), SER (shoot elongation rate), t50 (time to 50% germination).*

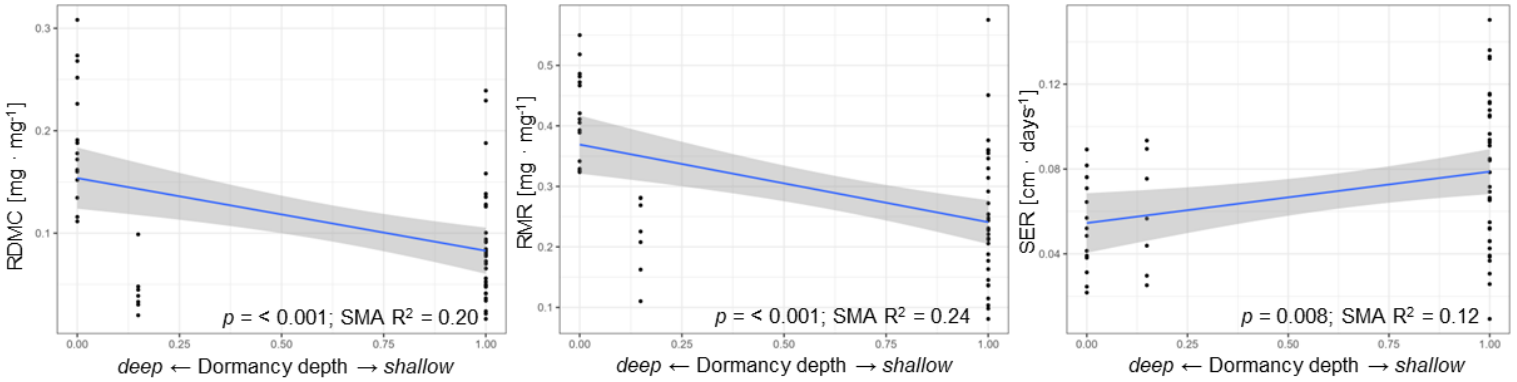


FIG. 3.12. Bivariate relationships between depth of dormancy and root dry matter content (RDMC), root mass ratio (RMR), and shoot elongation rate (SER) with linear regression lines. Coefficients of determination (R^2) and *p*-values from the standard major axis regression are shown on each plot.

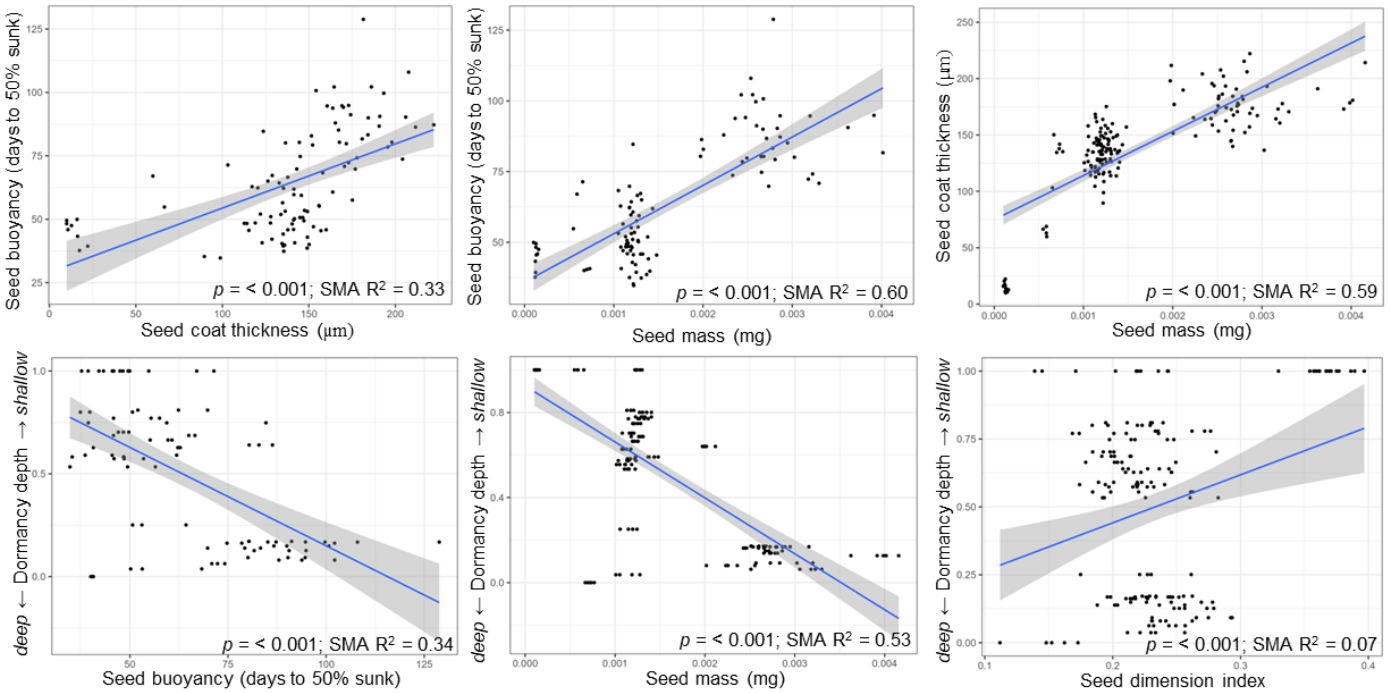


Figure 3.13. Bivariate relationships between seed buoyancy, seed mass, seed coat thickness, and depth of dormancy with linear regression lines. Coefficients of determination (R^2) and *p*-values from the standard major axis regression are shown on each plot.

CHAPTER 4

MODELING GERMINATION, SURVIVAL, AND CLONAL DEVELOPMENT: IMPLICATIONS FOR INVASION RESISTANCE FOLLOWING SEED-BASED WETLAND RESTORATION[1]

Abstract

Invasion resistance is a common goal during ecological restoration but is complicated by high seedling mortality during seed-based restoration. When restoring native plants via seed, the cumulative effects of early regenerative processes, including the probability of germination, survival, and clonal production, may drive early invasion resistance and can help elucidate recruitment bottlenecks that limit restoration outcomes. Assessing life stage transition probabilities, particularly with the inclusion of seedling clonal production, is an emerging field of study and is not well understand, particularly in wetland ecosystems. Here, we grew six wetland species sourced from a total of 12 populations in greenhouses across temperature and water regimes for eight-weeks. We tracked germination, seedling survival, clonal production per seedling, and percent cover outcomes across treatments for each species × population. *Phragmites australis* experienced the highest probability of germination across abiotic conditions relative to the other tested species, followed by *D. spicata*. Both species achieved high native cover and developed clones during the first eight-weeks, though the variation in clonal transitions was be mediated by water availability and temperature. *Eleocharis palustris*, a slow-growing Cyperaceae, achieved high end-of-season cover largely from extensive clonal production in high water levels, making it an ideal restoration candidate to impose biotic resistance in certain contexts. In general, high-water levels enhanced the

[1]Co-authored with Margaret Hallerud, Peter Adler, and Karin Kettenring

probability of germination across species, while high temperatures increased the likelihood of rapid clonal development. Given the paucity of mechanistic assessments of wetland plants through germination, survival, and clonal production, this research provides key insights that can guide in the planning and implementation for seed-based wetland restoration.

Key words

Life stage transitions, clonality, logistic regression, invasion resistance, seed-based restoration, wetlands, plant population dynamics, community assembly, demographic processes

Introduction

The ability of native plant communities to resist invasion is a well-established ecological concept (i.e., 'biotic resistance'; Elton, 1958; Levine et al. 2004), and a common goal during ecological restoration (e.g., Byun et al. 2013; Nemec et al. 2013; Byun et al. 2020; Weidlich et al. 2020). Despite many decades of research in this realm, the mechanisms underlying invasion resistance are still not well understood (Lockwood et al. 2013; Hess et al. 2020*a*). Further, research regarding community-level invasion resistance has primarily focused on the mechanisms that drive adult plant competition for resources (e.g., 'limiting similarity'; Funk et al. 2008; Byun et al. 2013; Bakker & Wilson, 2004; Goldstein & Suding, 2014). Less focus has been paid to the mechanisms driving early resistance to invasion as plant communities assemble from seed (but see, Hess et al. 2020*b*). However, numerous studies suggest that reducing invasive species at the seedling stage can be effective due to higher invasive plant vulnerability (relative to

mature invasive plants) combined with the importance of seedling dynamics in shaping subsequent community assembly (Kitajima & Fenner, 2000; Fraser & Karnezis, 2005; Larson & Funk, 2016). Invasion resistance could be, in part, driven by the net effects of early regenerative processes, including the probability of germination, first-season survival, and clonal production (James et al. 2011). Thus, deepening our understanding of regeneration processes among native and invasive plant species, across abiotic conditions, can help guide seed-based restoration choices that facilitate rapid native plant growth and invasion resistance.

Wetland ecosystems are among the most biologically productive systems on Earth (Millennium Ecosystem Assessment, 2005), yet have been degraded and lost at an alarming rate (>70% global wetland loss; Kingsford et al. 2016) relative to their small land cover (<10%; Zedler, 2000). Invasive species are particularly prevalent in wetland ecosystems and significantly contribute to widespread wetland degradation (Galatowitsch et al. 1999; Zedler & Kercher, 2004). Treatment and control methods for wetland invaders have been identified and applied successfully in some contexts (e.g., Keyport et al. 2019; Rohal et al. 2019; Sinks et al. 2021; Polzer & Wilcox, 2022), but desired native wetland plants that facilitate critical ecosystem functions are often slow or unable to return (Zedler, 2000; De Steven et al. 2006; Luckeydoo et al. 2006; Aronson & Galatowitsch, 2008; Carlson et al. 2009; Rohal et al. 2019). The inability of many wetland ecosystems to passively recover native species following invasive species control or general ecosystem disturbance points to insufficient and altered native seed banks (Seabloom & van der Valk, 2003; Lishawa et al. 2015; Bansal et al. 2019; Rohal et al. 2021), leading to disturbed wetlands that are highly susceptible to re-invasion or

secondary invasion (Kettenring & Adams, 2011; Pearson et al. 2016). Seed-based restoration is a promising active revegetation strategy that can have numerous benefits relative to other active revegetation approaches, including logistical benefits (e.g., easier to apply seeds over large scales; van der Valk, 2009; Löf et al. 2019), financial benefits (e.g., generally cheaper than other active revegetation strategies; van der Valk, 2009; Palmerlee & Young, 2010; Ede et al. 2018; Raupp et al. 2020), and ecological benefits (e.g., greater adaptive potential of restored plant community; Godefroid et al. 2011; Reynolds et al. 2012). However, seed-based restoration outcomes in wetlands have been unpredictable and largely unsuccessful due to high seedling mortality during vulnerable stages of plant growth (e.g., Smith et al. 2016), necessitating a deeper understanding of demographic processes that yield such variable outcomes (Kettenring & Tarsa, 2020).

In the last decade, numerous studies have quantified demographic transitions and processes that drive seeds and seedlings with the intention of optimizing seed-based restoration outcomes. However, an astonishingly large portion of these studies have focused on the recruitment dynamics of terrestrial species in arid or grassland ecosystems (e.g., Radford et al. 2002; James et al. 2011; Larson et al. 2015). The findings from these and other studies indicate that, despite germination requirements being met, establishment rates in grassland species often fall below 10% (James et al. 2011; James et al. 2019; Jensen et al. 2022). This bottleneck is generally between germination and emergence, and has been linked to several biotic and abiotic pressures, including annual precipitation and temperature variation (Rawlins et al. 2012; James et al. 2019), seedling herbivory (Edwards & Crawly, 1999), frost (Boyd & Lemos, 2013; Roundy & Madsen, 2016), and drought (Larson et al. 2015).

Compartively less attention has been paid to recruitment dynamics in wetlands, which limits the development of synthetic understanding of these dynamics across systems and hinders predictions of how and why wetland species fail to germinate, survive, and produce sufficient native cover. While there is likely overlap in recruitment constraints between systems (e.g., seed granivory; Greer et al. 2007; Bricker et al. 2010), there are also additional biotic and abiotic factors that may yield differences in seedling recruitment dynamics in wetland species relative to terrestrial species. For example, while there is limited comparative data evaluating systematic seed dormancy patterns across taxa, many wetland species, particularly in the Cyperaceae family, possess strong initial dormancy (Baskin & Baskin, 1971; Clevering 1995), require light for germination (Clevering 1995; Poschlod et al. 1996; Kettenring 2016), and depend on high, fluctuating temperatures for germination relative to species from other temperate habitats (Thompson & Grime, 1983; Grime et al. 1981; Baskin & Baskin, 1998). The strong initial dormancy may shift regenerative bottlenecks from early emergence (as evidenced in grasslands; James et al. 2011; Larson et al. 2015) to pre-germination. Furthermore, wetland plants are predominantly clonal (Sosnová et al. 2010), thus fully assessing early life stage dynamics requires the inclusion of clonal development in addition to seed germination and seedling growth patterns.

Clonality is an important, but largely unexplored, regenerative process that results in the development of semi-autonomous ramets connected to the original ‘mother plant’ (Mony et al. 2010; Orbony et al. 2012; Albert et al. 2022). Development of clones is prevalent across habitats and environmental regimes, but the variation in clonal response has been attributed to differences in productivity and wetness (Klimešová & Herben,

2015). The ability to produce clones can provide an advantage to plants growing in frequently disturbed, nutrient-poor, or heterogeneous environments by allowing ramets to 'forage' for more favorable sites (Herben et al., 1997) and via physiological clonal integration (i.e., resource translocation among clonal units; Liu et al. 2016; Estrada et al. 2020). Further, clonality at early life stages can enhance competitive ability by allowing for more extensive or rapid colonization of space (Herben et al., 1997; Gough et al. 2002; Kun & Oborny, 2003). Thus, incorporating the probability of clonal development in early life stages, in addition to seed germination and seedling survival probabilities, can deepen our understanding of which clonal species will perform and compete best following seed-based wetland restoration. This mechanistic view can also help disentangle the contribution of early recruitment dynamics across species, elucidating differing strategies at early life stages. For example, two species may appear equally competitive at the end of the first growing season, but for different reasons: one species may gain high cover through high germination and survival probabilities with minimal clonal production, whereas a second species may have low germination rates but achieves high cover through prolific clonal production. To date, demographic plant studies have largely ignored the influence of clonality, which can bias estimations of demographic characteristics (Janovský et al. 2017; Klimešová et al. 2021) and distort early life stage contributions to later invasion resistance.

Quantifying the probability of germination, survival, and clonal production is critical to better identify demographic bottlenecks and regenerative strategies that might influence restoration outcomes in wetlands. Further, understanding the inter- and intraspecific variation in these probabilities across abiotic conditions that drive early

seedling dynamics in wetlands (e.g., temperature and water availability; Koller, 1972) can allow for more targeted decisions on which species to include in seed mixes, where those seeds should be sourced, and which site conditions should be maintained to maximize plant community recovery (Kettenring & Tarsa, 2020). In addition to early demographic processes, native cover achieved in the first year of growth can also facilitate invasion resistance via light-limitation to neighboring or later-arriving plant species (Young et al. 2017). Thus, studies should incorporate a mechanistic understanding of the full spectrum of these early processes (germination, survival, clonality, final cover) to better assess which species, populations, and conditions might best facilitate invasion resistance.

In this study, we modeled early inter- and intraspecific demographic processes and final percent cover of six wetland species grown across temperature and water levels during the first eight weeks of plant growth. We compared five native and one invasive species (*Phragmites australis*) to disentangle factors that might drive early invasion resistance among native species relative to *P. australis* early plant dynamics. We were interested in exploring two questions:

(1) How does the probability of transitioning through germination, survival, and clonal development vary across source population abiotic conditions for each species during the first eight weeks of plant growth?

(2) How do species identity, source population, and abiotic conditions influence native cover over time and end-of-season native cover?

Based on performance of the study species in previous experiments (e.g., Tarsa et al. *in press*), we expected to see high end-of-season cover and high probability of

germination and survival for the two robust *Poaceae* species (including the focal invader *P. australis*), but we anticipated substantial variation across time and abiotic conditions for all species. In addition to higher probabilities of early life stage success, we also predicted that the robust *Poaceae* species would be less sensitive to abiotic conditions and would be able to maintain high germination, survival, and rapid clonal production across treatments. We also expected to see some evidence of population-level differentiation in performance in the native species across abiotic conditions that indicated greater population performance in conditions similar to the maternal seed collection site.

Methods

Species selection and population sampling

We chose five native species that are often targeted in restoration efforts regionally and nationally for their ability to provide high-quality forage and habitat to wildlife (Downard et al. 2017; Rohal et al. 2018)—*Bolboschoenus maritimus* (L.) Palla (alkali bulrush), *Schoenoplectus acutus* var. *acutus* Muhl. ex Bigelow (hardstem bulrush), *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller (threesquare bulrush), *Distichlis spicata* (L.) Greene (saltgrass), and *Eleocharis palustris* (L.) Roem. & Schult. (Common spikerush). Additionally, we studied early plant growth dynamics of the invasive *Phragmites australis* (Cav.) Trin. ex Steud for a total of six focal species. Seeds from three species (*D. spicata, E. palustris, P. australis*) were composed of a composite seed mix sourced from Great Salt Lake wetlands in 2018 (*D. spicata, E. palustris*) and 2020 (*P. australis*). We were interested in capturing intraspecific variation of plant responses for our three bulrush species (*B. maritimus, S. acutus, S. americanus*), thus we

grew three populations of each sourced from various wetlands across the Intermountain West, USA in 2018 (Figure 4.1). After collection, seed viability tests were performed using standard tetrazolium procedures from Miller et al. 2010, and seeds were stored in paper bags at room temperature (20–23°C) prior to the experiment.

Experimental design and seed sowing

The experiment was conducted in Utah State University's research greenhouses in Logan, Utah, USA. We set up a completely randomized block design across three greenhouse rooms. Within each greenhouse, we constructed four wooden reservoirs (dimensions: 1.5 × 2.4 × 0.2 m) lined with 30 mil PVC pond liner, within which we randomly assigned one of two day/night temperatures regimes (32/15℃ and 36/20℃) and one of two water regimes (high, low; see below). We set the temperatures of all greenhouses to the low temperature treatment (32/15℃). To achieve the high temperature treatment (36/20℃), we installed a space heater suspended within the reservoir attached to a temperature controller (Inkbird ITC-308; Inkbird Tech. Co., Ltd., Shenzhen, P.R. China; https://inkbird.com/products/temperature-controller-itc-308) to maintain the desired day and night-time temperatures. To retain heat in the high-temperature reservoirs, we covered these reservoirs with a clear plastic tent mounted to a 4-sided PVC with a top (5-sides total). To ensure there was no light effect across our two temperature conditions, we installed a similar tent on the 'low' temperature treatments but only covered the top of the frame with plastic to expose those plants to similar light quality but allow for air movement through the reservoir at the temperature of the greenhouse (32/15℃). Both temperature treatments were monitored every other day using 4 iButtons placed within each reservoir (48 total). We maintained the reservoir water levels every

other day at either: 1) 13–15 cm from the bottom of the reservoir for the high-water treatment, which resulted in saturated soil (water level equal to soil level), or 2) 3–5 from the bottom of the reservoir for the low-water treatments. During set-up, water height was measured throughout the reservoirs as the reservoirs were leveled with shims to ensure that the water level was uniform across the entire reservoir. Growing lights were spaced throughout the greenhouse to ensure an equal distribution of between 400–450 μmol m^{-2} s^{-1} of light to each growing container during a 16-h photoperiod. We applied Peter's Professional Hydroponic Solution (5-11-26) at the start of the experiment and two times during the experiment to ensure nutrients were not limiting growth.

Within each reservoir, we set up 12 growing containers (dimensions: 0.51 m × 0.38 m × 0.18 m) containing all species × population combinations growing in monotypic stands (1 species × population per container). We filled each growing container with Sunshine #3 propagation mix, which is comprised of *Sphagnum* peat moss, vermiculite, and dolomitic limestone (Sungro Horticulture; Agawam, MA, USA). This media was chosen to mimic natural wetland soil drainage patterns and prevent emergence of species from the seed bank of native soil. To simultaneously track life-stage transitions and percent cover, we divided each growing container into two using a mesh net: a larger side for percent cover measurements (subsequently referred to as 'cover side'; dimensions: 0.51 m × 0.38 m × 0.18 m) and a smaller side to track life-stage transitions (subsequently referred to as 'life stage side'; dimensions: 0.51 m × 0.38 m × 0.18 m). Then, we placed growing containers into the appropriate reservoir and floated foam strips on the water between growing containers to minimize evaporation and algae growth. After growing containers were prepared and randomly placed in the appropriate reservoirs, we evenly

gridded a known number of seeds on the life-stage side based on seed lot viability and expected emergence rates (30 pure-live seed ('PLS', the number of living seeds that accounts for non-seed debris and non-viable seeds in a seed lot): *B. maritimus*, *S. acutus*, *S. americanus*, *E. palustris*; 15 PLS: *P. australis*; 10 PLS: *D. spicata*). On the cover side, we sowed species at a rate of 360 PLS, adjusted for viability, which reflects the low-density sowing treatment commonly used in Great Salt Lake wetlands (Tarsa et al. 2022). We added an additional 25 PLS to each treatment to account for seedlings that we later removed for trait data collection. We assembled 360 PLS + 25 PLS for each species by weight after counting out 3 replicates of the target seed number for each species, weighing each replicate, and averaging replicate weights. After calculating seed totals for the life-stage side and the cover side, but before sowing, we broke physiological seed dormancy for seeds of *S. acutus*, *S. americanus*, and *D. spicata* by cold stratifying at 4°C for 39 days following the methods of Marty and Kettenring (2017). To break deep physiological dormancy for *E. palustris* and *B. maritimus*, and to account for substantial variation in depth of dormancy for these species (Tarsa, Chapter 3), we split each species' seed sample in two and placed one half in a 3% bleach solution for 24 hours and the other half for 48 hours (Marty & Kettenring, 2017). Following bleach treatments, the seeds were rinsed thoroughly and immediately seeded. *Phragmites australis* does not exhibit dormancy and was not pre-treated prior to seeding. All seeds were sown on January 13, 2021. See Appendix D: Figure S.4.1 for a schematic of the experimental design.

Data collection

On the life-stage side, surveys were conducted every 2–4 days for eight weeks (20 data collection periods total). To determine germination, we recorded the number of

newly germinated seeds when a radicle of >2mm was observed. To track seedling survival, we recorded the presence or death (differentiated by the presence or absence of green photosynthetic tissue) of periously germinated seedlings. To assess clonal development, we counted the number of additional ramets growing from the original seedling as a non-destructive means of determining capacity and rate of clonal growth. The clonal data was counted and assigned a clonal class to track the rate and extent of clonal production in each treatment, species, and population. Clonal classes were assigned per seedling and designated as follows: 'none' — 0 clones produced, 'low' — 1–2 clones produced, 'medium' — 3–5 clones produced, 'high' — >5 or more clones produced. Life stage classes were assigned as follows: germinated (> 2mm radicle observbed), survived (maintained presence of green photosynthetic tissue), died (no green photosynthetic tissue observed), no clones were produced *or* 1-2 clones were produced per seedling, 3-5 clones were produced per seedling, and 5 or more clones were produced per seedling.

On the cover side, we visually estimated percent cover once per week throughout the growing season to assess native cover development over time using a classification system based on Brohman and Bryant (2010). We modified these cover classes to capture 0% cover, 0–1% cover, and 99–100% cover for a total of 13 cover classes (Appendix D: Table S.4.1). Cover was assessed by the same observer (E. Tarsa) for the duration of the 8-week experiment.

Statistical analysis

All statistical analyses were performed in R version 4.0.2 (R Core Development Team, 2020), with data visualization using the 'ggplot2' package version 3.3.6 (Wickham

et al., 2016). Prior to conducting early life stage models, we plotted the percentage of individual recruits across life stages to visualize recruitment bottlenecks for each species, population, and abiotic treatment. We also calculated cumulative germination, cumulative survival, and aggregate counts of clonal categories to visualize overall regenerative patterns for each species × population.

To calculate transition probabilities (TP), we first defined six classes that a seed or seedling could occupy (Figure 4.2), each of which was calculated at the population level for each abiotic treatment and species/population: (1) TP_1 was the probability of a seed germinating after seeds were sown (i.e., germination probability). (2) TP_2 was the probability that a germinated seed did not survive during the 8-week period (i.e., mortality probability). We assumed that seedlings that died were not able to produce clones, which was supported by visual observations throughout the study. (3) TP_3 was the probability that a germinated seed survived but did not produce any clones over the 8-week period. For TP_2 and TP_3, when a seedling moved into either of those classes, it was not able to further transition to subsequent clonality stages. (4) TP_4 was the probability that a germinated seed survived and produced 1–2 clones, which was a direct trade-off from TP_3 and represented the starting point for the clonality transitions. In other words, unless a seedling died (TP_2 transition) it <u>either</u> transitioned into and remained in the no clonal production state (TP_3) <u>or</u> it started the clonality transitions in TP_4. (5) TP_5 was the probability that a germinated seed survived with 1–2 clones and went on to produce 3–4 clones (i.e., an additional 1–2 clones); and (6) TP_3 was the probability that a germinated seed survived with 3–4 clones and went on to produce 5 or more clones over the 8-week period.

Differences in transition probabilities between populations, temperature regime, and water level were analyzed with logistic mixed effects models using the glmmTMB package (Brooks et al. 2017). Separate models were run for each species (6) and each transition probability (6), for a potential total of 36 models. Because not all populations transitioned through each stage, a total of 23 models were developed. For species with multiple populations (*B. maritimus*, *S. acutus*, *S. americanus*), the transition probability (TP_1– TP_6) was included as the response variable and temperature regime (2 levels), water level (2 levels), and source population (3 levels) were included as fixed effects. Random effects included greenhouse and reservoir nested within greenhouse. For single population species (*D. spicata*, *P. australis*, *E. palustris*), the transition probability (TP_1–TP_6) was included as the response variable and temperature regime (2 levels) and water level (2 levels) were included as fixed effects. Random effects included greenhouse and reservoir nested within greenhouse. After running each model, we inspected residuals using the DHARMa package (v 0.4.1; Hartig, 2020). We used Tukey HSD *post-hoc* comparisons to test for significant differences ($\alpha = 0.05$) in transition probabilities across water levels, temperatures regimes, and, where relevant, source population.

For the percent cover analysis, we first plotted percent cover change over time for each species, population, temperature regime, and water level to visualize rates of change in the cover response. We analyzed end-of-season percent cover by converting percent cover data to midpoint values, then converting values to a continuous proportion with ± 0.001 added to zero or one values to ensure the data were within the [0,1] bounds required for a beta distributed model (Douma & Weedon, 2019). Generalized linear mixed effects models with a beta distribution and logit link were ran using the glmmTMB

package for: 1) all species (combined over populations), 2) *B. maritimus* populations, 3) *S. acutus* populations, and 4) *S. americanus* populations (v 1.0.2.1; Brooks et al. 2017). Model residuals were inspected using the DHARMa package (v 0.4.1; Hartig, 2020). We used Tukey HSD *post-hoc* comparisons to test for significant differences ($\alpha = 0.05$) in percent cover across species/populations for each treatment and between treatments for each species/population.

Results

Recruitment bottlenecks and early life stage abundance

Visual inspection of the percentage of recruits across life stages indicated that germination was the primary recruitment bottleneck across species and populations, but the magnitude of this bottleneck was highly variable (Figure 4.3). Despite dormancy-breaking treatments, *B. maritimus* and *S. americanus* experienced the most restrictive bottleneck with ~ 5–15% of the sown seeds reaching germination for the 'BLHO', 'FABA', and 'RRVABW' populations (i.e., 85–95% failure rate; Figure 4.3). The *B. maritimus* 'PAHR' population (southernmost latitude) and the *S. americanus* 'HACR' population (Great Salt Lake) experienced slightly higher germination (~25–32%) in the hot temperatures and high-water levels relative to other intraspecific populations and treatments (Figure 4.3). Germination percentages averaged around 25% for *S. acutus*, but there was quite a bit of intraspecific variation across abiotic treatments—the 'FROU' population (northernmost latitude) exhibited 15–25% germination regardless of abiotic treatment, whereas the 'PAHR' population (southernmost latitude) experienced ~25% higher germination in high-water levels at hot temperatures relative to other abiotic treatments. The *S. acutus* 'THNA' population (Great Salt Lake) had a 25% reduction in

germination when grown in the ‘hot temperature, low-water’ condition and the ‘cool temperature, high-water’ condition relative to the other two abiotic treatments. *Phragmites australis* had the least restrictive recruitment bottleneck, with ~60–100% of sown seeds reaching germination, followed by *D. spicata* (~38–65% germination; Figure 4.3). *Eleocharis palustris* germination ranged from 28% in the ‘cool temperature, high-water’ treatment to 80% in the ‘hot temperature, high-water’ treatment (Figure 4.3). For all species, if a seed germinated, the subsequent seedling had a high likelihood of survival during the first eight weeks (Appendix D: Figure S.4.2).

High clonal production (5+ clones per seedling) was evident for two populations of *B. maritimus* (‘BLHO’, ‘PAHR’) in high water levels at high temperatures (Figure 4.4). *Schoenoplectus acutus* sourced from ‘PAHR’ (southernmost latitude) also produced a high number of clones, while *D. spicata* clonal production increased to 3–4 clones per seedling (‘med’ category; Figure 4.4) in hot temperatures (Figure 4.4). The target invader, *P. australis*, and many of the other tested native species and populations experienced minimal clonal growth across abiotic conditions during the first 8-weeks of growth (Figure 4.4). *Eleocharis palustris* seedlings produced far more clones than any other tested species or populations driven by high water levels, regardless of temperature, and we observed an apparent tradeoff for this species regarding germination and clonal development (Figure 4.3, 4.4). For example, in the cool temperature treatment at high-water levels, *E. palustris* experienced only ~28% germination and ~25% seedling survival (Figure 4.3), but ~75% of the survived seedlings went on to produce 5 or more clones (Figure 4.4). Conversely, in the cool temperature treatment at low-water levels, *E. palustris* exhibited high germination and survival (~75%; Figure 4.3), but ~23% of them

produced 3–4 clones (Figure 4.4). Both treatments achieved high and statistically indistinguishable end-of-season *E. palustris* cover (see below).

Transition probabilities

Bolboschoenus maritimus. We found a significant interaction between temperature regime, water level, and source population for *B. maritimus* transitioning from sown seed to germinated seed (TP_1; Table 4.1). High water levels increased the probability of germination for every population—in cool conditions, the probability of germination increased significantly by 10% for 'BLHO', 9% for 'FABA', 21% for 'PAHR' (Appendix D: Figures S.4.3-S.4.5; Figure 4.5). In the hot temperature regime, the probability of germination was significantly higher for 'FABA' (11%) and 'PAHR' (16%) in high-water relative to low-water levels, but there was no significant difference for 'BLHO' (Appendix D: Figures S.4.3-S.4.5; Figure 4.5). Temperature and water levels did not have a significant effect on mortality or any clonal production transitions for *B. maritimus* (TP_3, TP_4-TP_5; Table 4.1).

Schoenoplectus acutus. We found marginally significant interactions between 'water level × population' and 'temperature × population' for *S. acutus* seed germination probability (TP_1; Table 4.2). High water levels increased the probability of germination by 20–30% across populations, with 'FROU' exhibiting the highest germination probability relative to the other populations (Appendix D: Figures S.4.6-S.4.8; Figure 4.6A). The 'temperature × population' interaction was driven by the 'PAHR' population, which was 10% more likely to germinate in the hot temperature than in the cool temperature (Appendix D: Figures S.4.6-S.4.8; Figure 4.6B). For the transition from germinated seed to seedling death (TP_2), *S. acutus* 'THNA' population exhibited a

modest (3%), but significant, increase in the probability of mortality in the high-water levels relative to the low-water level (Appendix D: Figures S.4.6-S.4.8; Figure 4.7). Across all *S. acutus* populations, there was a significant effect of temperature on the transition from germinated seed into no clonal production (TP_3) such that the cold temperature regime yielded a 10–50% increase (depending on population) in the likelihood that seedlings produced no clones (Table 4.2; Appendix D: Figures S.4.6-S.4.8; Figure 4.8). In other words, because the TP_3 and TP_4 represent a 'trade-off' state, the cool temperature regime inhibited clonal production while the hot temperature regime accelerated clonal production for all *S. acutus* populations, which is evidenced in the significant temperature × water × population interaction for the TP_4 transition (Table 4.2; Figure 4.9). However, this acceleration in clonal production in the hot temperature was mediated by water level for some populations more than others—the 'FROU' and 'PAHR' populations had either unchanged or reduced probability of transitioning into clonal production (TP_4) in low-water levels, while the 'THNA' population demonstrated the same pattern of increasing TP_4 probability across temperature regardless of water level (Appendix D: Figures S.4.6-S.4.8; Figure 4.9). Finally, we found a significant effect of water level on the transition from 1–2 clones to 3–4 clones (TP_5), which was driven by a 45% higher likelihood of the TP_5 transition for the 'PAHR' population in high-water levels relative to low-water levels (Table 4.2; Appendix D: Figures S.4.6-S.4.8; Figure 4.10).

Schoenoplectus americanus. We found a significant interaction between water level and population for *S. americanus* transitioning from sown seed to germinated seed (TP_1; Table 4.3). For all populations, high-water levels increased the probability of

germination by 5–25% (depending on the population) relative to low-water levels (Appendix D: Figures S.4.9-S.4.11; Figure 4.11). Across populations, the 'RRVABW' population had a significantly lower probability of germination in the high-water levels relative to the 'SASP' and 'HACR' populations (Figure 4.11). The 'HACR' population outperformed the 'SASP' and 'RRVABW' populations across water levels in terms of germination probabilities— 'HACR' was 10–15% more likely to germinate at low-water levels and 15–20% more likely to germinate at high-water levels relative to 'SASP' and 'RRVABW' (Appendix D: Figures S.4.9-S.4.11; Figure 4.11). We found no effect of temperature regime or water level on mortality (TP_2) and there was insufficient data to estimate transition probabilities beyond the TP_2 transition for *S. americanus*.

Distichlis spicata. There was no significant effect of temperature regime or water level on germination probability (TP_1) or probability of mortality (TP_2) for *D. spicata* (Table 4.4). We did find a significant interaction between temperature regime and water level for the transition from germinated seed to no clonal production (TP_3), which indicated a marginally significant increase TP_3 probability at the high-water level treatment (Appendix D: Figure S.4.12, Figure 4.12A). However, the model had difficulties estimating these parameters, as evidenced by the wide standard error bars (Figure 4.12A). There was also a marginally significant 'temperature × water' interaction for the transition from germinated seed to the first stage of clonal development (TP_4), which indicated a slight increase in clonal development in low-water conditions at the hot temperature regime (Table 4.4; Figure 4.12B). As with the previous model, there were large standard errors in the TP_4 transition model, indicating difficulties in estimating the true population means with this dataset. Finally, we found a significant 'temperature ×

water' effect on the transition from 1–2 clones to 3–4 clones (TP_5) for *D. spicata* (Table 4.4). In the hot temperature treatment, seedlings were 57% more likely to develop 3–4 clones (i.e., transition through TP_5) in high water levels relative to low-water levels (Appendix D: Figure S.4.12, 4.12C).

Phragmites australis. For the *P. australis* models, we identified a significant interaction between temperature regime and water level for seed germination probability (TP_1; Table 4.5). There was no statistical difference in germination probability between high- and low- water levels within the cool temperature or the hot temperature treatments (Appendix D: Figure S.4.13, Figure 4.13A); but, at low-water levels, there was a 25% higher likelihood of *P. australis* germination in the hot temperature regime relative to the cool temperature regime (Appendix D: Figure S.4.13, Figure 4.13A). There was also a significant interaction between temperature and water for the transition from germinated seed into no clonal production (TP_3; Table 4.5). In the cool temperature regime, seedlings were 40% more likely to not produce clones in high-water levels relative to low-water levels, and 50% more likely to not produce clones relative to high-water levels at the high temperature regime (Appendix D: Figure S.4.13, 4.13B). In the hot temperature regime, seedlings were 25% more likely to not produce clones in low-water conditions relative to high-water conditions (Appendix D: Figure S.4.13, 4.13B). A significant temperature and water interaction was also observed for the TP_4 transition into clonal development (Table 4.5). At the high-water treatment, there was a 48% increase the probability of clonal development in the hot temperature regime relative to the cool temperature regime (Appendix D: Figure S.4.13, 4.13C). There was no significant difference in TP_4 probabilities across temperatures in the low-water treatment (Appendix D: Figure S.4.13,

4.13C). Considering the models results of the TP_3 and TP_4 together, the hot temperature regime induced clonal production when water levels were high (Figure 4.13C), while low temperatures hindered *P. australis* clonal production (Figure 4.13B). Interestingly, there was less fluctuation in clonal responses across temperatures at the low-water level relative to the high-water level (Figure 4.13B, C). Temperature and water levels did not have a significant effect on mortality or clonality transitions above TP_4 for *P. australis* (TP_2, TP_5; Table 4.1).

Eleocharis palustris. Water level had a significant effect on *E. palustris* transitioning from sown to germinated seed (TP_1), revealing a 49% and 53% higher likelihood of germination at high-water levels relative to low-water levels in the hot temperature regime and the cool temperature regime, respectively (Table 4.6; Appendix D: Figure S.4.14; Figure 4.14A). There was a marginally significant effect of water level on the transition from germinated seed to no clonal growth (TP_3), which highlighted a 23% increase in the probability of seedling not producing clones in the hot temperature at the low water level (Table 4.6; Appendix D: Figure S.4.14, Figure 4.14B). The model also identified a significant effect of water level on the transition to the highest measured clonal production (TP_6; Table 4.6C). The probability of producing the highest number of clones was related to water level, particularly in the cool conditions in which there was a 66% higher probability of more than 5 clones per seedling in the high-water condition relative to the low water condition (Appendix D: Figure S.4.14, Figure 4.14).

Percent cover change over time

Visual inspection of plant cover plots over time revealed some consistent patterns in percent cover response for each species, population, and environmental treatment

(Figure 4.15). In general, species and populations exhibited the fastest accumulation of cover in the 'hot' temperature treatment at 'high' water levels, with the slowest (and lowest) cover accumulation in the 'cool' temperature treatment at 'low' water levels. *Distichlis spicata* and *P. australis* reached nearly 100% plant cover in the shortest amount of time (Figure 4.15). *Schoenoplectus americanus* had the lowest cover across treatments overall, with a similar intraspecific pattern across populations (Figure 4.15).

End-of-season plant cover across species, population, temperature regime, and water level

Interspecies percent cover models indicated a significant interaction between water level and species identity (Table 4.7). There was no significant difference between end-of-season percent cover across low- and high-water levels for *D. spicata*, *P. australis*, and *E. palustris* (Figure 4.16A). The three bulrush species (*B. maritimus, S. acutus, S. americanus*) had significantly higher end-of-season cover in high-water levels relative to low-water levels, but *B. maritimus* and *S. americanus* cover remained significantly lower than that of the other focal species (Figure 4.16A). In the high-water level, final cover for *S. acutus* at the high-water level was not statistically distinguishable from the final cover of *D. spicata, P. australis*, or *E. palustris* in the high-water level (Figure 4.16A). The model also identified a significant interaction between temperature regime and species identity, with a similar species pattern as in the water level × species interaction (Table 4.7; Figure 4.16B).

Within *B. maritimus* populations, the model results identified a significant three-way interaction between temperature regime, water level, and population (Table 4.8a). The 'BLHO' population (sourced from the highest latitude) had significantly higher final percent cover in the cool temperature regime at low water levels relative to the 'FABA'

and ‘PAHR’ populations (Figure 4.17A). At the high temperature regime and low-water level, the ‘PAHR’ population (sourced from the lowest latitude) experienced a large increase in final percent cover and was significantly higher than the ‘FABA’ and ‘BLHO’ populations (Figure 4.17A). The ‘FABA’ population had significantly higher cover in the low-water, high temperature treatment relative to the low-water, cool temperature treatment, but the ‘BLHO’ population cover was not significantly different between the two treatments (Figure 4.17A). At the high-water level, the ‘PAHR’ population had significantly higher final percent cover in the cool temperature regime relative to the other two populations (Figure 4.17B). The final percent cover at the high-water, high temperature regime was not statistically distinguishable between the three populations (Figure 4.17B).

For the *S. acutus* populations, the model identified a significant interaction between temperature regime and population (Table 4.8b). End-of-season cover remained high across these populations (relative to *B. maritimus* and *S. americanus*) but was significantly higher in the ‘THNA’ population relative to ‘FROU’ (highest latitude) and ‘PAHR’ (lowest latitude) at the cool temperature regime (Figure 4.18A). All populations experienced a modest, but significant, increase in cover at the hot temperature regime relative to the cool temperature regime, but the populations were not statistically distinguishable from one another (Figure 4.18A). The *S. americanus* model identified a significant two-way interaction between water level and population (Table 4.8c). The ‘SASP’ and ‘RRVABW’ populations experienced a significant increase in final percent cover between the low-water level and high-water level, but there was no significant difference in cover between water levels for the ‘HACR’ population, which maintained

significantly higher final cover at each treatment relative to the other two populations (Figure 4.18B).

Discussion

Restoring invasion resistant plant communities is a common goal in wetland restoration and can be enhanced with a mechanistic understanding of demographic processes during plant regeneration (James et al. 2011). Here, we quantified early life stage transition probabilities, including the probability of seedling clonal development, and percent cover development across focal native and invasive wetland species and abiotic conditions during the first eight-weeks of growth. In line with our predictions, we observed high performance (high germination, survival, and cover) in the two *Poaceae* species. The non-native, invasive grass *Phragmites australis* had high germination probabilities regardless of abiotic conditions, as did, to a lesser extent, *D. spicata*. Both species achieved high cover and developed clones during the first 8 weeks, though the variation in clonal transitions was mediated by water availability and temperature. To our surprise, *Eleocharis palustris*, a slow-growing perennial species that typically exhibits low germination and growth rates (Grime et al. 1981; Wagner & Olinger, 2017; Robinson, 2022), achieved high end-of-season cover in this study, largely from extensive clonal production at high (i.e. saturated) water levels. The generally poor performance of the bulrush species, particularly *B. maritimus* and *S. americanus*, was not surprising given previous research indicating low germination and growth rates (*Tarsa*, Chapter 3; Robinson, 2022). There was some evidence of population-level differentiation among the three-bulrush species (*B. maritimus, S. acutus, S. americanus*) in response to the interactive effects of temperature and water level, which may be driven by site-specific

selective pressures. Some of the differentiation we observed across populations reflected conditions similar to that of the maternal seed collection site, though the patterns were not noticeably consistent across life stage transitions. Overall, our findings highlight key points in the recruitment process that limit recruitment (e.g., low germination rates in *S. americanus*) or facilitate growth that can yield invasion resistance (e.g., high clonal production in *E. palustris*) during wetland restoration. Given the paucity of mechanistic assessments of wetland plants through germination, survival, and clonal production, this research provides key insights that can be used to guide the planning and implementation of seed-based wetland restoration.

Regeneration bottlenecks in seed-based wetland restoration

Identifying bottlenecks during the plant recruitment process is critical to maximizing restoration outcomes as points of high mortality can be addressed via species selection (Kettenring & Tarsa, 2020), seed treatments (Madsen et al. 2016), or targeting abiotic conditions that facilitate germination and growth (Copeland et al. 2021). Here, we found that the largest bottleneck in recruitment happened prior to germination, and the mortality that did occur was prior to clonal production. In some ways, this finding is contrary to studies of upland species that identified post-germination and pre-emergence as the biggest recruitment bottleneck (e.g. James et al. 2011, Larson et al. 2015). Part of this divergence could be related to the deep physiological dormancy that is characteristic of many of the *Cyperaceae* species in this study (Baskin & Baskin, 1998). Despite dormancy-breaking treatments, many seeds failed to germinate which could indicate that the dormancy-breaking treatments we applied, although standard for these species (Marty & Kettenring, 2016; Rosbakh et al. 2019), were not sufficient. Another plausible

explanation for this pattern is related to an even more fine-grained assessment of early germination patterns—our study was not able to distinguish between the lack of germination caused by dormancy vs. the lack of measurable germination caused by seed mortality in the very early germination stages. In water-impermeable seeds with thick seed coats, germination occurs after 1) dormancy is broken, and 2) the water-gap opens and allows for water to enter the seed so that germination can commence (Baskin, 2003; Soltani et al. 2022). In this way, the water-gap process is an indirect control of the germination process (Baskin, 2003; Soltani et al. 2022). It is possible that the mortality we observed in this study occurred after dormancy release but before germination via pathogenic attack or desiccation via the water-gap. Future research is needed to disentangle the true mechanism driving lack of germination in many of these species.

Regardless of the specific pre-germination mechanism, from a restoration practitioner perspective, the findings of this study point to the significance of pre-germination in limiting seed-based wetland restoration. Thus, the focus should be on ameliorating barriers through extensive dormancy break (Kettenring & Galatowitsch, 2007*a*; Kettenring & Galatowitsch, 2007*b*; Kildisheva et al. 2020), potentially applying seed enhancement technologies (Madsen et al. 2016), targeting seed sowing timing and locations for ideal conditions for seeds and seedling (i.e., “precision restoration”; Copeland et al. 2021; Govers et al. 2022), and renewing efforts to manage for wetland conditions that facilitate the highest probability of germination. In regard to abiotic conditions, we found that for four of the native species we tested (*B. maritimus*, *E. palustris*, *S. acutus*, and *S. americanus*), germination probabilities were significantly higher in high water levels and hot temperatures, indicating that these species should be

sown under saturated conditions in the summer when temperatures are hot. Interestingly, *E. palustris* germinated equally well in cool and hot temperatures at high-water levels (i.e., saturated soils), which may indicate that this species could be a good candidate for inducing native priority effects (i.e., ensuring that the native species has a temporal advantage over an invasive species such as *Phragmites*; Hess et al. 2020*b*; Tarsa et al. *in press*) at the restoration site given its high clonal potential in early-season, cool temperatures. However, future research should explore the bounds of the temperature requirements that facilitate high clonal production in *E. palustris*, particularly in a field setting. *Distichlis spicata* and *P. australis* were both less sensitive to abiotic influences during germination, indicating that these species will perform well across a wide range of abiotic conditions. In the case of *D. spicata*, this underscores the utility this species might have as a "workhorse" restoration species (Havens et al. 2015; Zinnen et al. 2020), while for *Phragmites*, these findings highlight the on-going challenge that restoration practitioners face in reestablishing native plant communities.

Inter- and intraspecific variation in regeneration traits and transition probabilities

We found notable interspecific differences in regeneration processes across focal species which has implications for the potential of these species to provide invasion resistance, particularly via clonal development. For several of the study species (*S. acutus*, *D. spicata*, *P. australis*), clonal development was accelerated in hot temperature regimes, indicating that these species prioritize clonal expansion during summer months to establish sufficient reserves for overwintering (Kun & Oborny, 2003). This interesting pattern also has implications for wetland plant communities in their short-term responses (i.e., increasing mean annual temperatures facilitating clonal development and

competition in first-year seedlings; Callaghan et al. 1992) and long-term responses (i.e., dominance of more effective clonal species; Callaghan et al. 1992) to a changing climate. High clonal development in *E. palustris* was associated with saturated water levels more than with temperature, which also has implications as wetland hydrologic regimes shift with a changing climate (Downard et al. 2014; Moomaw et al. 2018).

We also found some evidence of intraspecific differentiation among populations of bulrush species which has implications for sourcing seed for wetland restoration. *Bolboschoenus maritimus* seeds sourced from the southernmost latitude ('PAHR') had higher germination probabilities in hot temperatures relative to other tested populations, which is similar to the maternal-environmental conditions in which the seeds were sourced (Tarsa, *Chapter 3*). This pattern may indicate that seeds of *B. maritimus* sourced from high-temperature areas will perform superiorly in hot conditions, though this pattern needs further testing with genetic analyses across a wider range of temperatures and populations. Interestingly, the Great Salt Lake population of *S. acutus* ('THNA') had high clonal production in hot temperatures regardless of water levels while the Great Salt Lake population of *S. americanus* ('HACR') had significantly higher germination probability across temperatures relative to the other tested populations. In a previous study, Kettenring et al. (2019) found that all three bulrushes were broadly dispersed (likely from waterfowl) across the Intermountain West wetlands and that individual wetlands generally harbored a fair amount neutral genetic diversity (measured as genet richness). The findings from Kettenring et al. (2019), combined with the findings of the present study, suggest that seed collections from multiple sites along Great Salt Lake may

be sufficient to capture both neutral and adaptive genetic diversity, thus simplifying the logistical challenges of seed collections across broad regions.

Incorporating clonality into demographic research of early plant life stages was an important component of this study, which was particularly evidenced by the strong performance of *E. palustris* as a consequence of high clonal production. As increasing attention is given to identifying predictable patterns of seed and seedling functional trait expression among species (i.e., 'regeneration traits'; Larson & Funk, 2016), it is essential to consider clonality dynamics within clonal species which may skew the typically observed or expected functional trait relationships as predicated by the plant-economic spectrum (Wright et al. 2004; Reich, 2014). For example, clonal plants were observed to have higher below-ground biomass and greater root: shoot ratios in the first year of growth, making them more vulnerable to aboveground disturbance relative to non-clonal plants (Martínková et al. 2020). Further, clonality during the regeneration stage and beyond likely operates on its own spectrum of plant strategies and tradeoffs facilitated by functional traits unique to clonal species. For example, bud bank depth (i.e., belowground source of vegetative regrowth; Harper, 1977) can vary among species such that some species operating on the conservative end of the spectrum have deep bud banks that are resistant to freezing or disturbance, whereas other species operating on the competitive end of the spectrum have shallow bud banks that allow for rapid regrowth of aboveground structures (Grime, 1977; Pan et al. 2009; Lubbe & Henry, 2019). Thus, incorporating clonal traits into multidimensional assessments of plant regeneration can improve predictions of plant performance across species and systems.

Conclusion

To meet the growing need for improved restoration outcomes via seed, regenerative trait and early demographic plant studies should incorporate the net effects of germination, survival, clonality, and final percent cover outcomes to reflect the cumulative consequences of early plant growth. The proliferation of functional trait research to develop a mechanistic understanding of plant communities has been pivotal yet the focus on drivers of *established* communities has failed to capture the significance of regenerative processes and patterns, including clonality, at the seedling stage. Furthermore, the bias in the literature towards terrestrial plant communities limits synthetic understanding of early life stage dynamics in natural and restored wetland plant communities. In this study, we identified key points in the recruitment pathway that limited revegetation outcomes and, consequently, final plant cover. Further, this study was able to disentangle the contribution of germination vs. seedling clonal production to plant cover as seedlings transition through life stages across abiotic conditions within the first few weeks of growth. Detecting these patterns is critical for predicting plant community outcomes and applying a targeted restoration approach during seed-based wetland restoration.

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Tables and Figures

TABLE 4.1. Analysis of deviance results for logistic mixed effects model analyzing the effects of temperature regime ("Temp"), water level ("Water"), source population ("Source"), and their interactions, on each life stage transition probability for *Bolboschoenus maritimus* ('BOMA). Also reported are the variance estimates (logit scale; colon indicates nesting) for the modeled random effects. Type II significance tests at $P < 0.05$ are shown in bold. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling].*

BOMA: TP1	**Chi-sq**	**Df**	***P* value**
Temp	**5.34**	**1**	**0.021**
Water	**37.68**	**1**	**< 0.001**
Source	**10.78**	**2**	**0.005**
Temp × water	**4.71**	**1**	**0.030**
Temp × source	3.54	2	0.170
Water × source	2.03	2	0.363
Temp × water × source	**6.49**	**2**	**0.034**
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.022	0.148
BOMA: TP2	**Chi-sq**	**Df**	***P* value**
Temp	0.296	1	0.587
Water	1.001	1	0.317
Source	0.419	2	0.812
Temp × water	0.194	1	0.660
Temp × source	0.151	2	0.928
Water × source	0.268	2	0.874
Temp × water × source	0.074	2	0.964
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000
BOMA: TP3	**Chi-sq**	**Df**	***P* value**
Temp	0.588	1	0.443
Water	3.451	1	0.063
Source	2.830	2	0.243
Temp × water	0.039	1	0.844
Temp × source	0.045	2	0.978
Water × source	2.055	2	0.358
Temp × water × source	0.805	2	0.669

TABLE 4.1. (cont.)

Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.228	0.478
BOMA: TP4	**Chi-sq**	**Df**	***P* value**
Temp	0.746	1	0.388
Water	1.116	1	0.291
Source	2.152	2	0.341
Temp × water	0.022	1	0.883
Temp × source	0.209	2	0.901
Water × source	3.218	2	0.200
Temp × water × source	0.599	2	0.741
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.182	0.427
BOMA: TP5	**Chi-sq**	**Df**	***P* value**
Temp	8.785	1	0.118
Water	4.180	1	0.524
Source	5.775	2	0.566
Temp × water	4.058	1	0.132
Temp × source	4.316	2	0.229
Water × source	3.207	2	0.361
Temp × water × source	3.066	2	0.216
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000

TABLE 4.2. Analysis of deviance results for logistic mixed effects model analyzing the effects of temperature regime ("Temp"), water level ("Water"), source population ("Source"), and their interactions, on each life stage transition probability for *Schoenoplectus acutus* ('SCAC'). Also reported are the variance estimates (logit scale; colon indicates nesting) for the modeled random effects. Type II significance tests at $P < 0.05$ are shown in bold. Marginally significant interactions ($0.05 < P > 0.1$) are indicated by a +. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling].*

SCAC: TP1	**Chi-sq**	**Df**	***P* value**
Temp	1.756	1	0.185
Water	**43.206**	**1**	**< 0.001**
Source	4.078	2	0.130
Temp × water	0.637	1	0.425
Temp × source	5.391	2	0.068^{+}
Water × source	5.453	2	0.065^{+}
Temp × water × source	2.474	2	0.290
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.226	0.475
SCAC: TP2	**Chi-sq**	**Df**	***P* value**
Temp	1.226	1	0.268
Water	**6.721**	**1**	**0.009**
Source	3.391	2	0.184
Temp × water	1.101	1	0.294
Temp × source	3.883	2	0.143
Water × source	3.095	2	0.213
Temp × water × source	3.733	2	0.155
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000
SCAC: TP3	**Chi-sq**	**Df**	***P* value**
Temp	**8.015**	**1**	**0.004**
Water	0.009	1	0.925
Source	0.898	2	0.638
Temp × water	0.335	1	0.563
Temp × source	4.173	2	0.124
Water × source	2.029	2	0.363
Temp × water × source	1.235	2	0.539
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.849	0.922
Greenhouse		0.000	0.000

TABLE 4.2.2 (cont.)

SCAC: TP4	**Chi-sq**	**Df**	***P* value**
Temp	2.383	1	0.123
Water	0.021	1	0.886
Source	1.216	2	0.544
Temp × water	1.928	1	0.165
Temp × source	3.094	2	0.213
Water × source	**5.705**	**2**	**0.058**
Temp × water × source	**6.769**	**2**	**0.034**
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.469	0.685
Greenhouse		0.000	0.000
SCAC: TP5	**Chi-sq**	**Df**	***P* value**
Temp	1.812	1	0.178
Water	**4.423**	**1**	**0.035**
Source	2.432	2	0.296
Temp × water	0.395	1	0.530
Temp × source	0.025	2	0.988
Water × source	1.577	2	0.455
Temp × water × source	0.755	2	0.685
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.588	0.767
Greenhouse		0.208	0.456

TABLE 4.3. Analysis of deviance results for logistic mixed effects model analyzing the effects of temperature regime ("Temp"), water level ("Water"), source population ("Source"), and their interactions, on each life stage transition probability for *Schoenoplectus americanus* ('SCAM'). Also reported are the variance estimates (logit scale; colon indicates nesting) for the modeled random effects. Type II significance tests at $P < 0.05$ are shown in bold. Marginally significant interactions ($0.05 < P > 0.1$) are indicated by a +. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality].*

SCAM: TP1	**Chi-sq**	**Df**	***P* value**
Temp	**7.527**	**1**	**0.006**
Water	**21.938**	**1**	**< 0.001**
Source	**39.217**	**2**	**< 0.001**
Temp × water	1.882	1	0.170
Temp × source	3.438	2	0.179
Water × source	5.827	2	0.054^{+}
Temp × water × source	0.702	2	0.704
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000
SCAM: TP2	**Chi-sq**	**Df**	***P* value**
Temp	3.486	1	0.626
Water	3.167	1	0.674
Source	4.252	2	0.750
Temp × water	2.102	1	0.350
Temp × source	2.228	2	0.527
Water × source	2.974	2	0.396
Temp × water × source	1.823	2	0.402
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000

TABLE 4.4. Analysis of deviance results for logistic mixed effects model analyzing the effects of temperature regime ("Temp"), water level ("Water"), source population ("Source"), and their interactions, on each life stage transition probability for *Distichlis spicata* ('DISP'). Also reported are the variance estimates (logit scale; colon indicates nesting) for the modeled random effects. Type II significance tests at $P < 0.05$ are shown in bold. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

DISP: TP1	**Chi-sq**	**Df**	***P* value**
Temp	0.299	1	0.585
Water	0.007	1	0.932
Temp × water	1.661	1	0.198
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.902	0.950
Greenhouse		0.000	0.000
DISP: TP2	**Chi-sq**	**Df**	***P* value**
Temp	0.139	1	0.710
Water	0.139	1	0.710
Temp × water	0.139	1	0.709
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000
DISP: TP3	**Chi-sq**	**Df**	***P* value**
Temp	**0.588**	**1**	**0.086**
Water	3.451	1	0.750
Temp × water	**0.039**	**1**	**0.003**
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		7.406	2.721
DISP: TP4	**Chi-sq**	**Df**	***P* value**
Temp	0.480	1	0.489
Water	0.393	1	0.531
Temp × water	**5.903**	**1**	**0.015**
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		6.020	2.454
DISP: TP5	**Chi-sq**	**Df**	***P* value**
Temp	**10.782**	**1**	**0.001**
Water	**9.870**	**1**	**0.002**
Temp × water	2.478	1	0.115

TABLE 4.4. (cont.)

Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000
DISP: TP6	**Chi-sq**	**Df**	***P* value**
Temp	0.306	1	0.580
Water	0.306	1	0.580
Temp × water	0.280	1	0.560
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000

TABLE 4.5. Analysis of deviance results for logistic mixed effects model analyzing the effects of temperature regime ("Temp"), water level ("Water"), source population ("Source"), and their interactions, on each life stage transition probability for *Phragmites australis* ('PHAU). Also reported are the variance estimates (logit scale; colon indicates nesting) for the modeled random effects. Type II significance tests at $P < 0.05$ are shown in bold. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

PHAU: TP1	**Chi-sq**	**Df**	***P* value**
Temp	2.688	1	0.101
Water	0.033	1	0.857
Temp × water	**4.317**	**1**	**0.038**
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.126	0.355
Greenhouse		0.570	0.755
PHAU: TP2	**Chi-sq**	**Df**	***P* value**
Temp	0.007	1	0.932
Water	0.621	1	0.431
Temp × water	0.586	1	0.444
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000
PHAU: TP3	**Chi-sq**	**Df**	***P* value**
Temp	**9.035**	**1**	**0.002**
Water	0.180	1	0.671
Temp × water	**21.821**	**1**	**<0.001**
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.195	0.442
Greenhouse		0.000	0.000
PHAU: TP4	**Chi-sq**	**Df**	***P* value**
Temp	**6.564**	**1**	**0.010**
Water	0.049	1	0.825
Temp × water	**16.210**	**1**	**<0.001**
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000
PHAU: TP5	**Chi-sq**	**Df**	***P* value**
Temp	0.344	1	0.558
Water	0.056	1	0.813
Temp × water	0.482	1	0.488
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.756	0.870
Greenhouse		0.000	0.000

TABLE 4.6. Analysis of deviance results for logistic mixed effects model analyzing the effects of temperature regime ("Temp"), water level ("Water"), source population ("Source"), and their interactions, on each life stage transition probability for *Eleocharis palustris* ('ELPA'). Also reported are the variance estimates (logit scale; colon indicates nesting) for the modeled random effects. Type II significance tests at $P < 0.05$ are shown in bold. Marginally significant interactions ($0.05 < P > 0.1$) are indicated by a +. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

ELPA: TP1	**Chi-sq**	**Df**	***P* value**
Temp	0.235	1	0.628
Water	**11.952**	**1**	**0.001**
Temp × water	0.001	1	0.984
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.612	0.782
Greenhouse		0.000	0.000
ELPA: TP2	**Chi-sq**	**Df**	***P* value**
Temp	0.082	1	0.775
Water	0.475	1	0.491
Temp × water	1.249	1	0.264
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.464	0.681
ELPA: TP3	**Chi-sq**	**Df**	***P* value**
Temp	1.191	1	0.275
Water	3.477	1	0.062^{+}
Temp × water	3.082	1	0.079
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000
ELPA: TP4	**Chi-sq**	**Df**	***P* value**
Temp	0.983	1	0.322
Water	2.051	1	0.152
Temp × water	0.872	1	0.350
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000
ELPA: TP5	**Chi-sq**	**Df**	***P* value**
Temp	0.312	1	0.577
Water	1.498	1	0.221
Temp × water	0.330	1	0.566

TABLE 4.6. (cont.)

Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000
ELPA: TP6	**Chi-sq**	**Df**	***P* value**
Temp	0.944	1	0.331
Water	**6.923**	**1**	**0.009**
Temp × water	1.278	1	0.258
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.000	0.000

TABLE 4.7. Analysis of deviance results for mixed effects model analyzing the effects of temperature regime ("Temp"), water level ("Water"), species identity ("Species"), and their interactions, on percent cover. Also reported are the variance estimates (logit scale; colon indicates nesting) for the modeled random effects. Type II significance tests at $P < 0.05$ are shown in bold.

All species	**Chi-sq**	**Df**	***P* value**
Temp	**67.343**	**1**	**< 0.001**
Water	**86.689**	**1**	**< 0.001**
Species	**167.080**	**5**	**< 0.001**
Temp × water	0.007	1	0.932
Temp × species	**16.353**	**5**	**0.006**
Water × species	**17.754**	**5**	**0.003**
Temp × water × species	3.482	5	0.626
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.103	0.321

TABLE 4.8. Analysis of deviance results for (a) *B. maritimus*, (b) *S. acutus*, and (c) *S. americanus* mixed effects model analyzing the effects of temperature regime, water level, population, and their interactions, on percent cover. Also reported are the variance estimates (logit scale) for the modeled random effects. Type II significance tests at $P < 0.05$ are shown in bold.

(a) *B. maritimus*	**Chi-sq**	**Df**	***P* value**
Temp	**32.007**	**1**	**< 0.001**
Water	**51.553**	**1**	**< 0.001**
Population	**5.369**	**2**	**0.068**
Temp × water	1.421	1	0.233
Temp × population	**4.839**	**2**	**0.089**
Water × population	1.418	2	0.492
Temp × water × population	**10.342**	**2**	**0.006**
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.303	0.551

(b) *S. acutus*	**Chi-sq**	**Df**	***P* value**
Temp	**21.013**	**1**	**< 0.001**
Water	**76.729**	**1**	**< 0.001**
Population	**9.123**	**2**	**0.010**
Temp × water	**7.486**	**1**	**0.006**
Temp × population	**11.071**	**2**	**0.004**
Water × population	2.156	2	0.340
Temp × water × population	3.253	2	0.197
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.097	0.311
Greenhouse		0.133	0.365

(c) *S. americanus*	**Chi-sq**	**Df**	***P* value**
Temp	**41.487**	**1**	**< 0.001**
Water	**23.423**	**1**	**< 0.001**
Population	**20.625**	**2**	**< 0.001**
Temp × water	0.446	1	0.504
Temp × population	1.524	2	0.467
Water × population	**7.979**	**2**	**0.019**
Temp × water × population	0.654	2	0.721
Variance Estimates of Random Effects		**Variance (σ^2)**	**Std. Dev. (σ)**
Greenhouse: Reservoir		0.000	0.000
Greenhouse		0.316	0.562

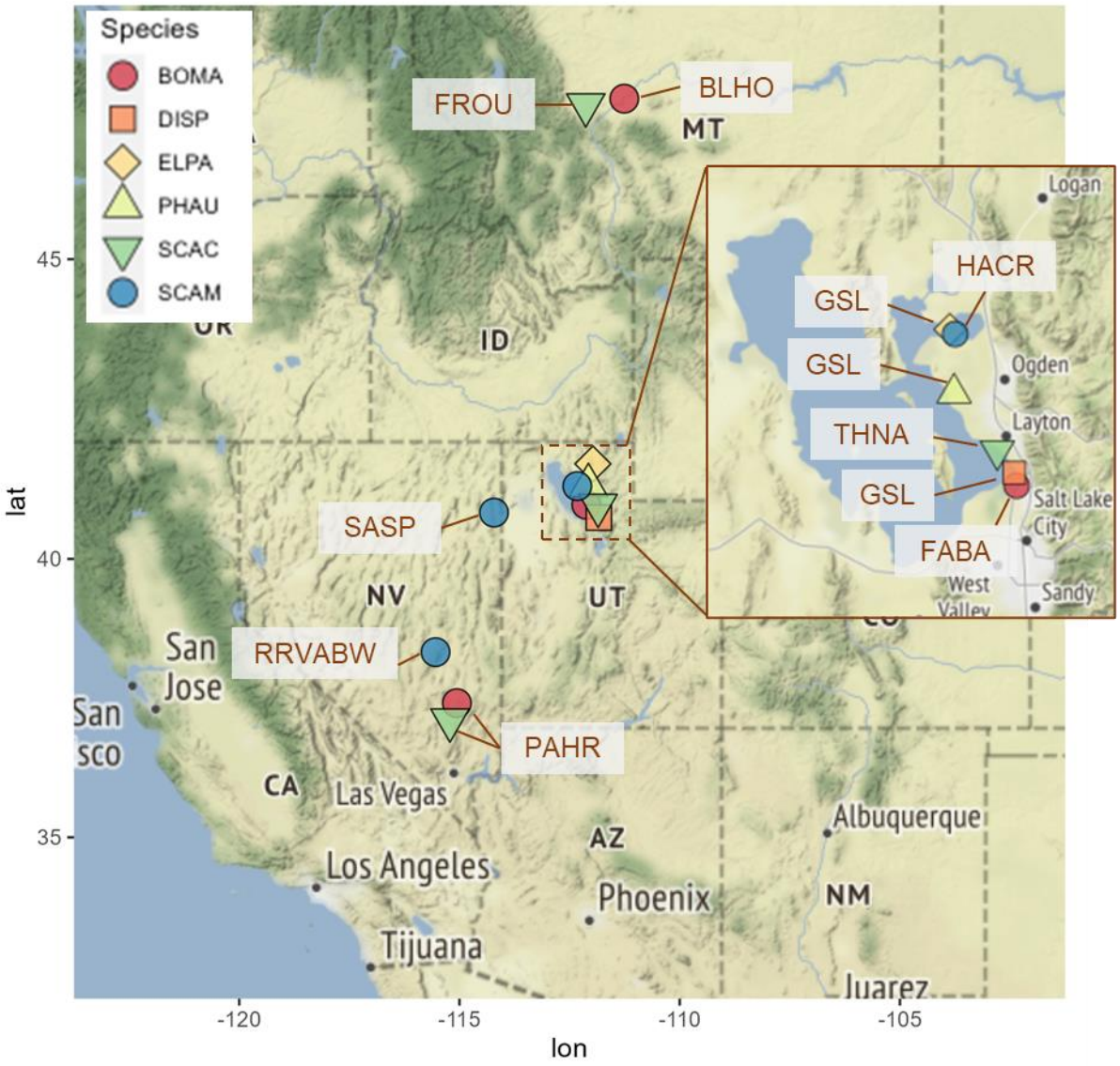

FIG. 4.1. Map of seed collection sites for species and populations in the Intermountain West of the USA. *Population codes*: *BLHO = Black Horse Lake; RRVABW = Railroad Valley Big Wells WMA; PAHR = Pahranagat NWR; FROU = Freezeout WMA; THNA = The Nature Conservancy (Shorelands Preserve); FABA = Farmington Bay WMA; HACR = Harold Crane WMA; SASP: Salt Springs WMA; GSL = Great Salt Lake.*

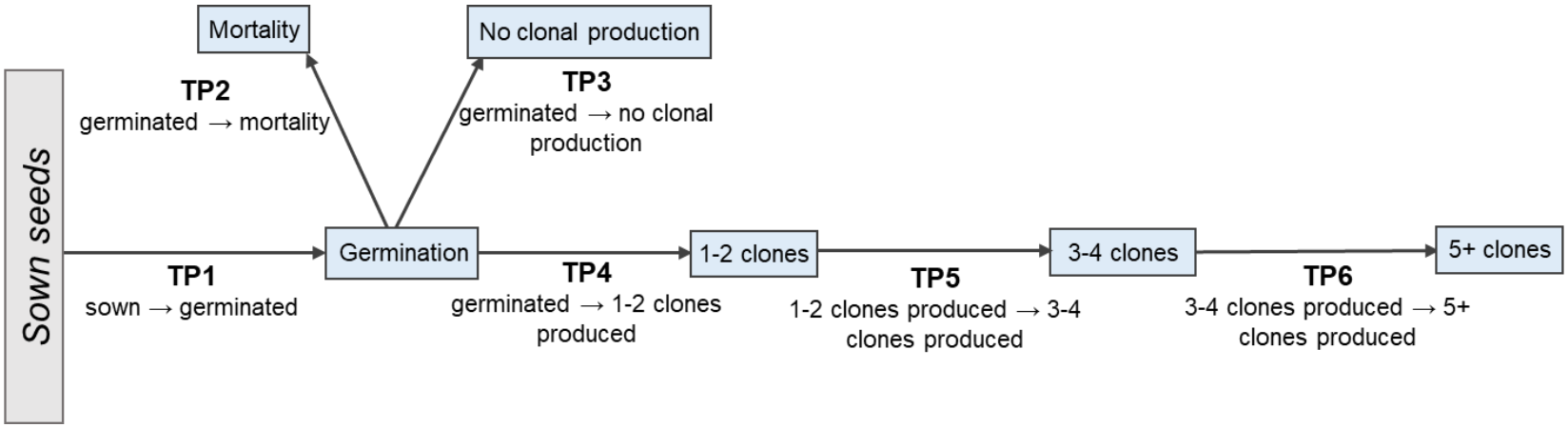

FIG. 4.2. Diagram of early life stage processes from sown seed to clonal development during the first 8-weeks of growth.

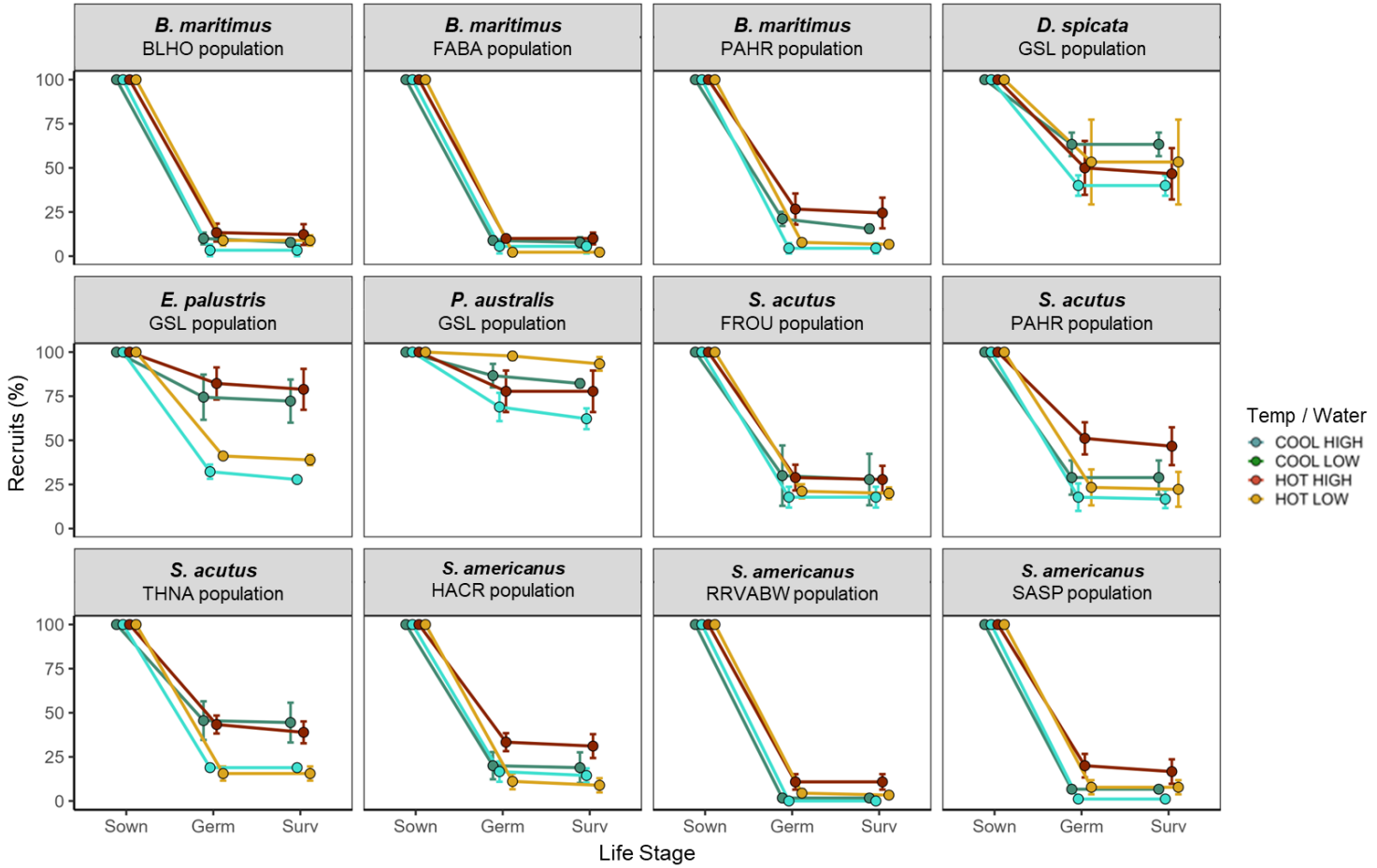

FIG. 4.3. Percentage of individual recruits across life stages ("Germ"=germination; "Surv"=survival) for species and population at each temperature regime ("Temp") and water level ("Water"). *Population codes*: *BLHO = Black Horse Lake; RRVABW = Railroad Valley Big Wells WMA; PAHR = Pahranagat NWR; FROU = Freezeout WMA; THNA = The Nature Conservancy (Shorelands*

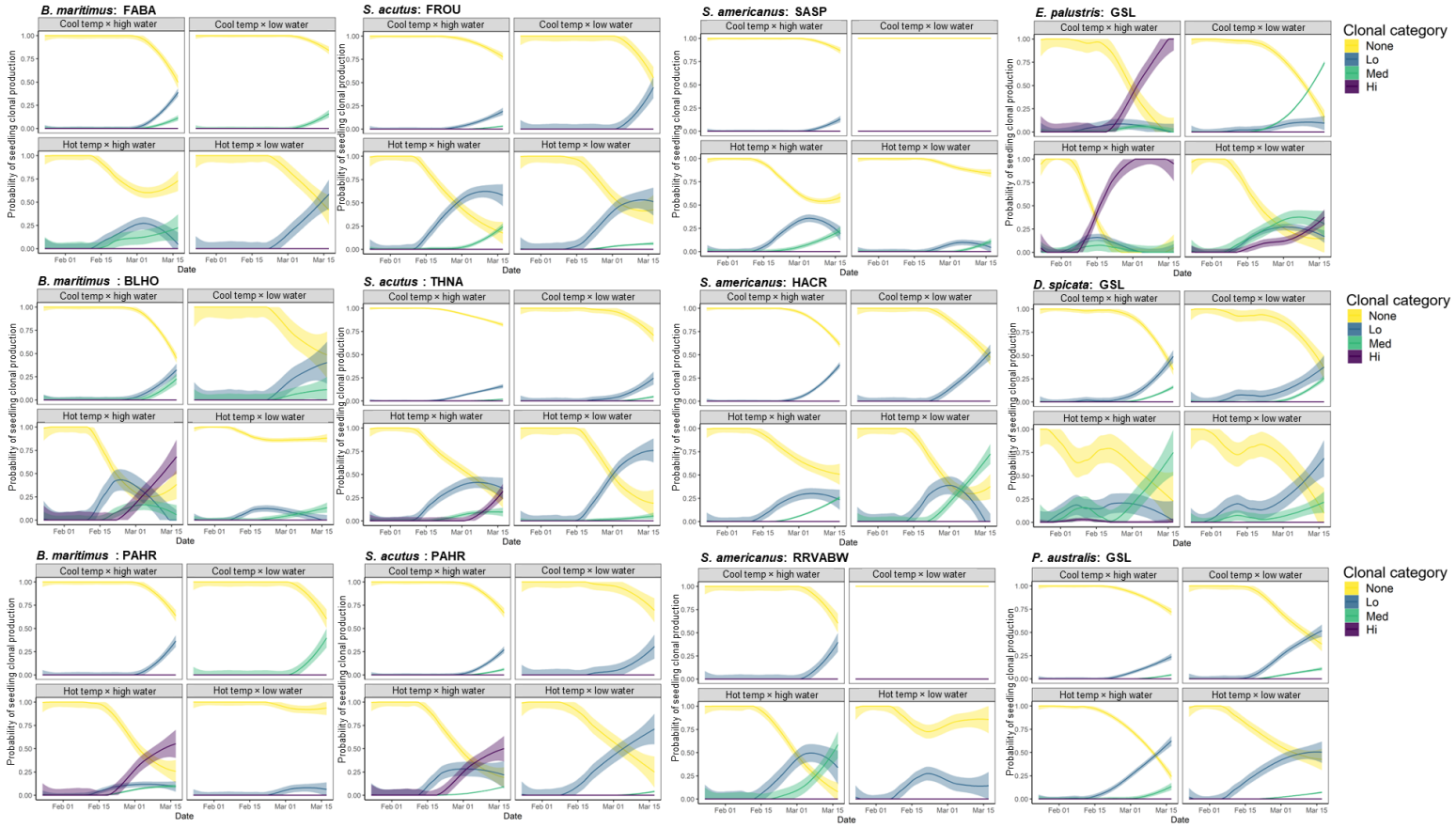

FIG. 4.4. Probability of seedling clonal production for each population and abiotic treatment over time. Data are displayed within clonal categories (*None = number of seedlings that produced no clones; Lo = number of seedlings that produced 1–2 clones; Med = number of seedlings that produced 3–4 clones; Hi = number of seedlings that produced 5+ clones*) and represent transitions through each category. *Population codes*: *BLHO = Black Horse Lake; RRVABW = Railroad Valley Big Wells WMA; PAHR = Pahranagat NWR; FROU = Freezeout WMA; THNA = The Nature Conservancy (Shorelands Preserve); FABA = Farmington Bay WMA; HACR = Harold Crane WMA; SASP: Salt Springs WMA; GSL = Great Salt Lake.*

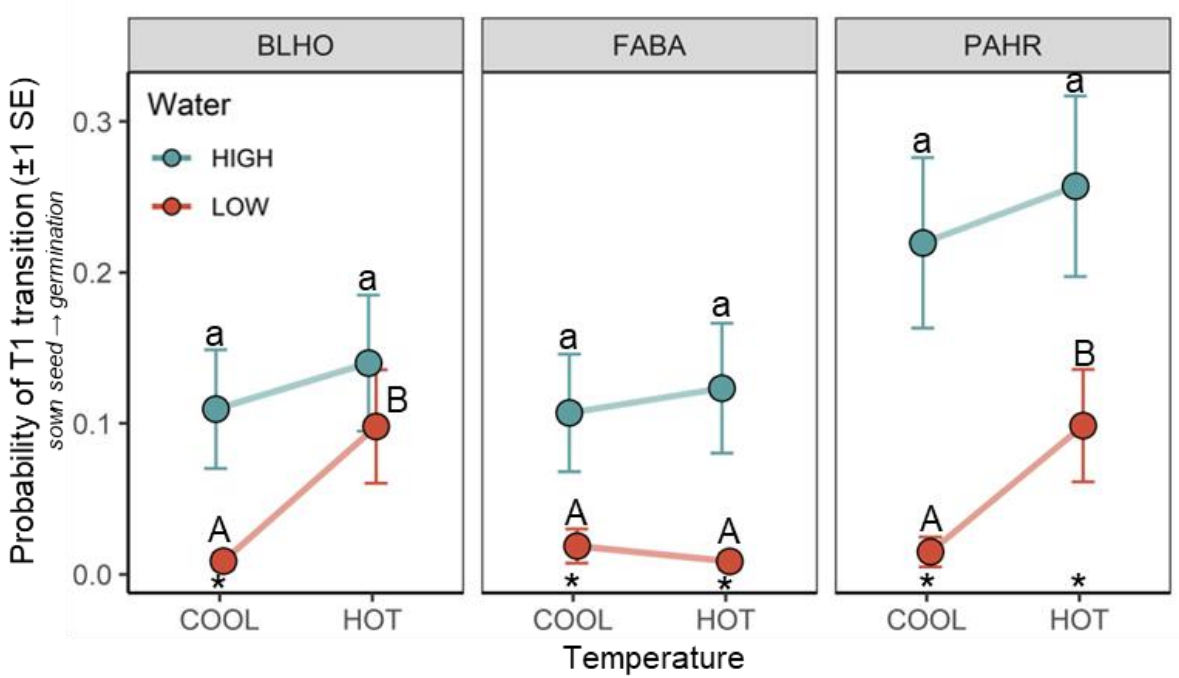

FIG. 4.5. Effect of temperature and water level on the probability of transition between sown seed to germinated seed [T1] for *Bolboschoenus maritimus* populations. Significant pairwise comparisons (Tukey HSD, α=0.05) between water levels at each temperature level for every population are indicated by an asterisk. Tukey post hoc significant values at an alpha level of 0.05 across water levels are shown in capital letters for low-water and lowercase letters for high-water conditions.

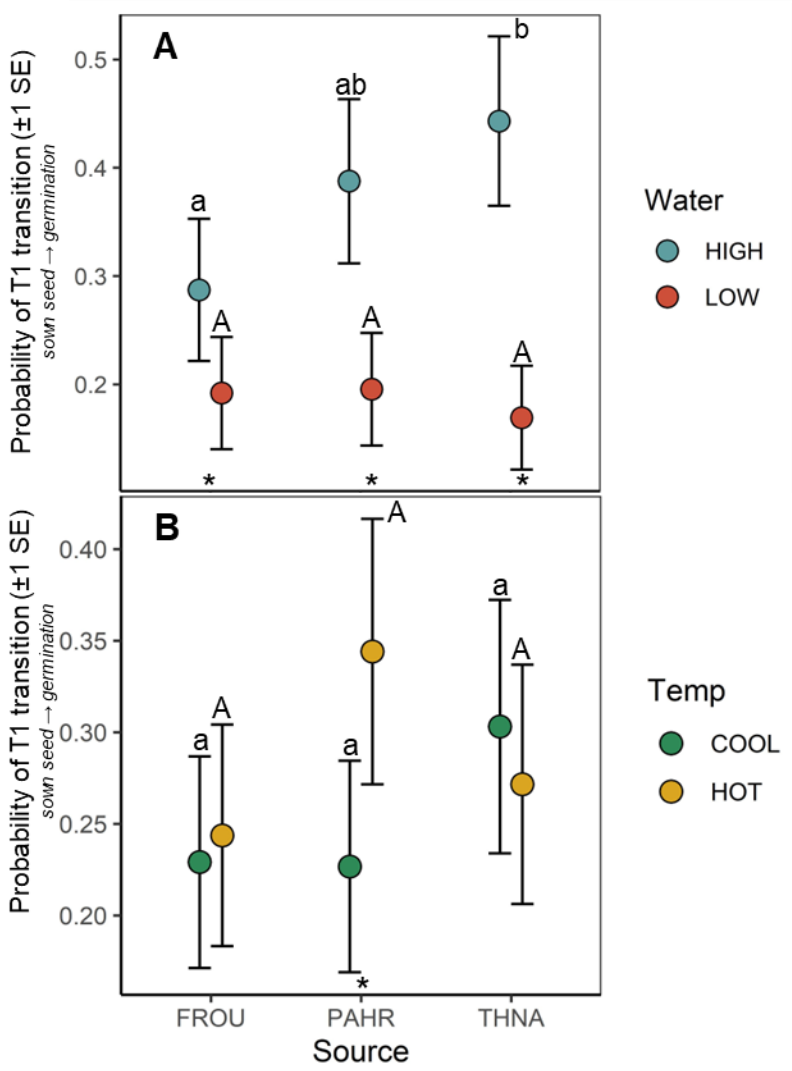

FIG. 4.6. Effect of temperature and water level on the probability of transition between sown seed to germinated seed [T1] for *Schoenoplectus acutus* populations. Significant pairwise comparisons (Tukey HSD, α=0.05) between abiotic conditions at each population are indicated by an asterisk. Tukey post hoc significant values at an alpha level of 0.05 are shown in capital letters for (A) low-water and (B) high-temperature; and lowercase letters for (a) high-water and (b) cool-temperature.

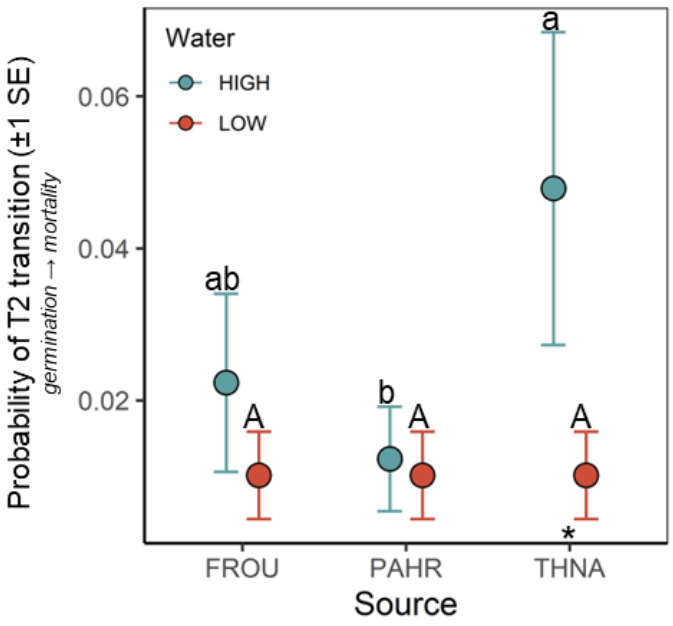

FIG. 4.7. Effect of water level on the probability of transition between germinated seed to death [T2] for *Schoenoplectus acutus* populations. Significant pairwise comparisons (Tukey HSD, α=0.05) between water levels at each population are indicated by an asterisk. Tukey post hoc significant values at α=0.05 across populations are shown in capital letters for low-water and lowercase letters for high-water conditions.

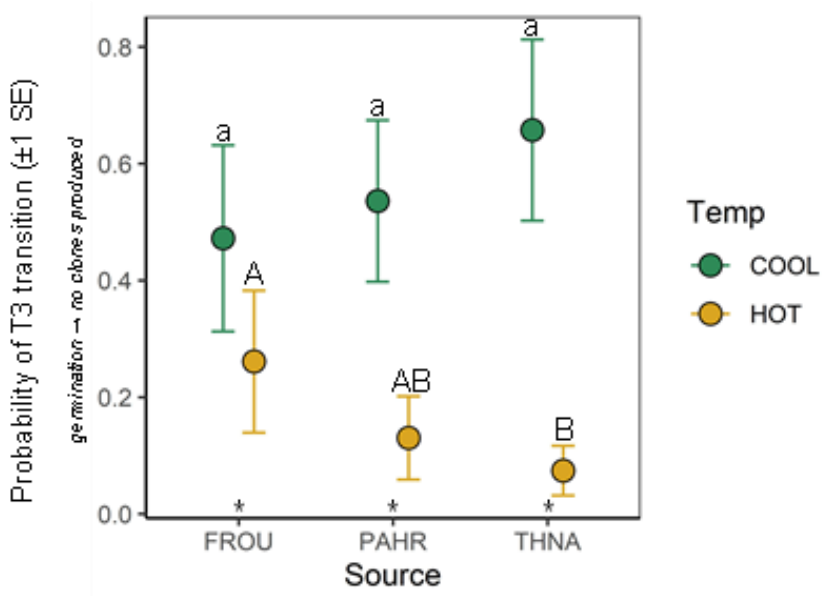

FIG. 4.8. Effect of temperature on the probability of transition between germinated seed to no clonal production [T3] for *Schoenoplectus acutus* populations. Significant pairwise comparisons (Tukey HSD, α=0.05) between temperature levels at each population are indicated by an asterisk. Tukey post hoc significant values at α=0.05 across populations are shown in capital letters for hot temperature and lowercase letters for cool temperature conditions.

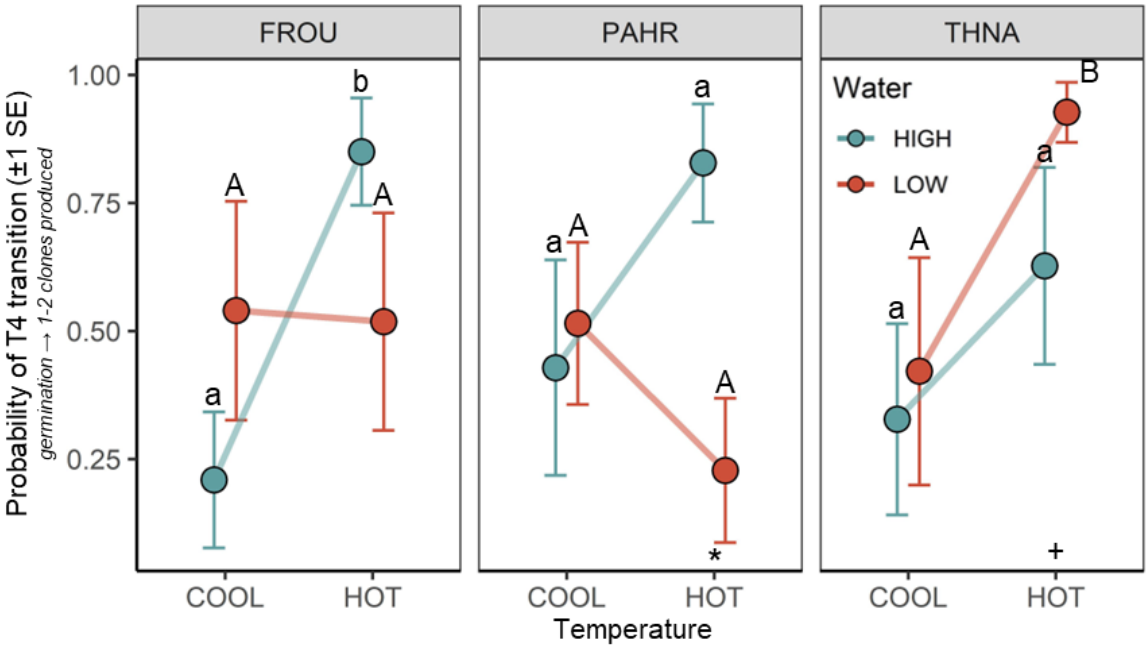

FIG. 4.9. Effect of temperature and water level on the probability of transition between germinated seed to low clonal production [T4] for *Schoenoplectus acutus* populations. Significant pairwise comparisons (Tukey HSD, α=0.05) between water levels at each temperature for each population are indicated by an asterisk. Moderately significant pairwise comparisons (Tukey HSD, $0.05 > \alpha < 0.10$ between water levels at each temperature for each population are indicated by a plus sign. Tukey post hoc significant values at an alpha level of 0.05 across temperatures are shown in capital letters for low-water and lowercase letters for high-water conditions.

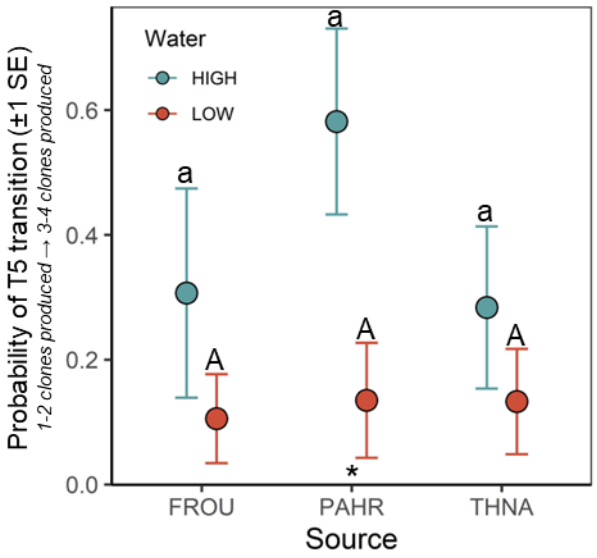

FIG. 4.10. Effect of water level on the probability of transition between the first clonal stage (1–2 clones produced) to the second clonal stage (3–4 clones produced) [T2] for *Schoenoplectus acutus* populations. Significant pairwise comparisons (Tukey HSD, α=0.05) between water levels at each temperature for each population are indicated by an asterisk. Tukey post hoc significant values at an alpha level of 0.05 are shown in capital letters for low-water and lowercase letters for high-water conditions.

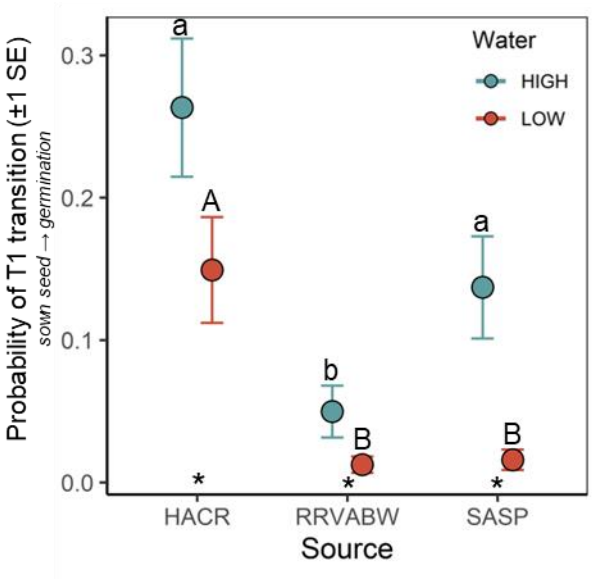

FIG. 4.11. Effect of temperature and water level on the probability of transition between sown seed to germinated seed [T1] for *Schoenoplectus americanus* populations. Significant pairwise comparisons (Tukey HSD, α=0.05) between water levels at each temperature for each population are indicated by an asterisk. Tukey post hoc significant values at an alpha level of 0.05 are shown in capital letters for low-water and lowercase letters for high-water conditions.

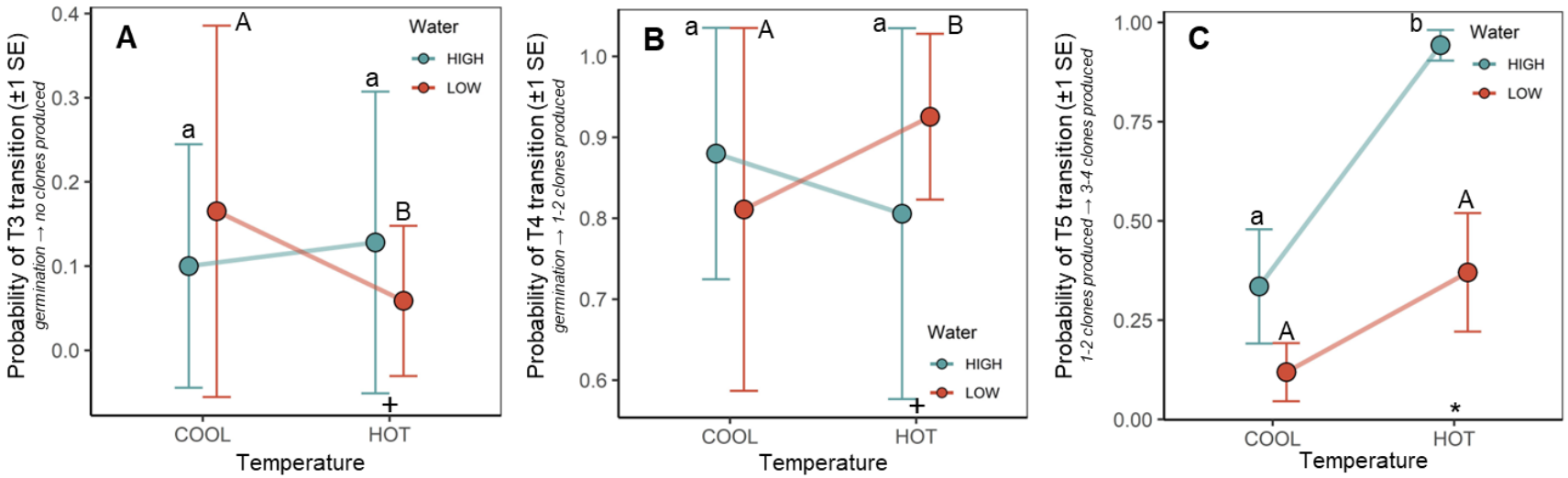

FIG. 4.12. Effect of temperature and water level on significant transition probabilities for *Distichlis spicata*. Graphs are presented for for the (A) TP_3 transition, (B) TP_4 transition, and (C) TP_5 transition. Significant pairwise comparisons (Tukey HSD, α=0.05) between water levels at each temperature for each population are indicated by an asterisk. Moderately significant pairwise comparisons (Tukey HSD, $0.05 > \alpha < 0.10$ between water levels at each temperature for each population are indicated by a plus sign. Tukey post hoc significant values at an alpha level of 0.05 are shown in capital letters for low-water and lowercase letters for high-water conditions.

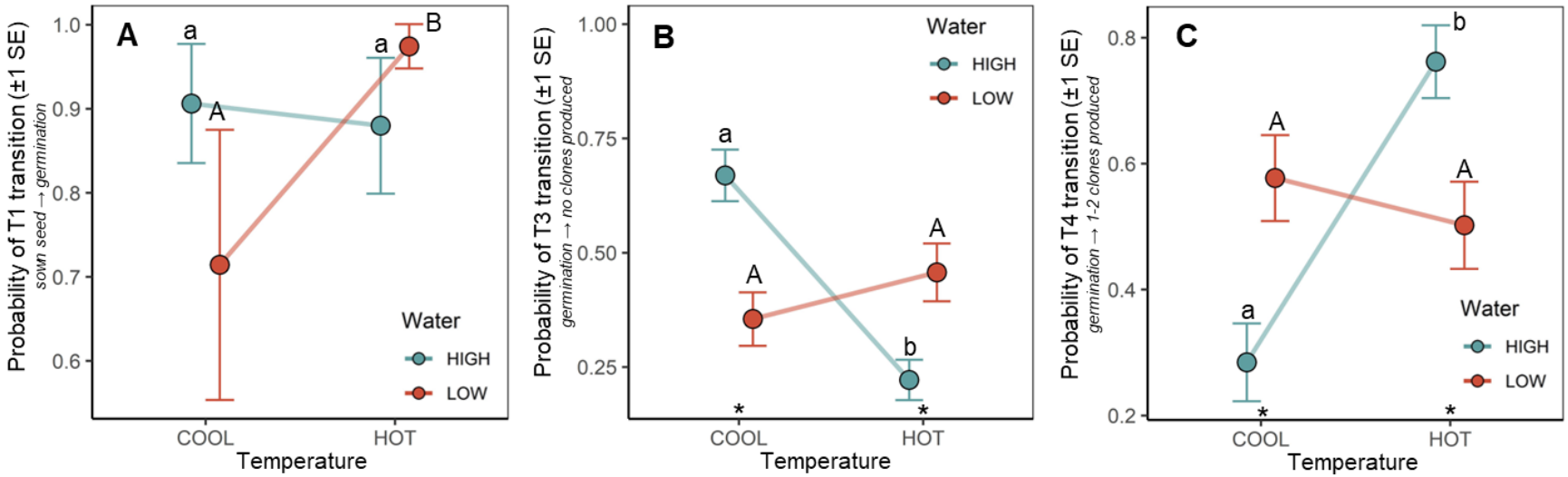

FIG. 4.13. Effect of temperature and water level on significant transition probabilities for *Phragmites australis.* Significant pairwise comparisons (Tukey HSD, α=0.05) between water levels at each temperature level for each population are indicated by an asterisk. Tukey post hoc significant values at an alpha level of 0.05 are shown in capital letters for low-water and lowercase letters for high-water conditions. Moderately significant pairwise comparisons (Tukey HSD, $0.05 > \alpha < 0.10$ between water levels at each temperature for each population are indicated by a plus sign. Tukey post hoc significant values at an alpha level of 0.05 are shown in capital letters for low-water and lowercase letters for high-water conditions.

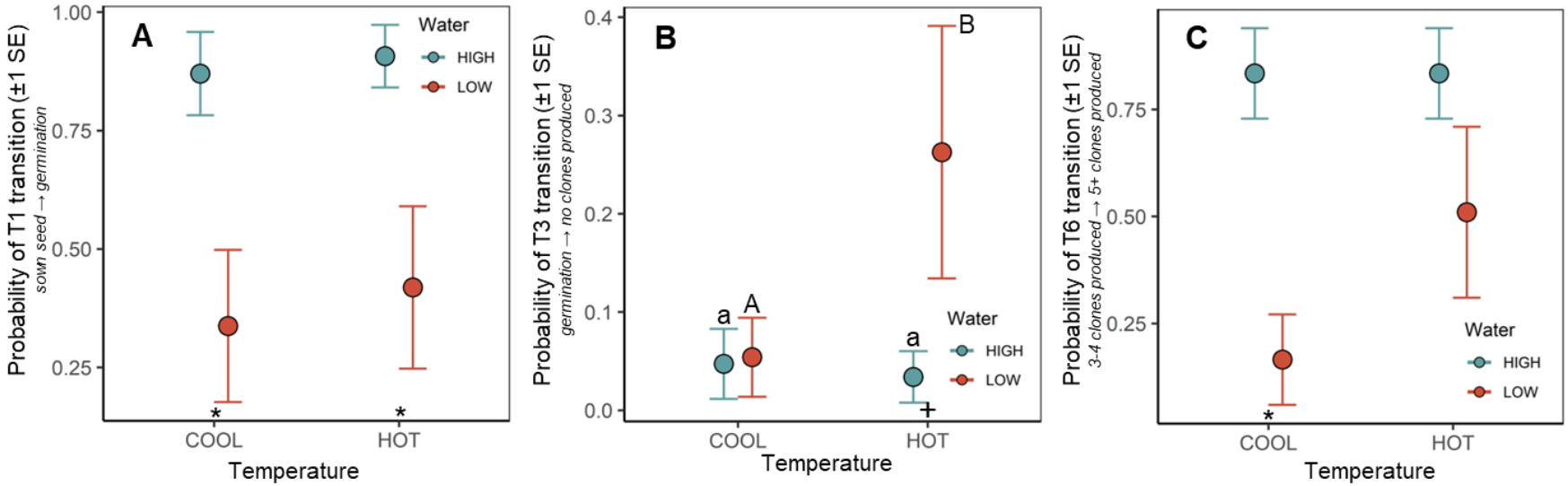

FIG. 4.14. Effect of temperature and water level on significant transition probabilities for *Eleocharis palustris.* Significant pairwise comparisons (Tukey HSD, α=0.05) between water levels at each temperature level for each population are indicated by an asterisk. Where significant, Tukey post hoc significant values at an alpha level of 0.05 are shown in capital letters for low-water and lowercase letters for high-water conditions. Tukey post hoc significant values at an alpha level of 0.05 are shown in capital letters for low-water and lowercase letters for high-water conditions.

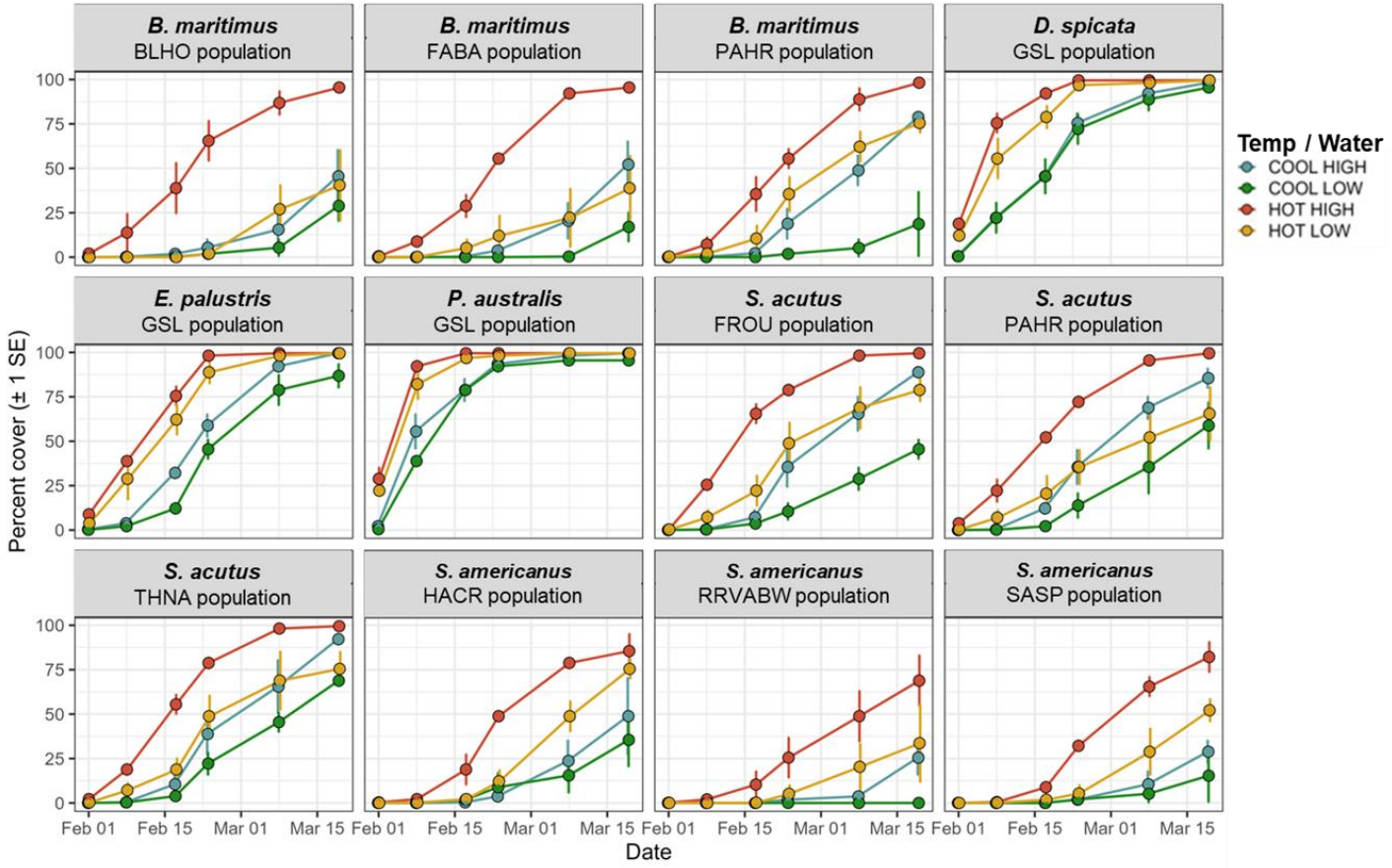

Figure 4.15. Percent cover of species and populations over data collection time periods for each temperature and water level treatment.

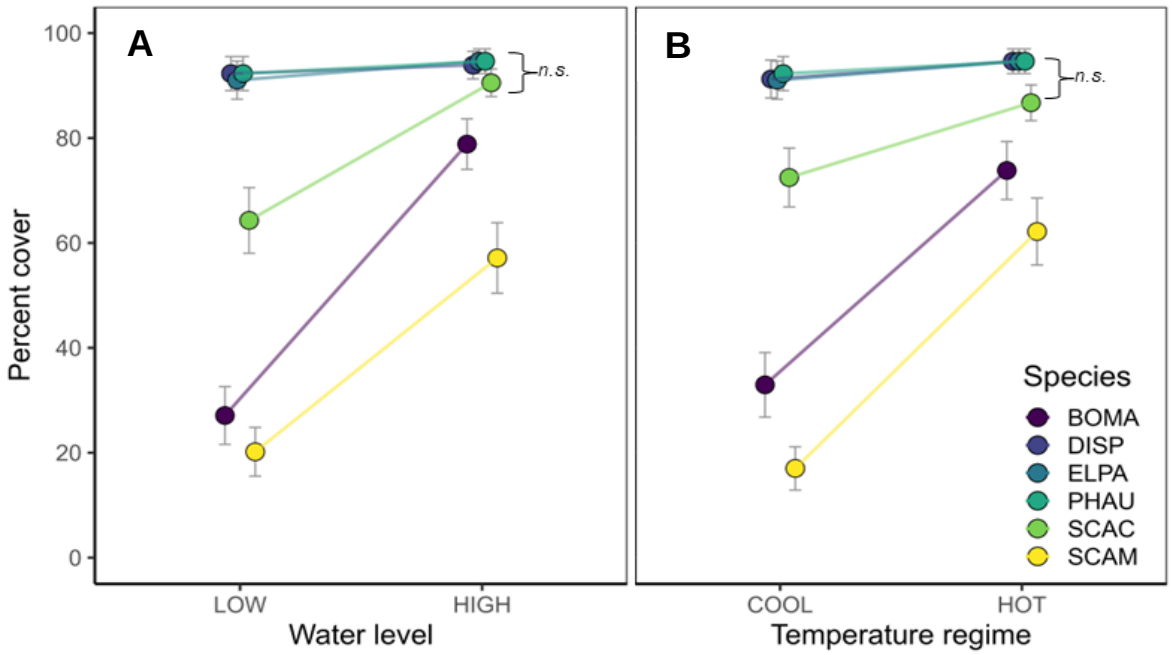

Figure 4.16. Modeled percent cover (± 1 SE) of species across (A) water level, and (B) temperature regime. Tukey post-hoc tests (α=0.05) were used to compare percent cover across species at each treatment and between treatments for each species. Non-significant (*n.s.*) species at each treatment level are displayed to highlight when cover differences were nominal.

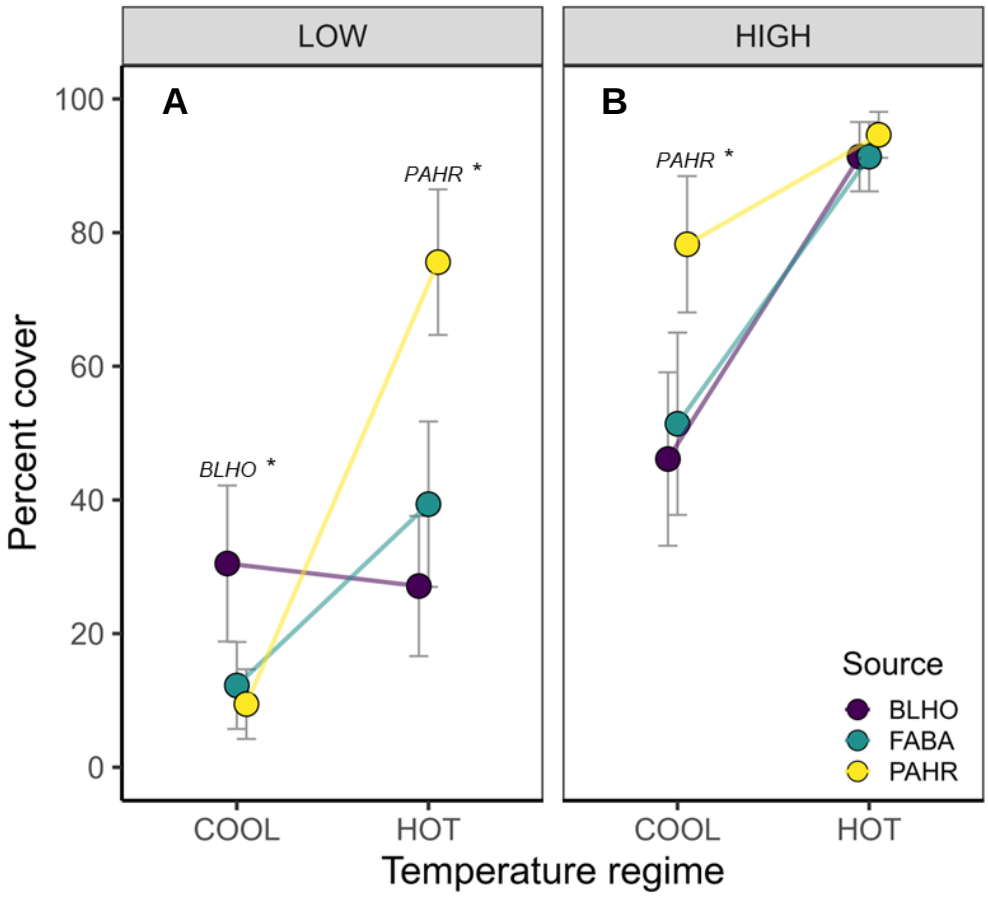

Figure 4.17. Modeled percent cover (± 1 SE) of *B. maritimus* populations at each temperature regime across (A) low water level and (B) high water level. Tukey post-hoc tests (α=0.05) were used to compare percent cover across populations at each treatment and between treatments for each population. Significant populations are denoted with an asterisk.

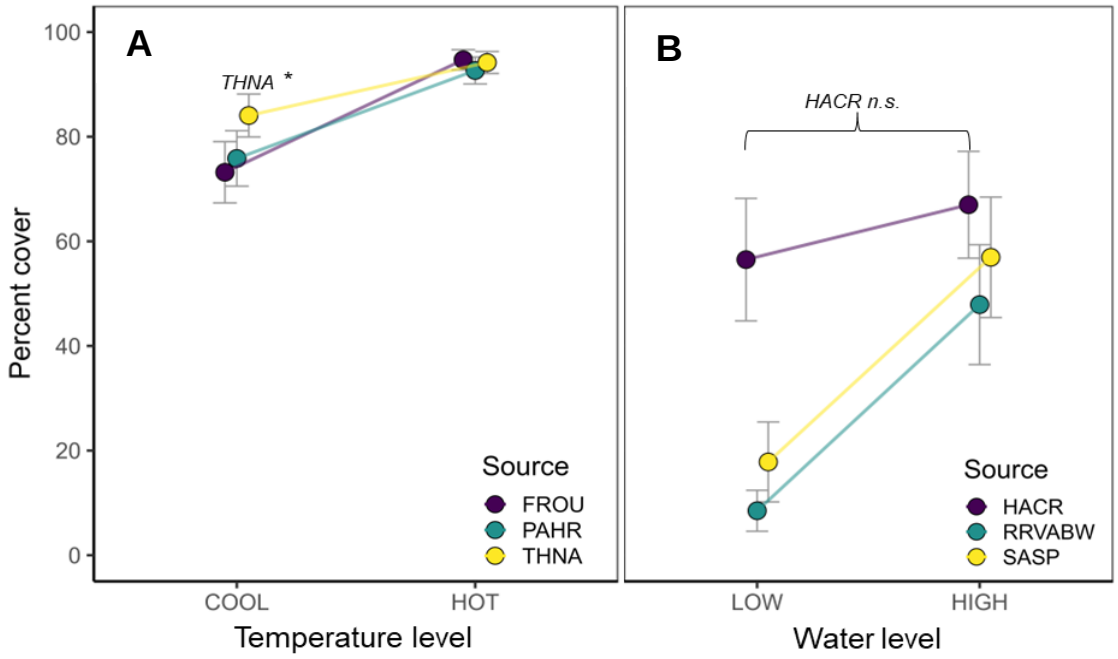

Figure 4.18. Modeled percent cover (± 1 SE) of (A) *S. acutus* populations at each temperature regime and (B) *S. americanus* populations at each water level. Tukey post-hoc tests (α=0.05) were used to compare percent cover across populations at each treatment and between treatments for each population. In (A), significant populations at each treatment are denoted with an asterisk; in (B), non-significant results between treatments are displayed to clarify statistical patterns.

CHAPTER 5

SUMMARY AND CONCLUSION

The application of native seeds is a common management practice in terrestrial and forest ecosystems (e.g., Kildisheva et al. 2016; Grossnickle and Ivetić, 2017), and has become increasingly common in degraded wetland systems with insufficient native seeds bank to support passive recruitment (Luckeydoo et al. 2006; Carlson et al. 2009; Rohal et al. 2019). Despite the global demand for restoration of native wetland species, empirical research to guide the application of seed-based restoration approaches in wetlands is limited (Kettenring & Tarsa, 2020). Further, high mortality during the early stages of recruitment can hinder the full potential of seeds, leading to unpredictable and largely unsuccessful outcomes (James et al. 2011). The research presented in this dissertation offers key insight into knowledge gaps surrounding seed-based wetland restoration by identifying: (1) restoration manipulations that maximize desired plant community outcomes, (2) functional trait strategies related to the dispersal, persistence, and growth of wetland seeds and seedlings, and (3) the probability of life stage transitions and clonal development across abiotic conditions. Here, we summarize the findings of this research, with an emphasis on management recommendations and contributions to restoration ecology.

Priority effects, native sowing density, and invasive propagule pressure across abiotic conditions

We found that applying higher native seed sowing rates can increase native plant cover and biomass, thus tipping community composition toward a more native-dominated state. Additional benefits occurred when native species were sown earlier in the season

and, interestingly, early-season benefits occurred regardless of sowing density. Thus, when financial realities limit higher native sowing densities, shifting strategies to early-season sowing can yield desired outcomes. However, an early-season sowing strategy must consider germination requirements of species included in the seed mix—native species that can germinate in cooler conditions should be prioritized. Further, restoration outcomes of early-season sowing can be maximized when including cool-germinating species that have functional traits that facilitate rapid growth rate (e.g., small seeds with thin seed coats, high elongation rates; Chapter 3). In Chapters 2-4, *Distichlis spicata* was a top restoration species and would be an ideal candidate for early-season sowing—it germinated well across a wide range of conditions and exhibited rapid growth rate following dormancy-break treatments. There are likely additional species, specifically wetland annual species that are adapted to early germination and rapid growth, that were not tested but would likely perform well in an early-season seed mix (Robinson, 2022). Our study did not capture realistic early-season field conditions well and was limited in the number of species tested, but given the significance of sowing timing here, future studies should investigate the role of priority effects in a field setting across a suite of functionally and phylogenetically diverse native species.

Increasing native sowing rates should be done secondary to (or in conjunction with) reducing *P. australis* propagule pressure, which was the most significant driver of plant community composition. This finding was not surprising and is supported widely in the literature (e.g., Holle & Simberloff, 2005; Lockwood et al. 2009), however there is surprisingly limited knowledge of seed bank dynamics for *P. australis*. Given the importance of *P. australis* propagule pressure in this study and the overwhelming number

of *P. australis* propagules in Great Salt Lake wetlands (Rohal et al. 2021), future research should investigate seed bank dynamics for this species. It would be beneficial to expand understanding of *P. australis* seed bank longevity and *P. australis* seed dispersal across the landscape to partition the contribution of propagule sources (i.e., seed bank persistence vs. annual seed rain) to newly assembling plant communities. From a management perspective, this would provide tangible knowledge that could be incorporated into wetland management plans to reduce *P. australis* propagule sources (e.g., focusing herbicide treatments/mowing on large *P. australis* stands contributing a high number of propagules), exhaust *P. australis* seeds that may be present in the seed bank (e.g., through repeated wet-dry cycling; Jordan, 2022; Tarsa, *unpublished data*), and prioritize restoration sites that are likely to yield desired outcomes.

Inter- and intraspecific variation in regeneration traits to predict seed and seedling performance

Utilizing functional traits of seeds and seedlings can enhance seed-based restoration outcomes and offers insight into how seeds and seedlings disperse, persist, and grow (Larson & Funk, 2016). Wetland plants have been generally underrepresented in regeneration trait-based ecological research, which limits our ability to generalize and predict recruitment patterns across systems. Through intensive lab measurements and growth chamber experiments, we identified specific seed and seedling traits and multidimensional strategies that aligned with the unique habitat and life-history of species. For example, flood-tolerant obligate wetland species, such as *B. maritimus*, exhibited seed traits conducive to habitat-specific dispersal (seed buoyancy), endozoochoric movement (thick seed coat), and subsequent seedling tolerance strategies

to withstand flooding (high biomass allocation). One surprising finding was that the flood tolerance seedling strategy that aligned with the obligate wetland species included both high biomass allocation and high specific leaf area (SLA), traits which have often been observed as representing oppositional strategies in upland species (e.g., Reich, 2014). Facultative wetland species in this study exhibited more acquisitive seed (e.g., fast germination, shallow dormancy) and seedling (high elongation rates) traits.

We found a high degree of intraspecific variation in seed and seedling traits among populations, and very weak effects of abiotic conditions on seedling trait expression. This could be explained by high phenotypic plasticity in wetland plants (Weiher & Keddy, 1995; Dorken & Barrett, 2004), which allows for wetland species to grow and adapt to a wide range of conditions. From a restoration practitioner perspective, this may be advantageous in that seed sourcing among long distances may not always be necessary to capture specific functional trait values in seeds and seedlings. However, there are several cautions and caveats to that finding. First, as climate change continues to negatively impact wetland communities, there will likely be an increasing need to source seeds from sites that consistently experience conditions similar to what is projected at the restoration site in order to introduce adapted genetic material (i.e., 'pre-restoration'; Butterfield et al. 2017). Thus, managers may still want to source seeds for seed-based wetland restoration from areas experiencing projected climate conditions in addition to locally sourcing seeds ("climate provenancing", Prober et al. 2016). Secondly, the reason for little effect of the abiotic conditions on seedling trait expression may have been a consequence of our methodology—the conditions we imposed may not have been extreme enough to see a substantial effect. Future research should investigate seedling

functional traits and germination traits growing in a wider range of abiotic conditions. Additionally, many of the species we tested were phylogenetically similar and, thus, we may see more of an effect of abiotic conditions on seedling trait expression in wetland plants across a more phylogenetically diverse species pool.

Quantifying life stage transitions and clonal development during early regeneration

Quantifying the probability of germination, mortality, and clonal production during early regeneration, as well as 'end-of-season' cover, can provide a mechanistic understanding of divergent recruitment outcomes across species and abiotic conditions. Here, we identified pre-germination as being the most restrictive point in recruitment, particularly for the three bulrushes, with less restrictions and less sensitivity to abiotic conditions for the non-native *P. australis* and the native *D. spicata*. From a management perspective, this underscores the importance of ameliorating barriers through extensive dormancy break (Kettenring & Galatowitsch, 2007*a*; Kettenring & Galatowitsch, 2007*b*; Kildisheva et al. 2020), targeting seed sowing timing and locations with ideal conditions for seeds and seedling (i.e., "precision restoration"; Copeland et al. 2021; Govers et al. 2022), and managing for wetland conditions that facilitate the highest probability of germination. Given that *D. spicata* exhibited similarly high germination probabilities relative to *P. australis*, this is an ideal restoration species in seed-based wetland restoration. Species exhibiting high clonal production, such as *E. palustris* in saturated soil conditions, can compensate for low germination probabilities and may provide high invasion resistance potential in the assembling plant community. More research is needed to characterize differences in transition probabilities of these species in field conditions and in the presence of competition, but this baseline mechanistic understanding provides

key insights into recruitment bottlenecks and abiotic conditions that can facilitate optimal recruitment after seed-based wetland restoration.

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APPENDICES

APPENDIX A

SUPPLEMENTS TO CHAPTER TWO

TABLE S.2.1. Nutrient application rates by experiment, treatment, and application time.

Experiment 1 - Nutricote 18-6-8 Type 100 (both app times)

Treatment	App time	Area of pool (m^2)	Volume of soil per pool (m^3)	Volume of soil per pool (gal)	App rate (g per pool)	Total N (18%; g)	NH3-N (9.7%; g)	NO3-N (8.3%; g)	P2O5 (6%; g)	K2O (8%; g)
none	1	1.76	0.16	42.24	211.2	38.016	20.4864	17.5296	12.672	16.896
none	2	1.76	0.16	42.24	211.2	38.016	20.4864	17.5296	12.672	16.896

TOTALS PER 1 m^2

Trt	App time	Total N (18%; g)	NH3-N (9.7%; g)	NO3-N (8.3%; g)	P2O5 (6%; g)	K2O (8%; g)
none	1	21.6	11.64	9.96	7.2	9.6
none	2	21.6	11.64	9.96	7.2	9.6

Experiment 2 & 3 - Nutricote 18-6-8 Type 100 (app time 1); Polyon 16-6-13 controlled release

Treatment	App time	Area of pool (m^2)	Volume of soil per pool (m^3)	Volume of soil per pool (gal)	App rate (g per pool)	Total N (g)	NH3-N (g)	NO3-N (g)	P2O5 (g)	K2O (g)
High	1	1.76	0.16	42.24	211.2	38.016	20.4864	17.5296	12.672	16.896
High	2	1.76	0.16	42.24	211.2	33.792	18.5856	15.2064	12.672	27.456
Low	1	1.76	0.16	42.24	52.8	9.504	5.1216	4.3824	3.168	4.224
Low	2	1.76	0.16	42.24	52.8	8.448	4.6464	3.8016	3.168	6.864

TOTALS PER 1 m^2

Trt	App time	Total N (g)	NH3-N (g)	NO3-N (g)	P2O5 (g)	K2O (g)
High	1	21.6	11.64	9.96	7.2	9.6
High	2	19.2	10.56	8.64	7.2	15.6
Low	1	5.4	2.91	2.49	1.8	2.4
Low	2	4.8	2.64	2.16	1.8	3.9

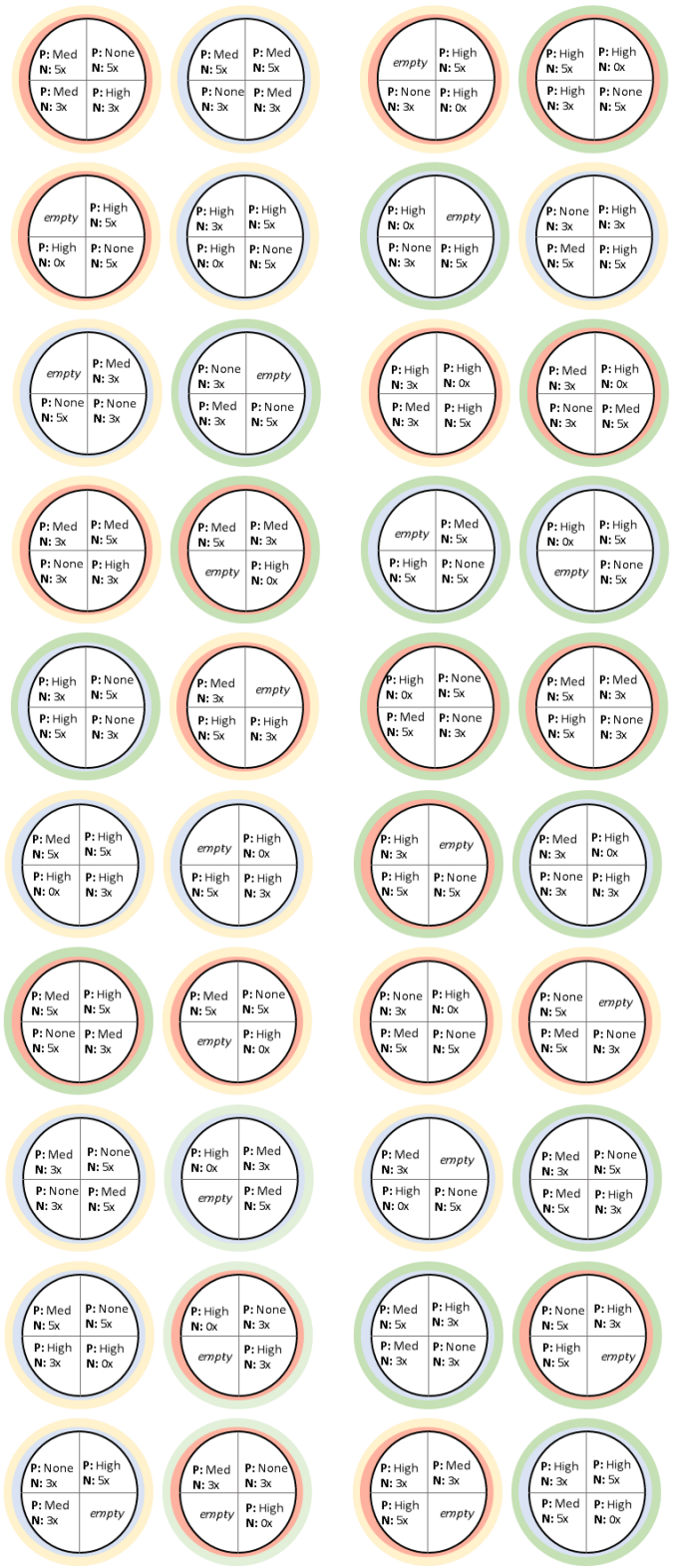
TABLE S.2.2. Percent cover classes, adapted from Brohman and Bryant's (2005) 10-percent class breaks, with an additional three classes to characterize no cover (0%), trace cover (<1%), and near complete cover (99-100%).

Class	Cover
0	0%
T	<1%
1	2-10%
2	11-20%
3	21-30%
4	31-40%
5	41-50%
6	51-60%
7	61-70%
8	71-80%
9	81-90%
10	91-99%
11	99-100%

P. australis	
Treatment	**Seeds/m^2**
Low	10
Med	500
High	5000

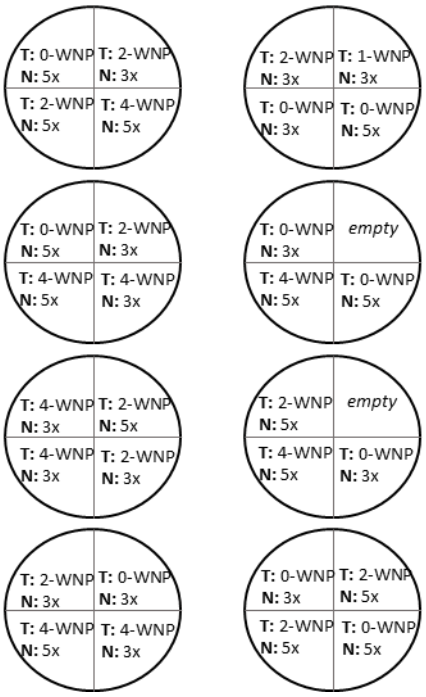
Native mix	
Treatment	**Seeds/m^2**
1x	1938
2x	3876
3x	5814
5x	9688

FIG. S.2.1. Experimental treatments, seed sowing densities, and photographs for Experiment 1 assessing the interaction between *P. australis* seed densities and native sowing densities.



P. australis	
Treatment	**Seeds/m²**
None	0
Med	500
High	5000
Native mix	
Treatment	**Seeds/m²**
0x	0
3x	5814
5x	9688
Water level	
Treatment	**Color**
Low	
High	
Nutrient level	
Treatment	**Color**
Low	
High	

FIG. S.2.2. Experimental treatments, seed sowing densities, and photographs for Experiment 2 assessing the interaction between *P. australis* seed densities, native sowing densities, water levels, and nutrient levels.



P. australis	
Treatment	**Seeds/m^2**
Med	500

Native mix	
Treatment	**Seeds/m^2**
3x	5814
5x	9688

Sowing timing	
Code	**Treatment**
4-WNP	4-week native priority
2-WNP	2-week native priority
0-WNP	0-week native priority

FIG. S.2.3. Experimental treatments, seed sowing densities, and photographs for Experiment 2 assessing the interaction between *P. australis* seed density, native sowing densities, and sowing timing.

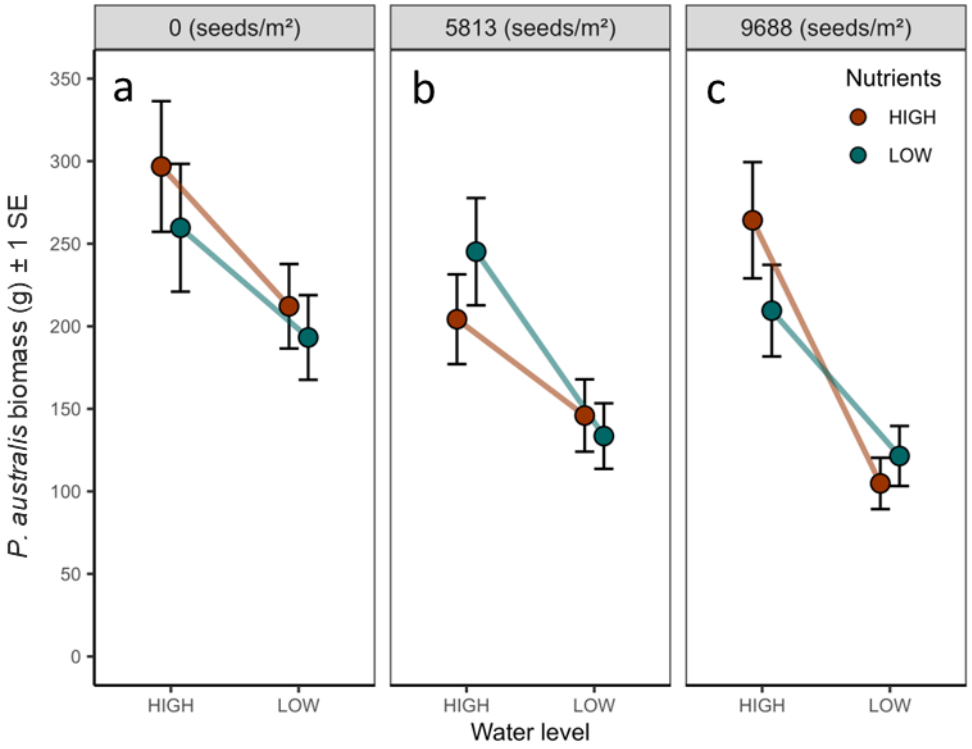


FIG. S.2.4. Biomass of the high-density *P. australis* treatment (5000 seeds m^{-2}) at three levels of native sowing density (a: 0 seeds m^{-2}; b: 5813 seeds m^{-2}; c: 9688 seeds m^{-2}) at high- and low-water levels on the x-axis and high (orange) and low (blue) nutrient levels. Nutrients was not identified as significant in our models.

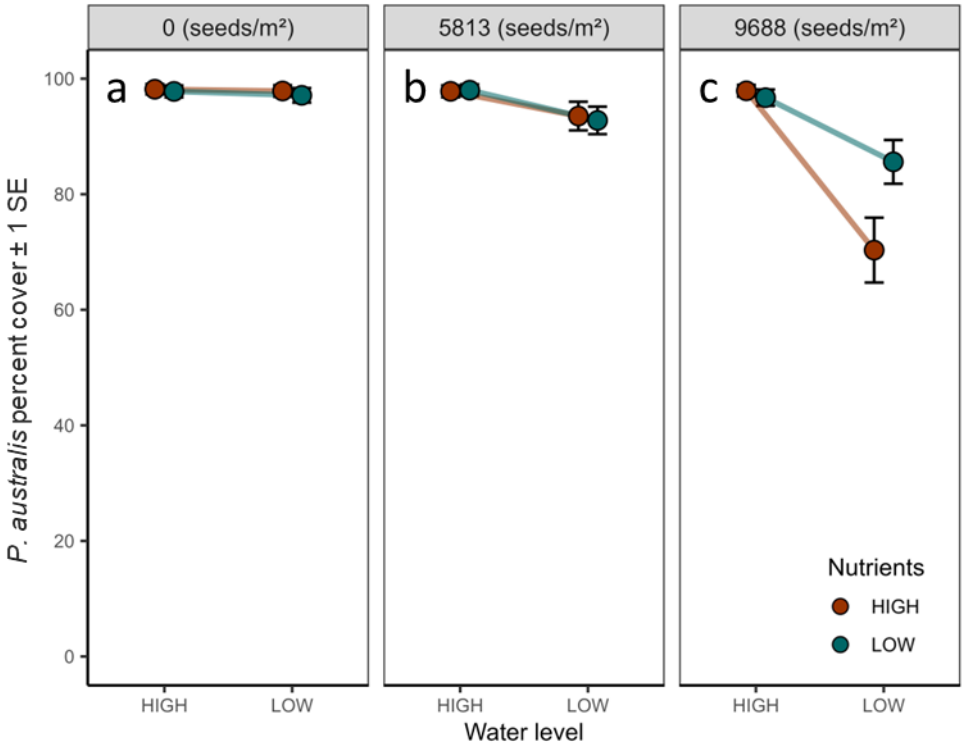


FIG. S.2.5. Percent cover of the high-density *P. australis* treatment (5000 seeds m^{-2}) at three levels of native sowing density (a: 0 seeds m^{-2}; b: 5813 seeds m^{-2}; c: 9688 seeds m^{-2}) at high- and low-water levels on the x-axis and high (orange) and low (blue) nutrient levels. Nutrients was not identified as significant in our models.

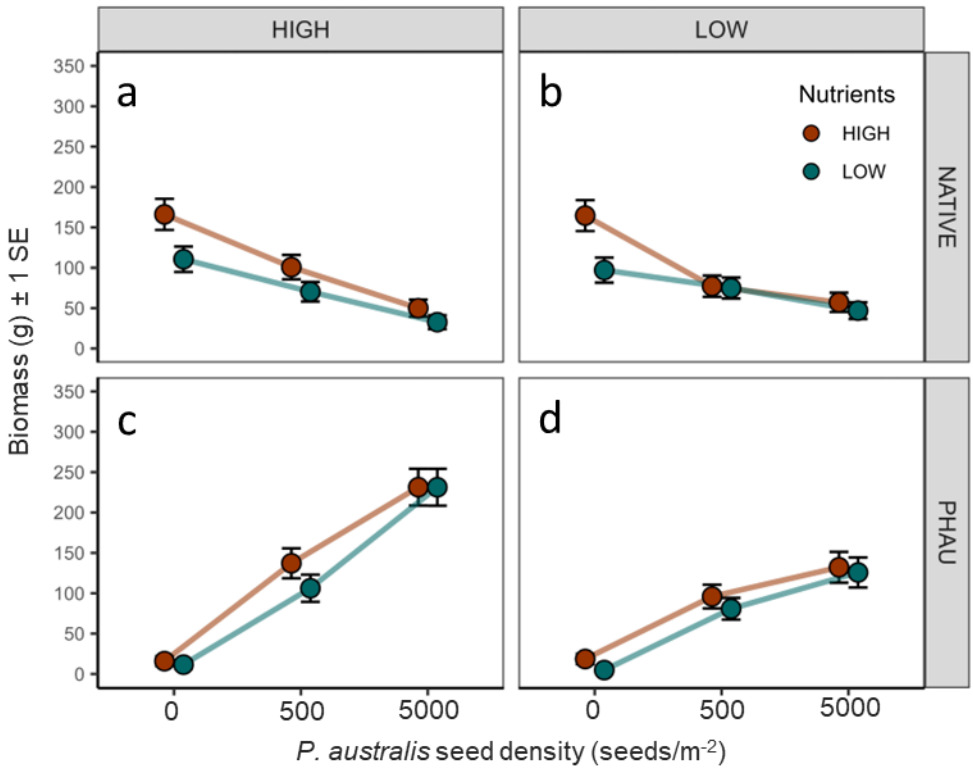


FIG. S.2.6. Biomass of (a, b) native species and (c, d) *P. australis* treatment at (a, c) high-water and (b, d) low-water levels across *P. australis* sowing densities and high nutrient (orange) and low nutrient (blue) conditions. Nutrients was not identified as significant in our models.

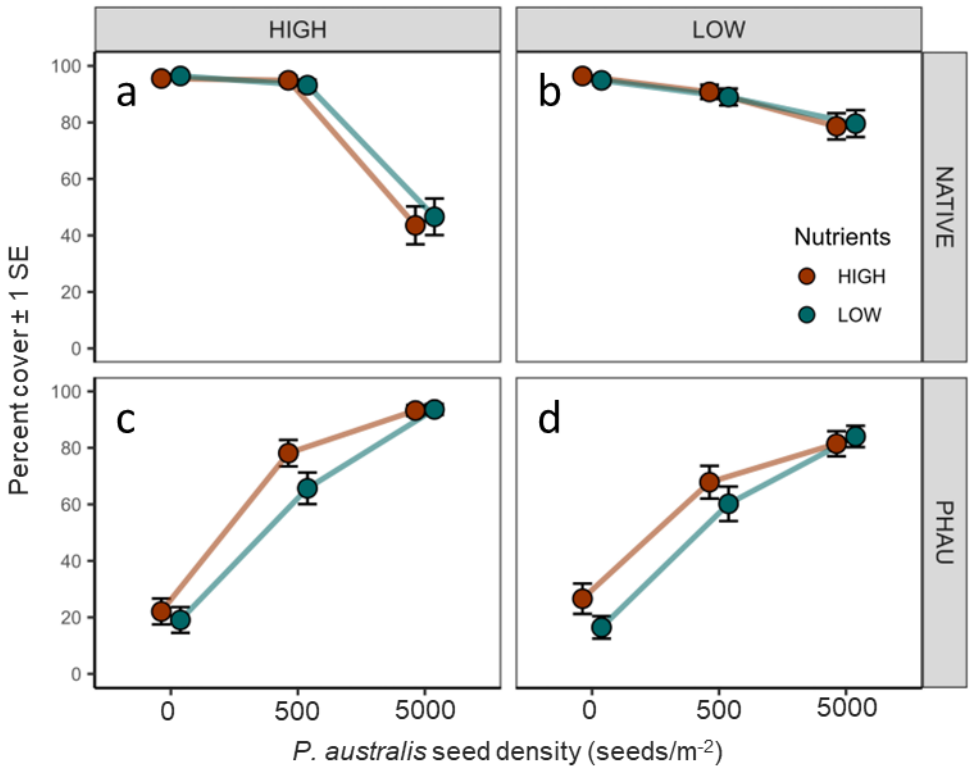


FIG. S.2.7. Percent cover of (a, b) native species and (c, d) *P. australis* treatment at (a, c) high-water and (b, d) low-water levels across *P. australis* sowing densities and high nutrient (orange) and low nutrient (blue) conditions. Nutrients was not identified as significant in our models.

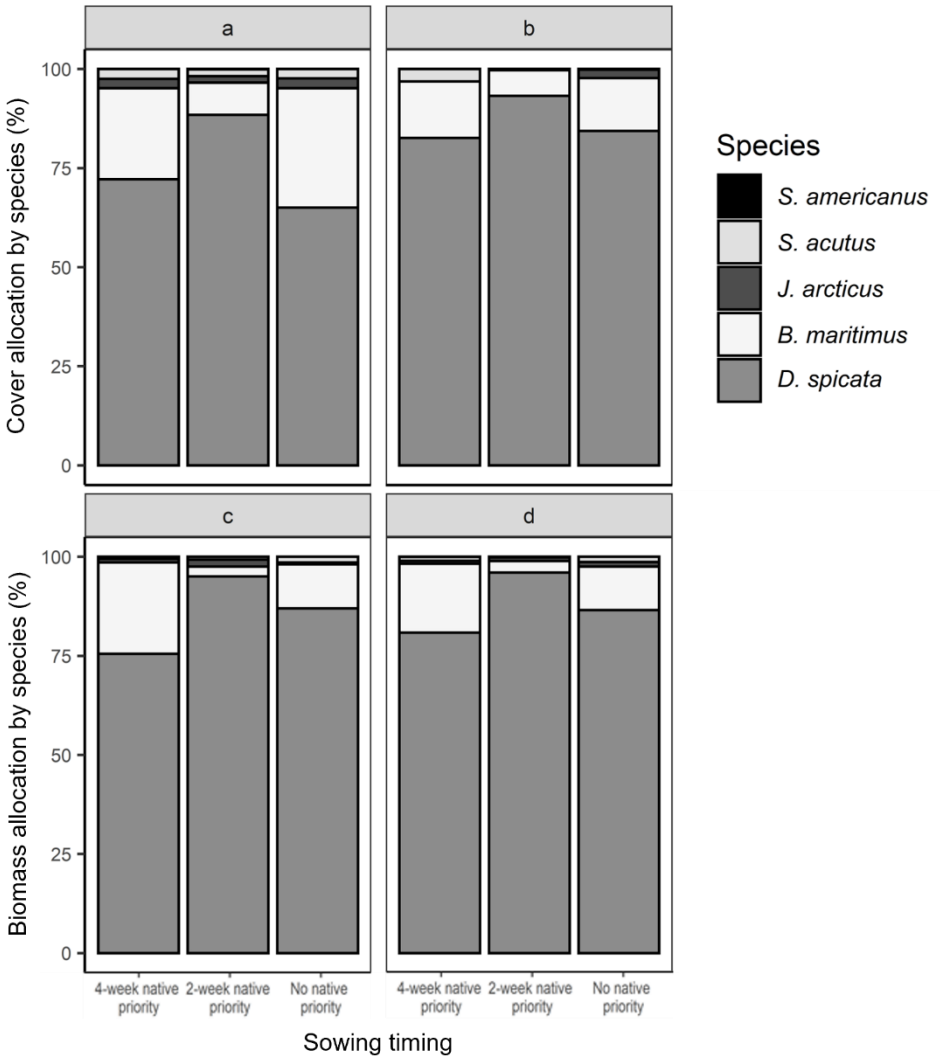


FIG. S.2.8. (Top) Percent cover and (bottom) biomass allocation by species across sowing timing at (a, c) the 3× sowing rate treatment (5813 seeds/m^2) and (b, d) the 5× sowing rate treatment (9688 seeds/m^2), scaled to 100% of the total native cover/biomass.

APPENDIX B

SUPPLEMENTS TO CHAPTER THREE

TABLE S.3.1. Collection date of seeds by species and population. Seeds were stored in paper bags at room temperature prior to seed trait measurements (conducted 02/2019 – 01/2020) and germination trails (conducted 12/2019 – 04/2020). Viability tests were conducted on each seed lot in early 2019. BOMA = *Bolboschoenus maritimus*; SCAC = *Schoenoplectus acutus*; SCAM = *S. americanus*; DISP = *Distichlis spicata*; PHAU = *Phragmites australis*; ELPA = *Eleocharis palustris*.

Species names	**Species code**	**Population code**	**Collection date**
Bolboschoenus maritimus	BOMA	PAHR	08/08/2018
Bolboschoenus maritimus	BOMA	RRVA-BW	09/08/2018
Bolboschoenus maritimus	BOMA	CLLA	08/08/2018
Bolboschoenus maritimus	BOMA	FISP	09/09/2018
Bolboschoenus maritimus	BOMA	WASP-UT	09/09/2018
Bolboschoenus maritimus	BOMA	ALK2	08/04/2017
Bolboschoenus maritimus	BOMA	FABA	09/2018
Bolboschoenus maritimus	BOMA	BERI	09/2018
Bolboschoenus maritimus	BOMA	SACR	08/2018
Bolboschoenus maritimus	BOMA	FROU	10/04/2018
Bolboschoenus maritimus	BOMA	BLHO	10/04/2018
Bolboschoenus maritimus	BOMA	BENLA	10/04/2018
Schoenoplectus acutus	SCAC	PAHR	08/08/2018
Schoenoplectus acutus	SCAC	KIWA	09/08/2018
Schoenoplectus acutus	SCAC	RRVA-BW	08/07/2018
Schoenoplectus acutus	SCAC	CLLA	08/08/2018
Schoenoplectus acutus	SCAC	FISP	08/06/2018
Schoenoplectus acutus	SCAC	PRBA	08/08/2018
Schoenoplectus acutus	SCAC	THNA	08/2018
Schoenoplectus acutus	SCAC	BERI	09/2018
Schoenoplectus acutus	SCAC	SACR	08/2018
Schoenoplectus acutus	SCAC	CUMA	08/2018
Schoenoplectus acutus	SCAC	MULA	10/03/2018
Schoenoplectus acutus	SCAC	WASP-MT	10/03/2018
Schoenoplectus acutus	SCAC	NIPI	08/13/2018
Schoenoplectus acutus	SCAC	FROU	08/14/2018
Schoenoplectus americanus	SCAM	RRVA-BW	08/07/2018
Schoenoplectus americanus	SCAM	FISP	08/06/2018
Schoenoplectus americanus	SCAM	SHAM	08/03/2017
Schoenoplectus americanus	SCAM	HACR	07/2018
Schoenoplectus americanus	SCAM	SASP	08/06/2018

TABLE S.3.1. (cont.)

Distichlis spicata	DISP	GSL	08/02/2017
Phragmites australis	PHAU	FABA	11/2018
Phragmites australis	PHAU	OGBA	11/2018
Phragmites australis	PHAU	BERI	11/2018
Eleocharis palustris	ELPA	GSL	08/2018

TABLE S.3.2. Environmental variables pulled from Climate NA (v 7.10; Wang et al. 2016; Daly et al. 2008) between 2017 – 2018. These variables were subsequently included in a principal component analysis to identify variables that explained most of the variation in the dataset. *Seasonal codes: AT: autumn Sept – Nov 2017; WT: winter Dec 2017 – Feb 2018; SP: spring Mar – May 2018; SU: summer Jun – Aug 2018.*

Environmental variable	Definition
Site variables	
Latitude	-
Longitude	-
Elevation	Elevation above sea level (m)
Seasonal variables	
TMAX_AT	Autumn mean maximum temperature (°C)
TMAX_WT	Winter mean maximum temperature (°C)
TMAX_SP	Spring mean maximum temperature (°C)
TMAX_SU	Summer mean maximum temperature (°C)
TMIN_AT	Autumn mean minimum temperature (°C)
TMIN_WT	Winter mean minimum temperature (°C)
TMIN_SP	Spring mean minimum temperature (°C)
TMIN_SU	Summer mean minimum temperature (°C)
TAVG_AT	Autumn mean temperature (°C)
TAVG_WT	Winter mean temperature (°C)
TAVG_SP	Spring mean temperature (°C)
TAVG_SU	Summer mean temperature (°C)
PPT_AT	Autumn precipitation (mm)
PPT_WT	Winter precipitation (mm)
PPT_SP	Spring precipitation (mm)
PPT_SU	Summer precipitation (mm)
DD_0_AT	Autumn degree-days below 0°C, chilling degree-days
DD_0_WT	Winter degree-days below 0°C, chilling degree-days
DD_0_SP	Spring degree-days below 0°C, chilling degree-days
DD_0_SU	Summer degree-days below 0°C, chilling degree-days
DD_5_AT	Autumn degree-days above 5°C, growing degree-days
DD_5_WT	Winter degree-days above 5°C, growing degree-days
DD_5_SP	Spring degree-days above 5°C, growing degree-days
DD_5_SU	Summer degree-days above 5°C, growing degree-days
DD_18_AT	Autumn degree-days below 18°C, heating degree-days
DD_18_WT	Winter degree-days below 18°C, heating degree-days
DD_18_SP	Spring degree-days below 18°C, heating degree-days
DD_18_SU	Summer degree-days below 18°C, heating degree-days
DD18_AT	Autumn degree-days above 18°C, cooling degree-days
DD18_WT	Winter degree-days above 18°C, cooling degree-days
DD18_SP	Spring degree-days above 18°C, cooling degree-days
DD18_SU	Summer degree-days above 18°C, cooling degree-days
CMD_AT	Autumn Hargreaves climatic moisture deficit (mm)

TABLE S.3.2. (cont.)

CMD_WT	Winter Hargreaves climatic moisture deficit (mm)
CMD_SP	Spring Hargreaves climatic moisture deficit (mm)
CMD_SU	Summer Hargreaves climatic moisture deficit (mm)
Annual variables	
MAT_2017	Mean annual temperature (°C); 2017
MAT_2018	Mean annual temperature (°C); 2018
MWMT_2017	Mean warmest month temperature (°C); 2017
MWMT_2018	Mean warmest month temperature (°C); 2018
MCMT_2017	Mean coldest month temperature (°C); 2017
MCMT_2018	Mean coldest month temperature (°C); 2018
MAP_2017	Mean annual precipitation (mm); 2017
MAP_2018	Mean annual precipitation (mm); 2018
AHM_2017	Annual heat: moisture index ((MAT + 10)/(MAP/1000)); 2017
AHM_2018	Annual heat: moisture index ((MAT + 10)/(MAP/1000)); 2018
SHM_2017	Summer heat: moisture index ((MWMT)/(MSP/1000)); 2017
SHM_2018	Summer heat: moisture index ((MWMT)/(MSP/1000)); 2018
NFFD_2017	Number of frost-free days; 2017
NFFD_2018	Number of frost-free days; 2018
FFP_2017	Frost-free period; number of days between last spring and first fall frost; 2017
FFP_2018	Frost-free period; number of days between last spring and first fall frost; 2018
bFFP_2017	Julian date on which FFP begins; 2017
bFFP_2018	Julian date on which FFP begins; 2018

TABLE S.3.3**.** Mean seed mass (mg) per individual seed (± S.E., *n* = 5) for the studied wetland species.

Species	Source	Mean (mg)	SE
BOMA	ALK2	0.0029	7.0986 -05
BOMA	BENLA	0.0031	1.4150 -04
BOMA	BERI	0.0027	2.6169 -05
BOMA	BLHO	0.0039	8.7976 -05
BOMA	CLLA	0.0025	4.5946 -05
BOMA	FABA	0.0027	3.6191 -05
BOMA	FISP	0.0027	6.7393 -05
BOMA	FROU	0.0029	1.1078 -04
BOMA	PAHR	0.0020	2.5569 -05
BOMA	RRVABW	0.0025	3.1435 -05
BOMA	SACR	0.0026	3.4339 -05
BOMA	WASPUT	0.0023	8.8055 -05
DISP	DIST	0.0006	1.6848 -05
ELPA	SHANE	0.0007	1.6752 -05
PHAU	BERI	0.0001	6.0992 -06
PHAU	FABA	0.0001	1.9391 -06
PHAU	OGBA	0.0001	4.1473 -06
SCAC	BERI	0.0012	2.1778 -05
SCAC	CLLA	0.0013	2.2874 -05
SCAC	CUMA	0.0013	4.2645 -05
SCAC	FISP	0.0012	1.6169 -05
SCAC	FROU	0.0011	5.0317 -05
SCAC	KIWA	0.0011	3.1205 -05
SCAC	MULA	0.0013	2.3416 -05
SCAC	NIPI	0.0012	3.1850 -05
SCAC	PAHR	0.0012	1.4610 -05
SCAC	PRBA	0.0011	1.8478 -05
SCAC	RRVABW	0.0012	1.4675 -05
SCAC	SACR	0.0013	3.7107 -05
SCAC	SHAC	0.0012	2.0080 -05
SCAC	THNA	0.0011	2.8823 -05
SCAC	WASPMT	0.0012	1.3121 -05
SCAM	HACR	0.0012	1.3948 -05
SCAM	RRVABW	0.0014	1.9580 -05
SCAM	SASP	0.0012	1.9775 -05
SCAM	SHAM	0.0013	1.5052 -05
SCAM	FISP	0.0013	2.8622 -05

TABLE S.3.4. Analysis of variance results from linear models analyzing the effect of source population on seed mass for (A) *B. maritimus*, (B) *Schoenoplectus acutus*, (C) *S. americanus*, and (D) the effect of species on seed mass.

Species: BOMA, Response: Seed mass, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	1.2342e-05	11	41.884	< 2.2e-16 ***
Residuals	1.2859e-06	48		

Species: SCAC, Response: Seed mass, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	4.6725e-07	13	8.9087	1.682e-09 ***
Residuals	2.2593e-07	56		

Species: SCAM, Response: Seed mass, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	1.5244e-07	4	18.916	1.421e-06 ***
Residuals	4.0294e-08	20		

Species: ALL, Response: log(Seed mass), Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Species	119.62	5	1748.2	< 2.2e-16 ***
Residuals	2.45	179		

TABLE S.3.5. Mean seed coat thickness per individual seed (± S.E., *n* = 25) for the studied wetland species.

Species	Source	Mean (µm)	SE
BOMA	ALK2	178.30	3.79
BOMA	BENLA	184.96	2.91
BOMA	BERI	168.17	3.98
BOMA	BLHO	189.59	4.80
BOMA	CLLA	171.58	2.42
BOMA	FABA	176.04	4.54
BOMA	FISP	184.59	4.12
BOMA	FROU	183.64	4.39
BOMA	PAHR	178.67	3.34
BOMA	RRVABW	177.85	2.84
BOMA	SACR	160.68	3.26
BOMA	WASPUT	166.55	3.04
DISP	DIST	72.82	2.96
ELPA	SHANE	149.55	2.62
PHAU	BERI	14.37	0.80
PHAU	FABA	14.25	0.47
PHAU	OGBA	16.65	0.63
SCAC	BERI	129.14	2.80
SCAC	CLLA	133.85	3.50
SCAC	CUMA	149.31	4.16
SCAC	FISP	134.51	2.58
SCAC	FROU	150.45	3.38
SCAC	KIWA	139.99	3.76
SCAC	MULA	135.46	2.90
SCAC	NIPI	148.68	2.63
SCAC	PAHR	118.85	2.39
SCAC	PRBA	124.50	2.41
SCAC	RRVABW	138.91	3.35
SCAC	SACR	134.77	3.51
SCAC	THNA	128.18	2.38
SCAC	WASPMT	139.06	3.26
SCAM	HACR	112.86	2.54
SCAM	RRVABW	139.34	3.53
SCAM	SASP	132.53	2.93
SCAM	SHAM	123.07	3.16
SCAM	FISP	123.76	2.87

TABLE S.3.6. Analysis of variance results from linear models analyzing the effect of source population on seed coat thickness for (A) *B. maritimus*, (B) *Schoenoplectus acutus*, (C) *S. americanus*, and (D) the effect of species on seed coat thickness.

Species: BOMA, Response: SCT, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	19805	11	5.2734	1.37e-07 ***
Residuals	97990	287		

Species: SCAC, Response: SCT, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	27974	13	8.8817	1.184e-15 ***
Residuals	80922	334		

Species: SCAM, Response: SCT, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	10161	4	11.12	1.047e-07 ***
Residuals	27412	120		

Species: ALL, Response: log(SCT), Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Species	368.52	5	3923.8	< 2.2e-16 ***
Residuals	16.66	887		

TABLE S.3.7. Seed dimension index per individual seed (± S.E., *n* = 25) for the studied wetland species. An index closer to 0 represents round seeds, while an index closer to one indicates more elongated seeds.

Species	Source	Mean	SE
BOMA	ALK2	0.24	0.004
BOMA	BENLA	0.26	0.006
BOMA	BERI	0.23	0.006
BOMA	BLHO	0.26	0.005
BOMA	CLLA	0.22	0.004
BOMA	FABA	0.24	0.004
BOMA	FISP	0.24	0.007
BOMA	FROU	0.26	0.005
BOMA	PAHR	0.22	0.005
BOMA	RRVABW	0.23	0.005
BOMA	SACR	0.24	0.003
BOMA	WASPUT	0.23	0.005
DISP	DIST	0.20	0.006
ELPA	SHANE	0.14	0.006
PHAU	BERI	0.35	0.006
PHAU	FABA	0.35	0.005
PHAU	OGBA	0.36	0.005
SCAC	BERI	0.21	0.007
SCAC	CLLA	0.20	0.004
SCAC	CUMA	0.21	0.005
SCAC	FISP	0.22	0.004
SCAC	FROU	0.22	0.007
SCAC	KIWA	0.19	0.005
SCAC	MULA	0.21	0.003
SCAC	NIPI	0.21	0.005
SCAC	PAHR	0.22	0.004
SCAC	PRBA	0.22	0.004
SCAC	RRVABW	0.21	0.004
SCAC	SACR	0.20	0.004
SCAC	THNA	0.20	0.006
SCAC	WASPMT	0.21	0.004
SCAM	HACR	0.22	0.005
SCAM	RRVABW	0.22	0.005
SCAM	SASP	0.55	0.005
SCAM	SHAM	0.23	0.005
SCAM	FISP	0.25	0.004

TABLE S.3.8. Analysis of variance results from linear models analyzing the effect of source population on the seed dimension index for (A) *B. maritimus*, (B) *Schoenoplectus acutus*, (C) *S. americanus*, and (D) the effect of species on the seed dimension index.

Species: BOMA, Response: Dim.inx, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	0.055841	11	8.0902	2.633e-12 ***
Residuals	0.180086	287		

Species: SCAC, Response: Dim.inx, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	0.025472	13	3.3806	6.653e-05 ***
Residuals	0.193579	334		

Species: SCAM, Response: Dim.inx, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	0.013982	4	5.4888	0.0004303 ***
Residuals	0.076423	120		

Species: ALL, Response: Dim.inx, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Species	1.4206	5	394.15	< 2.2e-16 ***
Residuals	0.6394	887		

TABLE S.3.9. Floating percentage (± S.E., n = 3) for the studied wetland species. The floating percentage indicates the number of days after which a set percentage of the seeds had sunk.

		FP 10%		FP 25%		FP 50%		FP 75%		FP 90%	
Species	**Source**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**
BOMA	ALK2	41.98	0.60	61.13	1.05	89.04	1.84	129.70	3.18	188.95	5.40
BOMA	BENLA	31.55	0.78	47.80	0.79	72.46	0.96	109.86	1.97	166.60	4.47
BOMA	BERI	35.84	2.70	52.68	3.35	77.45	3.99	113.91	4.50	167.58	4.57
BOMA	BLHO	38.31	1.61	58.38	2.26	89.04	3.89	135.88	7.47	207.51	14.47
BOMA	CLLA	38.16	5.55	56.96	6.98	85.13	8.58	127.40	10.35	190.87	12.62
BOMA	FABA	41.38	1.74	61.85	2.65	92.47	4.23	138.28	6.96	206.82	11.61
BOMA	FISP	52.78	4.77	76.94	6.45	112.17	8.66	163.54	11.56	238.46	15.29
BOMA	FROU	38.13	2.80	58.03	3.52	88.35	4.32	134.58	5.29	205.09	6.94
BOMA	PAHR	38.55	1.78	56.62	1.85	83.20	1.72	122.31	1.80	179.89	3.84
BOMA	RRVABW	37.17	3.58	55.38	4.68	82.54	6.05	123.06	7.81	183.55	10.17
BOMA	SACR	39.04	3.03	57.23	3.40	83.96	3.63	123.30	4.06	181.23	6.41
BOMA	WASPUT	43.07	1.93	63.84	2.74	94.65	4.13	140.36	6.61	208.21	10.98
DISP	DIST	22.77	4.14	38.17	4.79	64.42	4.96	109.41	5.95	186.96	14.39
ELPA	SHANE	9.91	0.34	20.00	0.36	40.38	0.19	81.58	1.34	164.91	5.45
PHAU	BERI	11.46	0.44	23.02	0.35	46.30	0.60	93.21	3.41	187.89	11.55
PHAU	FABA	13.73	0.49	25.40	0.96	47.02	1.91	87.05	3.86	161.15	7.83
PHAU	OGBA	10.86	1.19	21.44	2.14	42.34	3.84	83.64	6.81	165.26	12.01
SCAC	BERI	13.04	0.84	25.09	0.96	48.36	0.77	93.36	2.16	180.50	8.70
SCAC	CLLA	11.02	1.09	21.67	2.11	42.61	4.08	83.79	7.94	164.77	15.53
SCAC	CUMA	13.87	3.11	25.94	4.73	48.67	6.91	91.61	9.58	173.03	12.78
SCAC	FISP	22.00	9.42	36.25	11.59	61.16	13.09	105.68	13.69	186.83	21.05
SCAC	FROU	20.29	2.03	34.07	3.36	57.22	5.61	96.13	9.44	161.51	16.00
SCAC	KIWA	15.05	0.37	27.23	0.81	49.33	2.20	89.44	5.64	162.28	13.42
SCAC	MULA	17.03	3.14	31.68	4.70	59.13	6.67	110.82	8.96	208.51	12.60
SCAC	NIPI	18.65	2.03	32.31	2.97	56.02	4.20	97.18	5.75	168.71	7.66
SCAC	PAHR	20.56	3.36	35.45	4.40	61.41	5.15	106.88	5.35	186.96	9.50
SCAC	PRBA	17.57	3.57	31.10	5.19	55.25	7.27	98.53	9.82	176.39	13.40
SCAC	RRVABW	11.97	0.86	23.80	1.42	47.36	2.37	94.28	4.24	187.77	8.58
SCAC	SACR	15.18	1.77	28.32	2.55	52.93	3.60	99.14	5.51	186.07	10.82
SCAC	SHAC	11.84	1.54	22.91	2.37	44.40	3.44	86.20	4.68	167.68	6.69
SCAC	WASPMT	18.24	2.43	32.57	2.63	58.53	1.70	105.88	3.75	192.78	17.45
SCAM	HACR	11.47	1.14	22.45	1.81	44.06	2.77	86.67	4.16	170.91	6.67
SCAM	RRVABW	18.20	2.92	31.46	4.49	54.43	6.79	94.27	10.10	163.40	14.82
SCAM	SASP	11.57	1.81	23.28	3.39	46.88	6.41	94.49	12.34	190.66	24.34
SCAM	SHAM	10.88	0.52	21.85	0.96	43.86	1.74	88.06	3.14	176.78	5.59

TABLE S.3.10. Analysis of variance results from linear models analyzing the effect of source population on seed buoyancy for (A) *B. maritimus*, (B) *Schoenoplectus acutus*, (C) *S. americanus*, and (D) the effect of species on seed buoyancy.

Species: BOMA, Response: Buoy, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	3241.7	11	4.363	0.0008731 ***
Residuals	1823.7	27		

Species: SCAC, Response: Buoy, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	1514.6	13	1.2146	0.3202
Residuals	2685.8	28		

Species: SCAM, Response: Buoy, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Source	237.04	3	1.0408	0.4162
Residuals	759.16	10		

Species: ALL, Response: Buoy, Type II ANOVA				
	Sum Sq	DF	F value	Pr (>F)
Species	35838	5	70.586	< 2.2e-16 ***
Residuals	10561	104		

TABLE S.3.11. Variable loadings on Principal Components Axes for interspecific assessment of seed traits. The strongest positive loading and the strongest negative loading are bolded to aid in interpretation of the tradeoffs represented among each axis.

Variable	PC Axis 1	PC Axis 2
Seed mass	**-0.514**	0.221
Seed coat thickness (SCT)	-0.510	**-0.270**
Seed dimension index	0.223	**0.855**
Seed buoyancy	-0.450	0.372
Dormancy depth	**0.476**	-0.097
Variance explained (%)	63.37	21.86
Cumulative variance (%)	-	85.23

TABLE S.3.12. Variable loadings on Principal Components Axes for (top) *B. maritimus* seed traits and (bottom) *S. acutus* seed traits.

Variable	PC Axis 1	PC Axis 2
Seed mass	**-0.611**	0.128
Seed coat thickness (SCT)	0.275	0.600
Seed dimension index	-0.483	0.109
Seed buoyancy	0.079	**0.766**
Dormancy depth	**0.558**	**-0.168**
Variance explained (%)	38.40	23.14
Cumulative variance (%)	-	61.54

Variable	PC Axis 1	PC Axis 2
Seed mass	**0.593**	-0.195
Seed coat thickness (SCT)	0.327	**-0.721**
Seed dimension index	**-0.498**	-0.259
Seed buoyancy	-0.309	0.138
Dormancy depth	0.444	**0.597**
Variance explained (%)	35.32	22.78
Cumulative variance (%)	-	58.09

TABLE S.3.13. Variable loadings on principal component axes for collection-site environmental variables. Bolded values represent the variable that loads most strongly on each of the first three principal components.

Variable	PC Axis 1	PC Axis 2	PC Axis 3
Latitude	-0.148	-0.052	-0.181
Longitude	-0.079	-0.214	0.063
Elevation	0.004	0.075	**0.443**
Autumn mean maximum temperature (°C)	0.153	0.072	-0.041
Winter mean maximum temperature (°C)	0.152	0.082	-0.039
Spring mean maximum temperature (°C)	0.156	0.071	-0.006
Summer mean maximum temperature (°C)	0.156	0.030	0.117
Autumn mean minimum temperature (°C)	0.129	-0.173	-0.086
Winter mean minimum temperature (°C)	0.138	-0.127	0.022
Spring mean minimum temperature (°C)	0.143	-0.134	0.037
Summer mean minimum temperature (°C)	0.145	-0.112	0.066
Autumn mean temperature (°C)	0.158	-0.031	-0.064
Winter mean temperature (°C)	0.157	-0.010	-0.011
Spring mean temperature (°C)	0.160	-0.023	0.013
Summer mean temperature (°C)	0.156	-0.037	0.095
Autumn precipitation (mm)	-0.069	-0.273	0.025
Winter precipitation (mm)	-0.045	-0.279	-0.094
Spring precipitation (mm)	-0.058	-0.279	0.058
Summer precipitation (mm)	-0.127	0.023	-0.296
Autumn degree-days below 0°C	-0.145	0.060	-0.180
Winter degree-days below 0°C	-0.150	0.033	-0.132
Spring degree-days below 0°C	-0.138	0.043	-0.208
Autumn degree-days above 5°C	0.155	-0.022	-0.125
Winter degree-days above 5°C	0.132	0.035	-0.281
Spring degree-days above 5°C	0.160	-0.014	-0.064
Summer degree-days above 5°C	0.156	-0.037	0.097
Autumn degree-days below 18°C	-0.158	0.035	0.028
Winter degree-days below 18°C	-0.157	0.009	0.019
Spring degree-days below 18°C	-0.159	0.026	-0.048
Summer degree-days below 18°C	-0.138	0.053	-0.206
Autumn degree-days above 18°C	0.141	-0.007	-0.242
Spring degree-days above 18°C	0.137	-0.004	-0.255
Summer degree-days above 18°C	0.158	-0.032	0.063
Autumn Climate Moisture Deficit	0.125	0.193	-0.008
Winter Climate Moisture Deficit	0.106	0.209	-0.129
Spring Climate Moisture Deficit	0.120	0.203	-0.014
Summer Climate Moisture Deficit	0.146	0.047	0.202
Mean annual temperature (°C); 2017	0.160	-0.015	-0.032
Mean annual temperature (°C); 2018	**0.161**	-0.029	0.004
Mean warmest month temperature (°C); 2017	0.150	-0.066	0.047
Mean warmest month temperature (°C); 2018	0.151	-0.056	0.137
Mean coldest month temperature (°C); 2017	0.146	0.024	-0.148
Mean coldest month temperature (°C); 2018	0.154	-0.011	0.031
Mean annual precipitation (mm); 2017	-0.036	**-0.294**	0.047

TABLE S.3.13. (cont.)

Mean annual precipitation (mm); 2018	-0.067	-0.271	-0.027
Annual heat: moisture index; 2017	0.100	0.224	-0.148
Annual heat: moisture index; 2018	0.112	0.203	-0.122
Summer heat: moisture index; 2017	0.117	0.187	-0.006
Summer heat: moisture index; 2018	0.136	0.087	0.125
Number of frost-free days; 2017	0.138	-0.154	-0.069
Number of frost-free days; 2018	0.139	-0.150	-0.040
Beginning of frost-free period; 2017	-0.112	0.189	0.178
Beginning of frost-free period; 2018	-0.113	0.189	0.151
Frost-free period; 2017	0.122	-0.174	-0.164
Frost-free period; 2018	0.135	-0.165	-0.041
Variance explained (%)	**69.58**	**19.12**	**6.29**
Cumulative variance (%)	**-**	**88.70**	**94.99**

TABLE S.3.14. Pearson's correlation coefficients for the single abiotic variable that most strongly loaded on the first three principal components.

	MAT_2018	MAP_2017	Elevation
MAT_2018	-	-0.13	-0.03
MAP_2017	-0.13	-	-0.12
Elevation	-0.03	-0.12	-

TABLE S.3.15. Pearson's correlation coefficients for the top five environmental variables that loaded on to the first three principal components.

PC1	MAT_2018	Tave_sp	MAT_2017	DD5_sp	DD_18_sp
MAT_2018	-	0.99	0.99	0.99	-0.99
Tave_sp	0.99	-	0.98	0.98	-1.00
MAT_2017	0.99	0.98	-	0.99	-0.97
DD5_sp	0.99	0.98	0.99	-	-0.97
DD_18_sp	-0.99	-1.00	-0.97	-0.97	-
PC2	MAP_2017	PPT_sp	PPT_wt	PPT_at	MAP_2018
MAP_2017	-	0.96	0.91	0.97	0.94
PPT_sp	0.96	-	0.90	0.95	-1.00
PPT_wt	0.91	0.90	-	0.96	-0.97
PPT_at	0.97	0.95	0.91	-	-0.97
MAP_2018	0.94	0.96	0.96	0.95	-
PC3	Elevation	PPT_sm	DD5_wt	DD18_sp	DD18_at
Elevation	-	-0.37	-0.31	-0.37	-0.32
PPT_sm	-0.37	-	0.90	-0.43	-0.45
DD5_wt	-0.31	-0.33	-	0.97	0.98
DD18_sp	-0.37	-0.43	0.97	-	0.99
DD18_at	-0.32	-0.45	0.98	0.99	-

TABLE S.3.16. Results of robust linear regressions assessing the effect of collection site-level (top) 2018 mean annual temperature, (middle) 2017 mean annual precipitation, and (bottom) elevation on seed mass across *B. maritimus* populations.

Species: BOMA, Response: log(seed mass), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-5.73978	0.27575	-20.815	1.45e-09 ***
MAT_2018	-0.02033	0.02252	-0.903	0.388

Robust residual standard error 0.1071
Adjusted R-squared: 0.1551
Robustness weights:
One weight is ~= 1. The remaining 11 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.2510	0.9037	0.9592	0.8859	0.9894	0.9920

Species: BOMA, Response: log(seed mass), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-6.034818	0.0899134	-67.118	1.31e-14 ***
MAP_2017	0.000198	0.0002294	0.861	0.409

Robust residual standard error 0.1049
Adjusted R-squared: -0.0186
Robustness weights:
One weight is ~= 1. The remaining 11 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.05384	0.84800	0.96580	0.86090	0.99570	0.99900

Species: BOMA, Response: log(seed mass), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-6.232872	0.3202921	-19.460	2.8e-09 ***
Elevation	0.0002041	0.0002454	0.832	0.425

Robust residual standard error 0.1049
Adjusted R-squared: 0.0008145
Robustness weights:
Observation 9 is an outlier with |weight| = 0 (< 0.0083);
The remaining 11 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.8459	0.9064	0.9807	0.9488	0.9859	0.9982

TABLE S.3.17. Results of robust linear regressions assessing the effect of collection site-level (top) 2018 mean annual temperature, (middle) 2017 mean annual precipitation, and (bottom) elevation on seed coat thickness across *B. maritimus* populations.

Species: BOMA, Response: log(SCT), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	5.188146	0.174639	29.708	4.36e-11 ***
MAT_2018	-0.004526	0.014387	-0.315	0.76

Robust residual standard error 0.1914
Adjusted R-squared: -0.09223
Robustness weights:
One weight is ~= 1. The remaining 11 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.8370	0.9290	0.9609	0.9510	0.9828	0.9967

Species: BOMA, Response: log(SCT), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	5.169e+00	9.835e-02	52.560	1.5e-13 ***
MAP_2017	-9.738e-05	3.836e-04	-0.254	0.805

Robust residual standard error 0.1677
Adjusted R-squared: -0.09266
Robustness weights:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.8162	0.8932	0.9490	0.9366	0.9836	0.9988

Species: BOMA, Response: log(SCT), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	5.5384205	0.2377414	23.296	4.81e-10 ***
Elevation	-0.000320	0.0001884	-1.696	0.121

Robust residual standard error 0.1813
Adjusted R-squared: 0.003708
Robustness weights:
One weight is ~= 1. The remaining 11 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.8370	0.9270	0.9537	0.9464	0.9814	0.9944

TABLE S.3.18. Results of robust linear regressions assessing the effect of collection site-level (top) 2018 mean annual temperature, (middle) 2017 mean annual precipitation, and (bottom) elevation on seed dimension index across *B. maritimus* populations.

Species: BOMA, Response: log(seed dim), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-1.409380	0.024370	-57.832	5.8e-14 ***
MAT_2018	-0.001707	0.002252	-0.758	0.466

Robust residual standard error 0.04409
Adjusted R-squared: -0.08478
Robustness weights:
One weight is ~= 1. The remaining 11 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.2197	0.8859	0.9731	0.8740	0.9912	0.9986

Species: BOMA, Response: log(seed dim), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-1.45e+00	5.655e-02	-25.7	1.83e-10 ***
MAP_2017	8.342e-05	2.088e-04	0.4	0.698

Robust residual standard error 0.03725
Adjusted R-squared: -0.03071
Robustness weights:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.1470	0.8538	0.9746	0.8592	0.9901	0.9988

Species: BOMA, Response: log(seed dim), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-1.40e+00	3.699e-02	-37.744	4.06e-12 ***
Elevation	-2.57e-05	3.550e-05	-0.723	0.486

Robust residual standard error 0.0439
Adjusted R-squared: -0.09087
Robustness weights:
2 weights are ~= 1. The remaining 10 ones are summarized as:

1	2	3	4	6	7	8	9	11	12
0.2032	0.8733	0.7346	0.9530	0.8846	0.9887	0.9851	0.9977	0.9797	0.9917

TABLE S.3.19. Results of robust linear regressions assessing the effect of collection site-level (top) 2018 mean annual temperature, (middle) 2017 mean annual precipitation, and (bottom) elevation on seed buoyancy across *B. maritimus* populations.

Species: BOMA, Response: log(seed buo), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	4.406974	0.127811	34.481	9.97e-12***
MAT_2018	0.004658	0.011705	0.398	0.699

Robust residual standard error 0.09093
Adjusted R-squared: -0.07803
Robustness weights:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.4040	0.9066	0.9653	0.8973	0.9816	0.9975

Species: BOMA, Response: log(seed buo), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	4.4116088	0.0262731	167.914	<2e-16***
MAP_2017	0.0001295	0.0002093	0.619	0.55

Robust residual standard error 0.06054
Adjusted R-squared: -0.03007
Robustness weights:
Observation 3 is an outlier with |weight| = 0 (< 0.0083);
2 weights are ~= 1. The remaining 9 ones are summarized as:

1	2	4	6	7	8	9	10	12
0.9556	0.9480	0.9695	0.6881	0.3727	0.9823	0.9833	0.9923	0.8023

Species: BOMA, Response: log(seed buo), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	4.2928222	0.1865625	23.010	5.43e-10 ***
Elevation	0.0001329	0.0001498	0.888	0.396

Robust residual standard error 0.09678
Adjusted R-squared: -0.05483
Robustness weights:
2 weights are ~= 1. The remaining 10 ones are summarized as:

1	2	3	6	7	8	9	10	11	12
0.9890	0.9591	0.4719	0.8808	0.7775	0.9874	0.9671	0.9519	0.9892	0.9453

TABLE S.3.20. Results of robust linear regressions assessing the effect of collection site-level (top) 2018 mean annual temperature, (middle) 2017 mean annual precipitation, and (bottom) elevation on depth of dormancy across *B. maritimus* populations.

Species: BOMA, Response: log(dod), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-3.54343	0.69958	-5.065	0.000676 ***
MAT_2018	0.15377	0.07031	2.187	0.056534 .

Robust residual standard error 0.272
Adjusted R-squared: 0.6194
Robustness weights:
One weight is ~= 1. The remaining 10 ones are:

1	2	3	4	5	6	7	8	9	12
0.9665	0.8937	0.9908	0.9983	0.6846	0.9762	0.9299	0.9620	0.7988	0.3391

Species: BOMA, Response: log(dod), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-1.588921	2.611396	-0.608	0.558
MAP_2017	-0.001175	0.006874	-0.171	0.868

Robust residual standard error 0.3952
Adjusted R-squared: -0.01635
Robustness weights:
3 weights are ~= 1. The remaining 8 ones are:

1	2	4	5	6	7	8	12
0.9168	0.9433	0.9786	0.2787	0.9925	0.7055	0.9073	0.8561

Species: BOMA, Response: log(dod), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-3.985431	1.391934	-2.863	0.0187 *
Elevation	0.001553	0.001053	1.475	0.1742

Robust residual standard error 0.2507
Adjusted R-squared: 0.2159
Robustness weights:
Observation 5 is an outlier with |weight| = 0 (< 0.0091);
One weight is ~= 1. The remaining 9 ones are:

1	2	3	4	6	7	8	9	12
0.9298	0.9831	0.9567	0.9990	0.9986	0.6810	0.9549	0.8676	0.4670

TABLE S.3.21. Results of robust linear regressions assessing the effect of collection site-level (top) 2018 mean annual temperature, (middle) 2017 mean annual precipitation, and (bottom) elevation on seed mass across *S. acutus* populations.

Species: SCAC, Response: log(seed mass), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-6.666823	0.102512	-65.035	<2e-16 ***
MAT_2018	-0.005268	0.008622	-0.611	0.553

Robust residual standard error 0.07646
Adjusted R-squared: -0.04933
Robustness weights:
One weight is ~= 1. The remaining 13 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.4770	0.8956	0.9514	0.8958	0.9934	0.9980

Species: SCAC, Response: log(seed mass), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-6.759361	0.0442142	-152.878	< 2e-16 ***
MAP_2017	0.0001115	0.0001735	0.643	0.533

Robust residual standard error 0.08151
Adjusted R-squared: -0.04011
Robustness weights:
One weight is ~= 1. The remaining 13 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.6139	0.8429	0.9735	0.9103	0.9898	0.9985

Species: SCAC, Response: log(seed mass), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-6.80e+00	1.539e-01	-44.165	1.18e-14 ***
Elevation	5.473e-05	1.125e-04	0.487	0.635

Robust residual standard error 0.09328
Adjusted R-squared: -0.06995
Robustness weights:
3 weights are ~= 1. The remaining 11 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.7321	0.8817	0.9449	0.9160	0.9734	0.9933

TABLE S.3.22. Results of robust linear regressions assessing the effect of collection site-level (top) 2018 mean annual temperature, (middle) 2017 mean annual precipitation, and (bottom) elevation on seed coat thickness across *S. acutus* populations.

Species: SCAC, Response: log(SCT), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	5.105034	0.102525	49.793	2.82e-15 ***
MAT_2018	-0.015926	0.009816	-1.622	0.131

Robust residual standard error 0.1255
Adjusted R-squared: 0.05234
Robustness weights:
2 weights are ~= 1. The remaining 12 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.7271	0.8969	0.9451	0.9223	0.9725	0.9930

Species: SCAC, Response: log(SCT), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	4.8688502	0.0899939	54.102	1.05e-15 ***
MAP_2017	0.0002073	0.0002198	0.943	0.364

Robust residual standard error 0.1335
Adjusted R-squared: -0.01587
Robustness weights:
One weight is ~= 1. The remaining 13 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.7712	0.8749	0.9625	0.9312	0.9827	0.9960

Species: SCAC, Response: log(SCT), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	4.9144230	0.4327422	11.356	8.92e-08 ***
Elevation	0.0000200	0.0003126	0.064	0.95

Robust residual standard error 0.1214
Adjusted R-squared: -0.08251
Robustness weights:
One weight is ~= 1. The remaining 13 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.6454	0.8505	0.9799	0.9115	0.9871	0.9967

TABLE S.3.23. Results of robust linear regressions assessing the effect of collection site-level (top) 2018 mean annual temperature, (middle) 2017 mean annual precipitation, and (bottom) elevation on seed dimension index across *S. acutus* populations.

Species: SCAC, Response: log(seed dim), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-1.562200	0.040928	-38.170	6.73e-14 ***
MAT_2018	-0.002289	0.004617	-0.496	0.629

Robust residual standard error 0.1017
Adjusted R-squared: -0.07921
Robustness weights:
2 observations c(6,12) are outliers with |weight| = 0 (< 0.0071);
The remaining 12 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.5867	0.8866	0.9914	0.9072	0.9982	0.9989

Species: SCAC, Response: log(seed dim), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-1.677703	0.1245412	-13.47	1.32e-08 ***
MAP_2017	0.0002691	0.0002991	0.90	0.386

Robust residual standard error 0.09985
Adjusted R-squared: 0.08591
Robustness weights:
2 observations c(6,12) are outliers with |weight| = 0 (< 0.0071);
The remaining 12 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.7001	0.9076	0.9668	0.9207	0.9751	0.9956

Species: SCAC, Response: log(seed dim), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-1.55e+00	4.116e-01	-3.769	0.00267 **
Elevation	-2.44e-05	3.519e-04	-0.069	0.94594

Robust residual standard error 0.08432
Adjusted R-squared: -0.08104
Robustness weights:
2 observations c(6,12) are outliers with |weight| = 0 (< 0.0071);
One weight is ~= 1. The remaining 11 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.4389	0.7674	0.9800	0.8593	0.9926	0.9981

TABLE S.3.24. Results of robust linear regressions assessing the effect of collection site-level (top) 2018 mean annual temperature, (middle) 2017 mean annual precipitation, and (bottom) elevation on seed buoyancy across *S. acutus* populations.

Species: SCAC, Response: log(seed buo), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	4.23164	0.34527	12.256	9.36e-08 ***
MAT_2018	-0.02755	0.04214	-0.654	0.527

Robust residual standard error 0.07561
Adjusted R-squared: 0.308
Robustness weights:
One weight is ~= 1. The remaining 12 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.008324	0.741300	0.969200	0.800400	0.991600	0.998900

Species: SCAC, Response: log(seed buo), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	4.1237641	0.4510535	9.143	1.8e-06 ***
MAP_2017	-0.000329	0.0009624	-0.342	0.739

Robust residual standard error 0.06814
Adjusted R-squared: 0.1738
Robustness weights:
One weight is ~= 1. The remaining 12 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.008097	0.730700	0.943900	0.774400	0.966800	0.978700

Species: SCAC, Response: log(seed buo), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	4.2749796	0.1418255	30.143	6.33e-12 ***
Elevation	-0.000226	0.0001182	-1.917	0.0816 .

Robust residual standard error 0.1359
Adjusted R-squared: 0.04389
Robustness weights:
One weight is ~= 1. The remaining 12 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.7997	0.9178	0.9612	0.9466	0.9904	0.9978

TABLE S.3.25. Results of robust linear regressions assessing the effect of collection site-level (top) 2018 mean annual temperature, (middle) 2017 mean annual precipitation, and (bottom) elevation on depth of dormancy across *S. acutus* populations.

Species: SCAC, Response: log(dod), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-0.50156	0.11041	-4.543	0.00084 ***
MAT_2018	0.01060	0.01038	1.021	0.32911

Robust residual standard error 0.2139
Adjusted R-squared: -0.04786
Robustness weights:
2 observations c(6,9) are outliers with |weight| <= 0.0047 (< 0.0077);
The remaining 11 ones are summarized as:

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
0.9081	0.9576	0.9730	0.9693	0.9904	0.9985

Species: SCAC, Response: log(dod), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	-0.203722	0.1115544	-1.826	0.0951 .
MAP_2017	-0.000519	0.0002845	-1.826	0.0950 .

Robust residual standard error 0.1156
Adjusted R-squared: 0.3078
Robustness weights:
2 observations c(6,9) are outliers with |weight| = 0 (< 0.0077);
One weight is ~= 1. The remaining 10 ones are:

1	2	3	4	5	9	12	13	14	15
0.9865	0.9465	0.7766	0.9961	0.9978	0.9782	0.9490	0.9640	0.9906	0.5922

Species: SCAC, Response: log(dod), Robust regression

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	0.2322162	0.1865192	1.245	0.23900
Elevation	-0.000459	0.0001340	-3.429	0.00563 **

Robust residual standard error 0.1757
Adjusted R-squared: 0.1413
Robustness weights:
2 observations c(6,9) are outliers with |weight| <= 0.0047 (< 0.0077);
One weight is ~= 1. The remaining 10 ones are:

1	2	3	4	5	8	9	12	14	15
0.9891	0.8487	0.9697	0.995	0.9844	0.9830	0.9977	0.9004	0.9400	0.9869

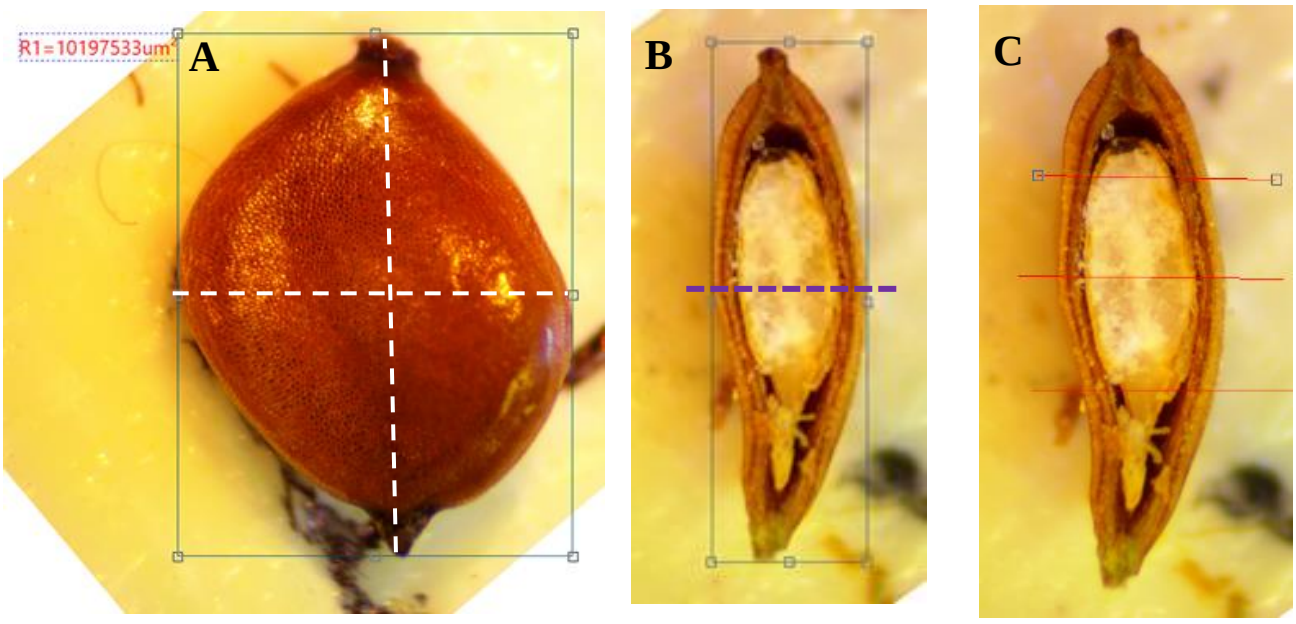


FIG S.3.1. Example images depicting *B. maritimus* seeds during measurements of seed coat thickness and seed dimensions. Measurements were taken using a 2×–225× zoom stereomicroscope (ZM-1TW3-FOD-10M; AmScope) equipped with a 10 MP digital camera (MU1000; AmScope). One seed view was (A) top-down of the seed to measure dimensions as the length (µm) and width (µm) of the longest point on each vertically aligned seed image (white dashed lines). Then, seeds were cut in half and cross-sectional images were used to calculate (B) the seed depth as the height (µm) of the cross section (purple dashed line). The cross-sectional image was also used to calculate (C) seed coat thickness, in which six equidistant lines were placed across the seed and the areas where lines cross the seed coat were identified, measured, and averaged to get a single seed coat thickness value (µm).

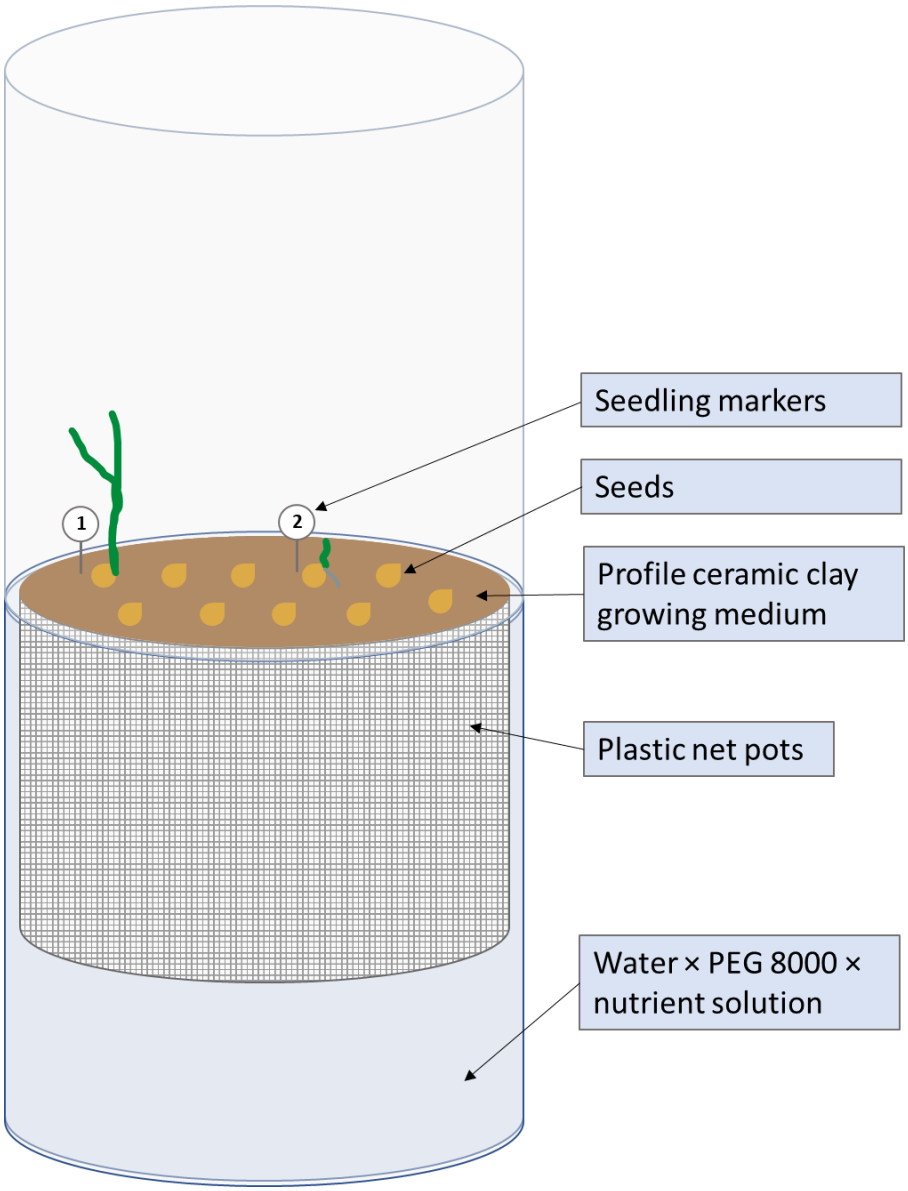


FIG S.3.2. Constructed growing containers to measure germination and seedling growth.

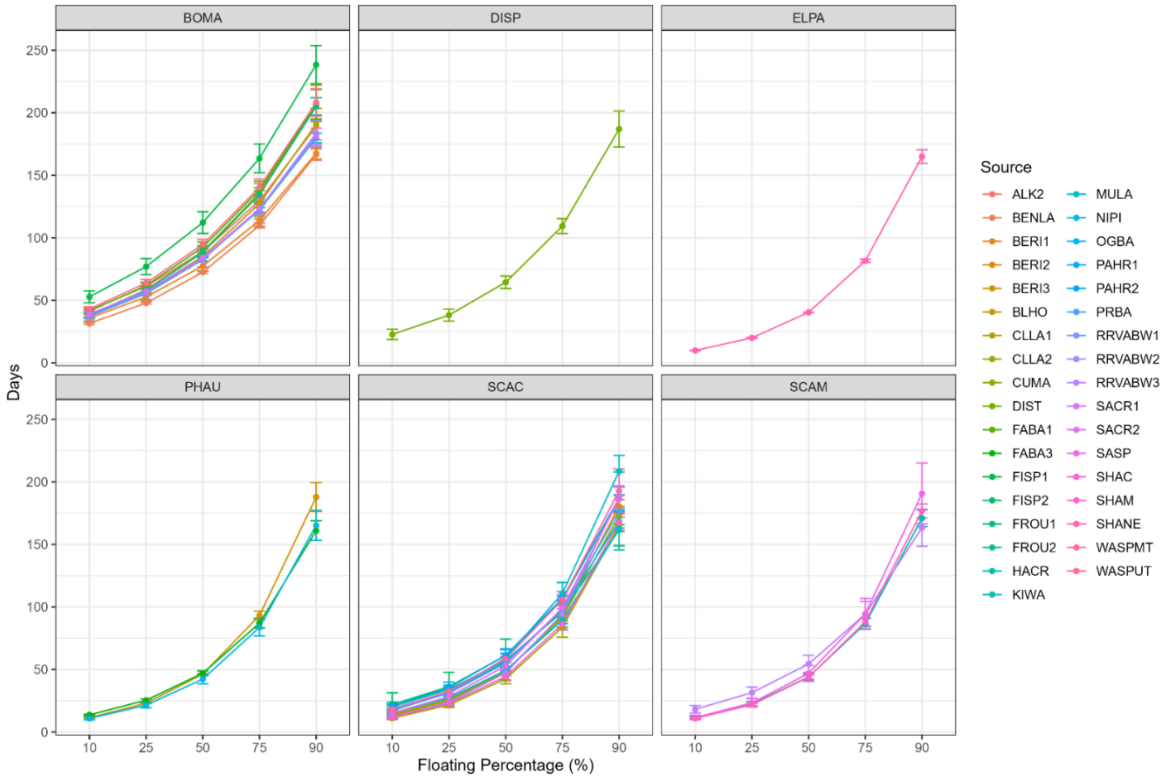


FIG S.3.3. The ‘Floating Percentage’, which indicates the number of days in which a set percentage of seeds had sunk, by days for each species and population.

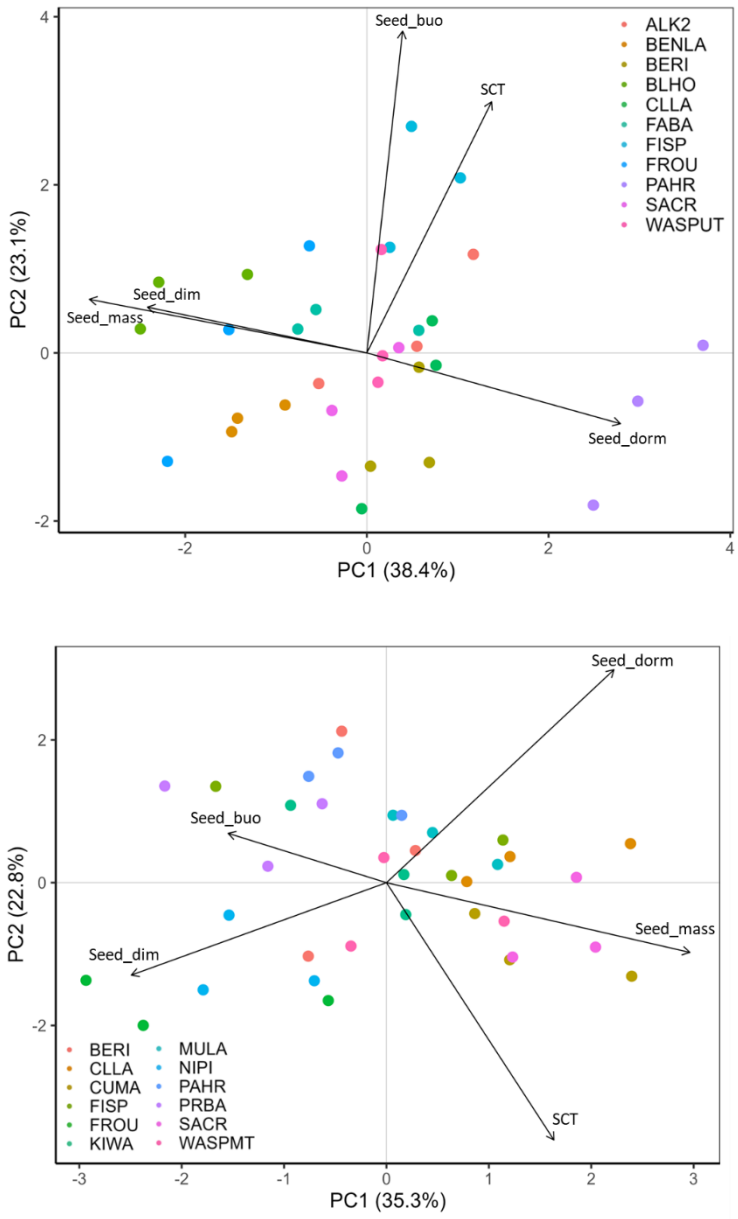


FIG S.3.4. Principal component analysis results for intraspecific assessment of seed trait variation across (top) *B. maritimus* populations and (bottom) *S. acutus* populations.

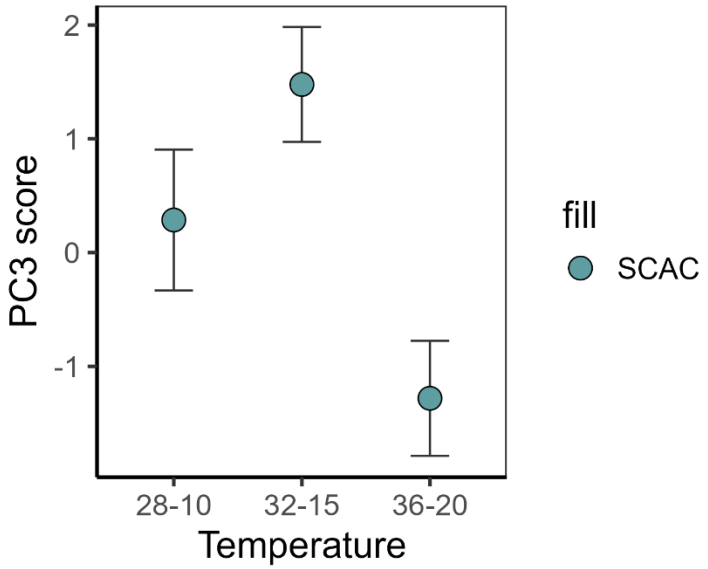


FIG S.3.5. Interaction between temperature and species for PC3 scores of *S. acutus*. Lower values of PC3 were most strongly correlated with increased shoot dry matter content, whereas higher values of PC3 were correlated with root elongation rate.

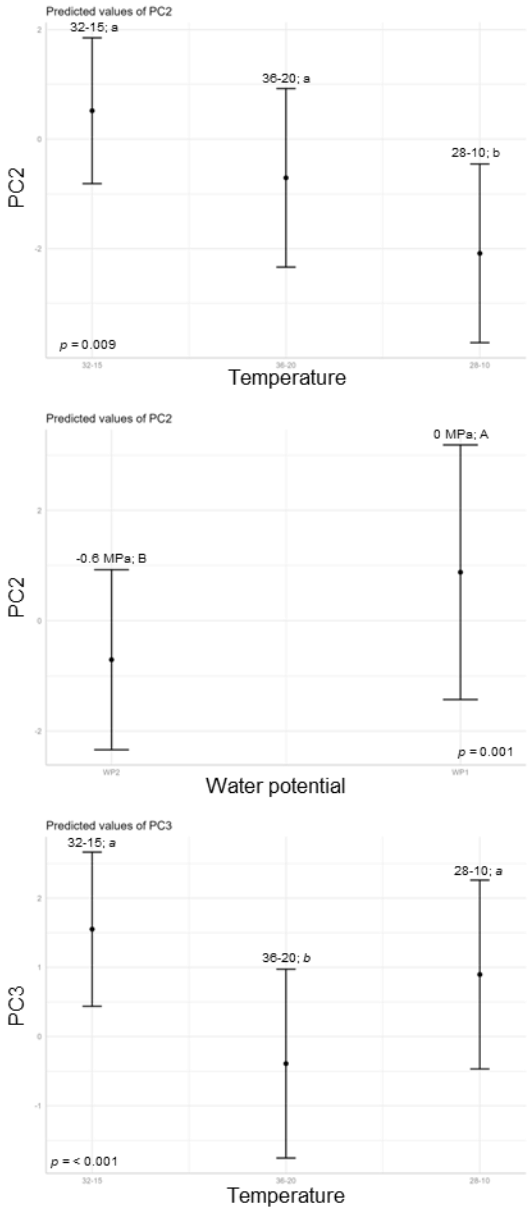


FIG S.3.6. Significant effects for top) temperature and PC2 scores, middle) water potential and PC2 scores, and bottom) temperature and PC3 scores for the *B. maritimus* principal component analysis. P values and letters of significance are reported from Tukey HSD *post-hoc* tests comparing the mean differences in PC scores across temperature and water potential treatments.

APPENDIX C

SUPPLEMENTS TO CHAPTER THREE

DEPTH OF DORMANCY INDEX

Depth of dormancy calculations

Ecological underpinning

Seed dormancy is a long-studied ecological phenomenon that allows for plants to 'block' germination of a viable seed in unfavorable conditions, thus reducing spatial and temporal risk to young seedlings (Baskin & Baskin, 2004; Satterthwaite, 2010; Willis et al. 2014). Variation in dormancy type and depth is known to vary not only across species (Baskin & Baskin, 2004), but also within species (Schütz & Milberg, 1997; Schutz & Rave, 2003; Gremer et al. 2020). This intraspecific variation in seed dormancy, and specifically depth of dormancy, can be attributed to both long-term and short-term ecological and physiological effects on the seed during development and maturation (Fernández Farnocchia et al. 2021). In the short-term, site-level abiotic conditions (termed 'maternal effects'; Mousseau & Fox, 1998) can modulate the depth of dormancy a seed may experience each year due to differences in temperature, water availability, or nutrient availability during seed development (Arnold et al. 1992). For example, lower temperatures can yield seeds that experience deeper dormancy levels (e.g., Huang et al. 2014; Springthorpe & Penfield, 2015). In the long-term, sustained climate differences between populations of a species can induce differences in dormancy depth that may persist across generations (Huang et al. 2018).

From a restoration perspective, understanding the relationship of dormancy depth across populations can assist in choosing seed source populations (or species) that exhibit

dormancy characteristics that will best meet restoration objectives. On one hand, species or sources that have lower depth of dormancy and require less cold stratification may require less logistical effort on the part of practitioners to reach maximum germination, which can enhance restoration outcomes. On the flip side, because dormancy depth can be an important adaptation to minimize spatial and temporal risk (Satterthwaite, 2010; Willis et al. 2014), practitioners may seek out more deeply dormant seeds as part of a seed mix to incorporate disturbance resiliency (Scott et al. 2010). Moreover, understanding the variation in depth of dormancy cannot be considered in isolation—understanding the trade-offs between dormancy traits and other seed functional traits can yield a more holistic understanding, and ultimately generalization, of how seed dynamics influence germination and early seedling growth (Larson & Funk, 2016).

To capture intra- and interspecific variation in depth of dormancy, we calculated one metric that represented the maximum germination observed across all tested cold stratification treatments. Our goal was to quantify the minimum cold stratification time needed to reach maximum germination for each tested species × population. We recognize that dormancy depth and dormancy cycling is nuanced and adequately capturing these dynamics is a perpetual challenge (Finch-Savage & Leubner-Metzger, 2006), but this calculation provided a standardized method of assessing the length of cold stratification necessary to maximally break dormancy, making it an appropriate depth of dormancy metric.

Calculating the data

As described in the main text, we subjected three replicates of all species × populations to one of seven cold stratification treatments: one untreated control (0 days of

cold stratification) and six cold stratification treatments at 30-day intervals (30-, 60-, 90-, 120-, 150-, 180-days of cold stratification). The cold stratification treated seed bags were buried on the same day and pulled out every 30 days for germination testing. Germination was conducted in Conviron growth chambers at one temperature regime (32/15°C; day/night) and germinated seeds were counted and removed every other day for 30 days.

To calculate the depth of dormancy metric, we used germination count data to calculate germination proportion and averaged across replicate treatments. We then extracted the maximum germination percentage across cold stratification treatments within every species × population combination. After identifying the maximum germination for each species × population, we plotted the mean final germination percentage by cold stratification treatment species × population. These relationships were not linear, indicating that a simple linear slope would not adequately capture dormancy dynamics for this data. We conducted Tukey HSD *post-hoc* comparisons of the means to identify for each species × population the lowest cold stratification time required to reach maximum germination, beyond which there were no significant increases in germination percentage with additional cold stratification. We divided the maximum germination percentage for each species × population by the length of cold stratification times identified in the Tukey HSD analysis to normalize the data, and then scaled the data between 0 and 1 to improve interpretation. For species that were not tested due to lack of dormancy (*P. australis*), the dormancy index was set to 1 to indicate no dormancy.

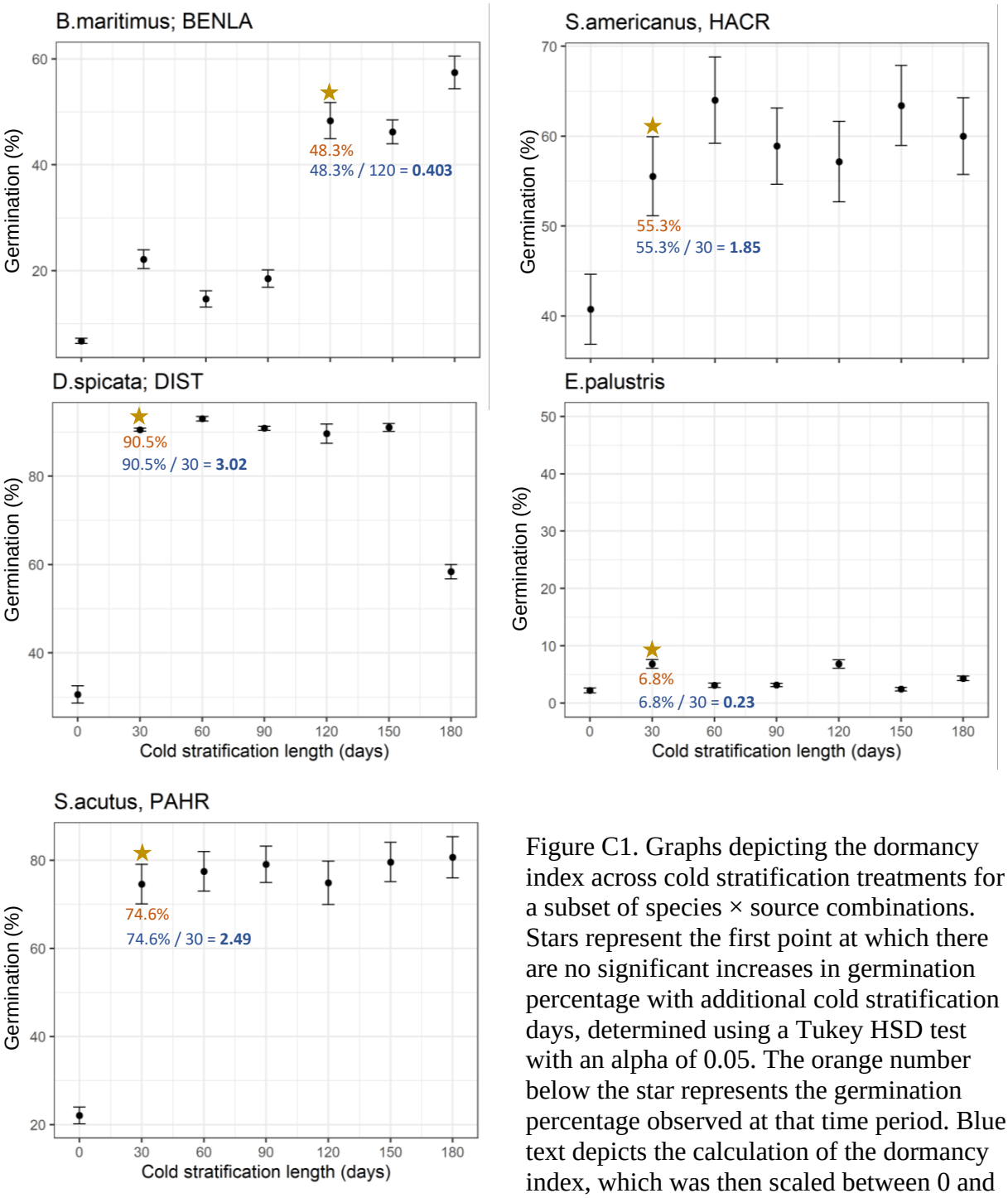


Figure C1. Graphs depicting the dormancy index across cold stratification treatments for a subset of species × source combinations. Stars represent the first point at which there are no significant increases in germination percentage with additional cold stratification days, determined using a Tukey HSD test with an alpha of 0.05. The orange number below the star represents the germination percentage observed at that time period. Blue text depicts the calculation of the dormancy index, which was then scaled between 0 and 1 across all species × source combinations.

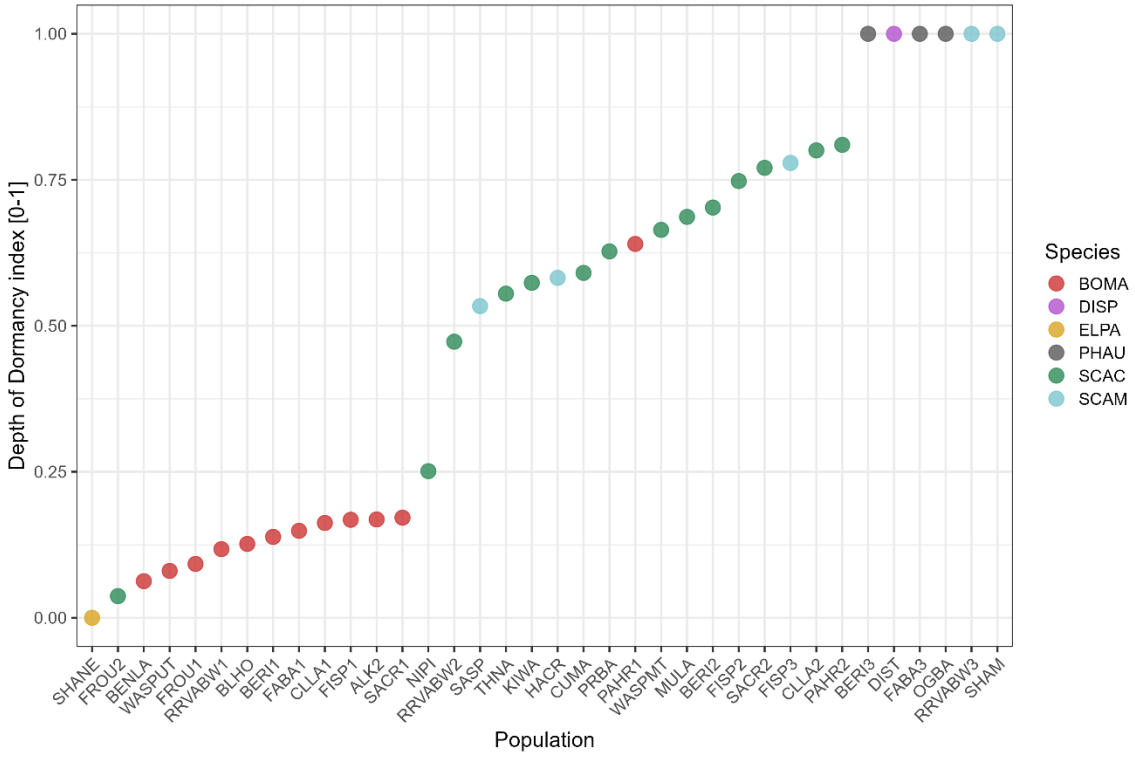


Figure C2. Depth of dormancy index values by population and species. The dormancy index ranges from 0 to 1, where populations with deeper dormancy have values closer to 0 and populations with less deep dormancy have values closer to 1.

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APPENDIX D

SUPPLEMENTS TO CHAPTER FOUR

TABLE S.4.1. Percent cover classes, adapted from Brohman and Bryant's (2005) 10-percent class breaks, with an additional three classes to characterize no cover (0%), trace cover (<1%), and near complete cover (99-100%).

Class	**Cover**
0	0%
T	<1%
1	2-10%
2	11-20%
3	21-30%
4	31-40%
5	41-50%
6	51-60%
7	61-70%
8	71-80%
9	81-90%
10	91-99%
11	99-100%

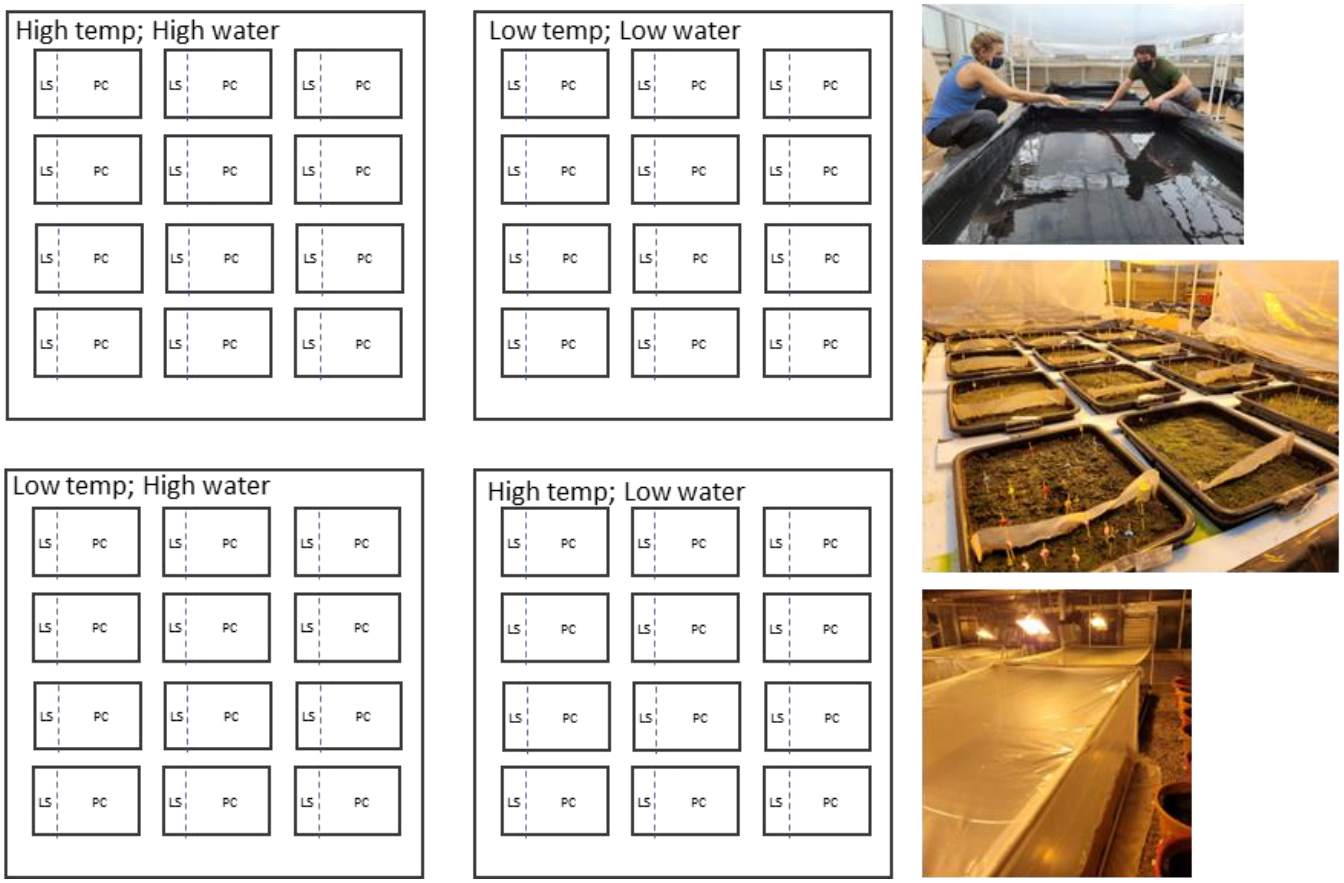

FIGURE S.4.1. Experimental design schematic in one of the three greenhouses. Each reservoir contained one of two temperature levels (36/20 ℃ or 32/15 ℃), modulated by plastic tents and space heaters, and one of two water levels (high: 13-15 cm of water; or low: 3-5 cm of water). There were four reservoirs per greenhouse and three total greenhouses. Each reservoir was wrapped in 30 mil PVC pond liner to retain water (https://www.pondliner.com/pond-liners). Within each reservoir, 12 growing containers were constructed for every monotypic species × population combination. Seeds were either sown on the life-stage side of the container (LS), where we tracked life-stage transitions, or the cover side of the container (PC), where we tracked percent cover throughout the experiment. Images on the right depict (top) leveling the reservoirs during setup to ensure water levels were consistent, (middle) growing containers within greenhouses, and (bottom) plastic tents constructed over reservoirs to retain heat.

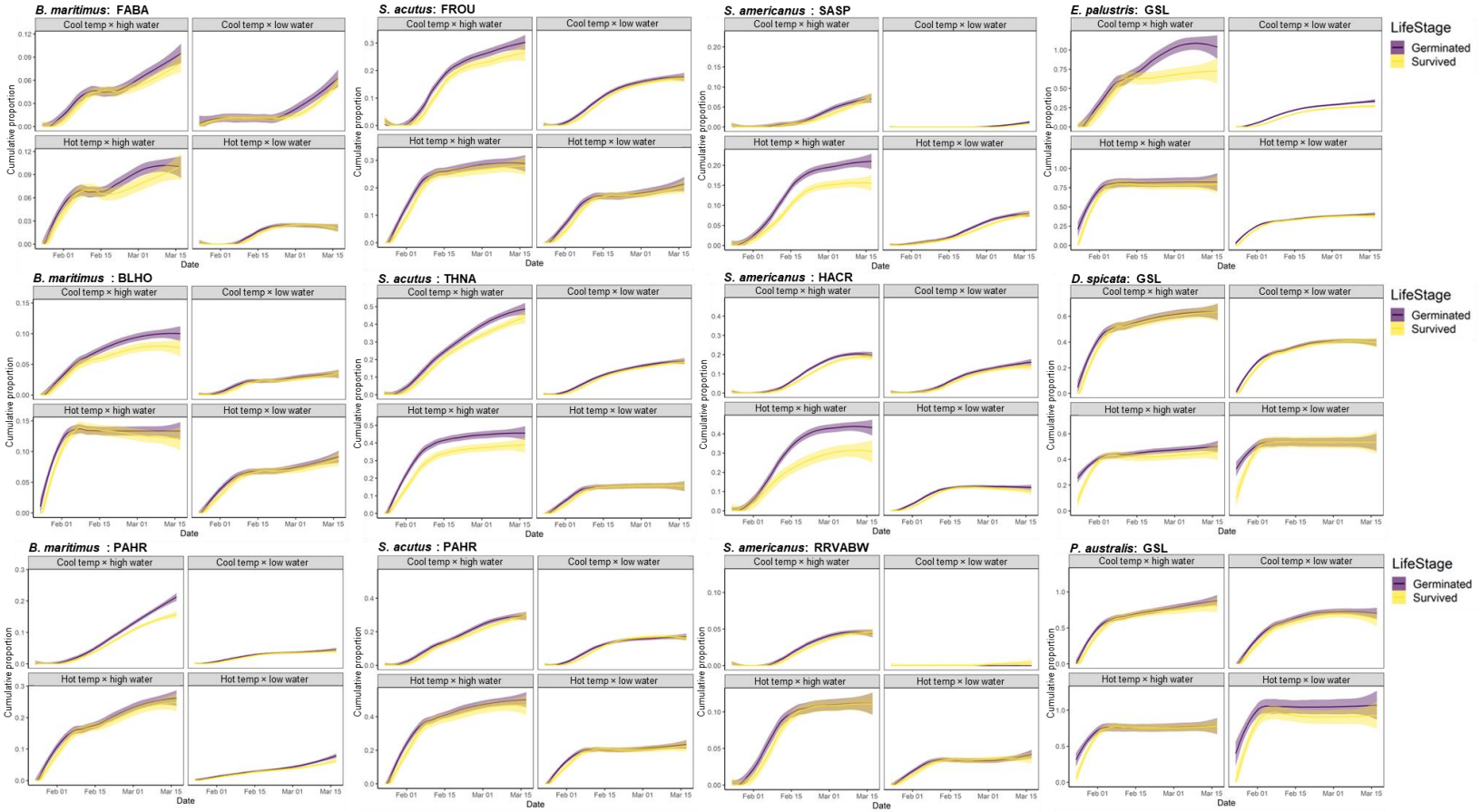

FIG. S.4.2. Smoothed raw data of the cumulative proportion of germinated seeds and survived seedlings over time. Note the variation in y-axis among populations, which was retained to showcase within-population differences between germination and survival. *Population codes*: *BLHO = Black Horse Lake; RRVABW = Railroad Valley Big Wells WMA; PAHR = Pahranagat NWR; FROU = Freezeout WMA; THNA = The Nature Conservancy (Shorelands Preserve); FABA = Farmington Bay WMA; HACR = Harold Crane WMA; SASP: Salt Springs WMA; GSL = Great Salt Lake.*

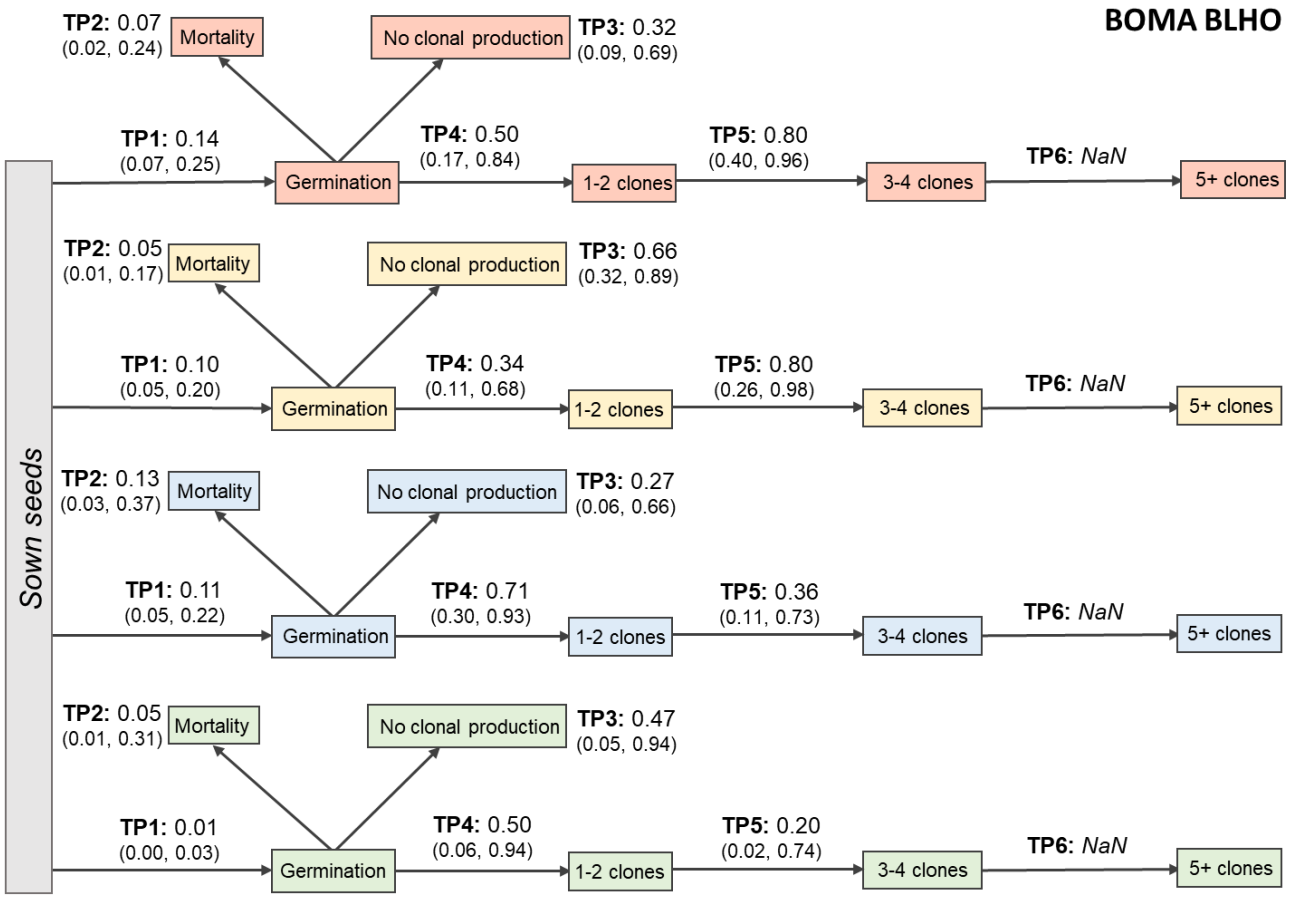

FIG. S.4.3. Life stage transition probabilities for *Bolboschoenus maritimus* ('BOMA') sourced from Black Horse Lake ('BLHO'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

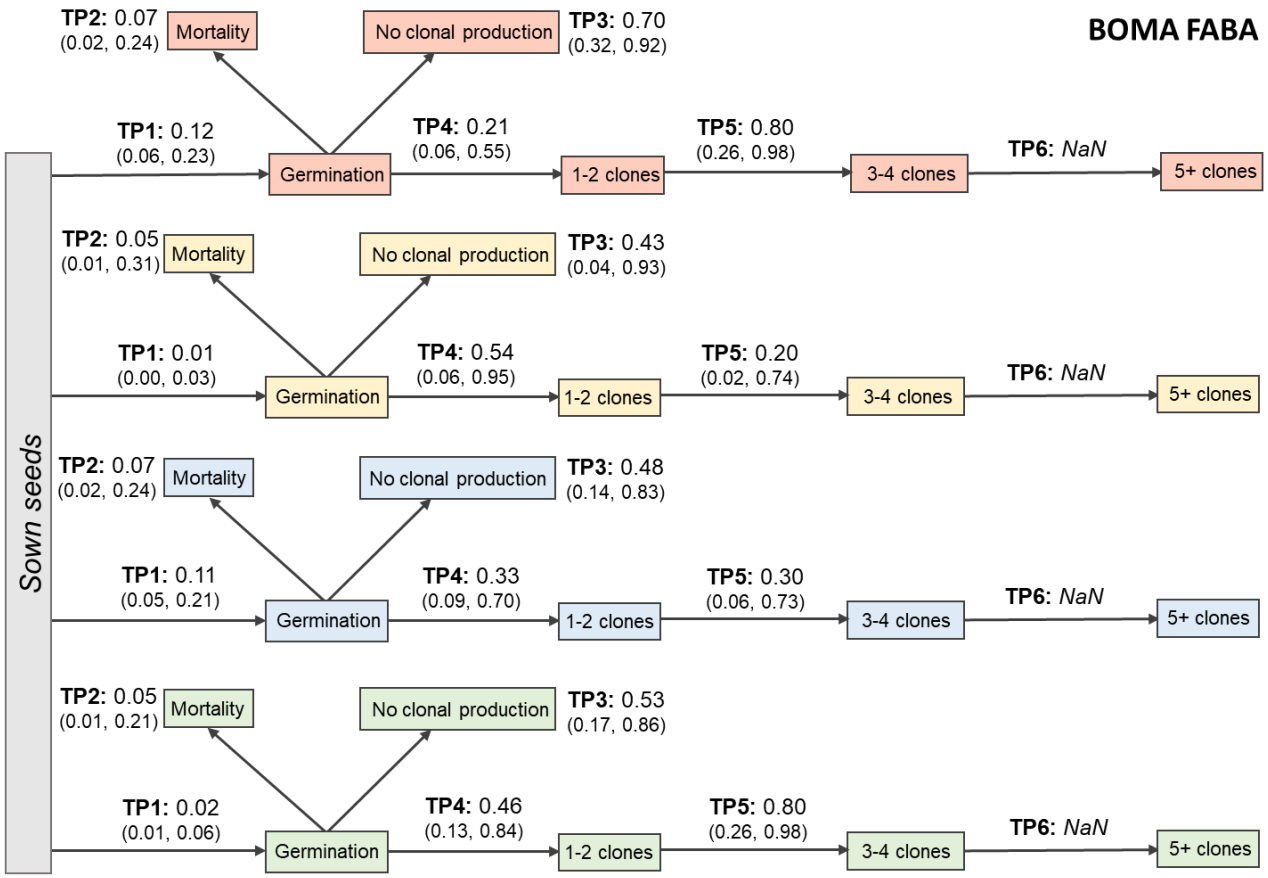

FIG. S.4.4. Life stage transition probabilities for *Bolboschoenus maritimus* ('BOMA') sourced from Farmington Bay Waterfowl Management Area ('FABA'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

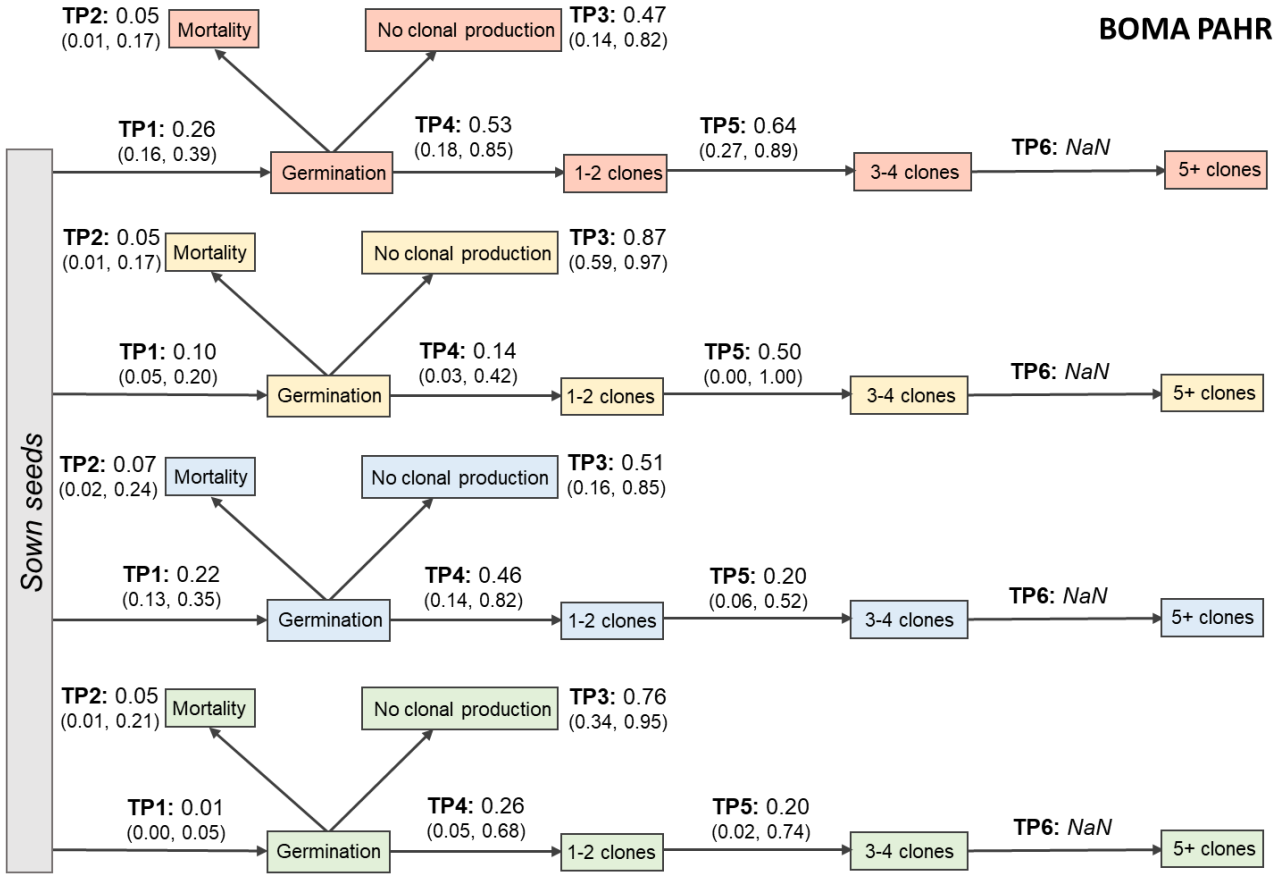

FIG. S.4.5. Life stage transition probabilities for *Bolboschoenus maritimus* ('BOMA') sourced from Pahranagat National Wildlife Refuge ('PAHR'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

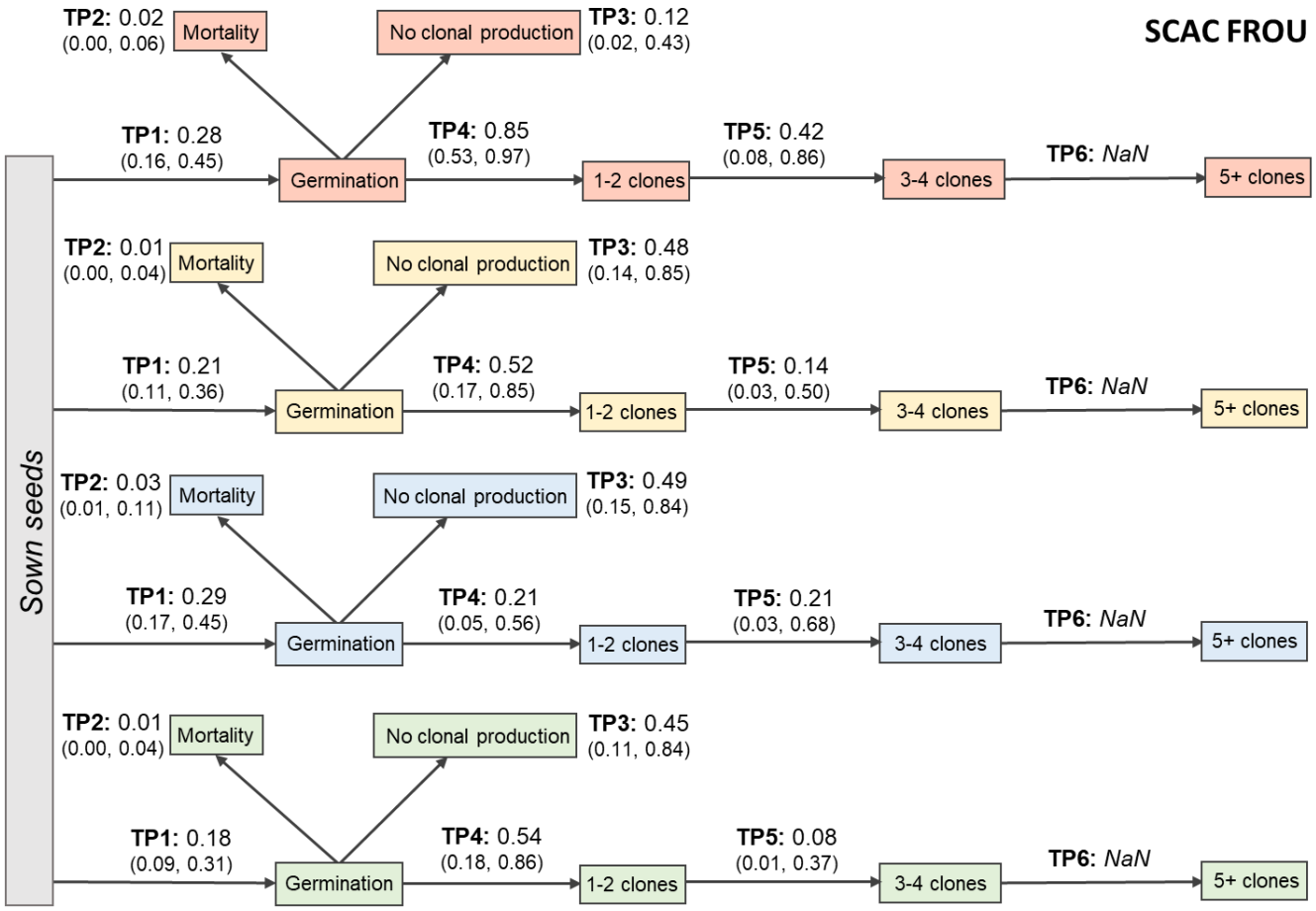

FIG. S.4.6. Life stage transition probabilities for *Schoenoplectus acutus* ('SCAC') sourced from Freezeout Lake Wildlife Management Area ('FROU'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

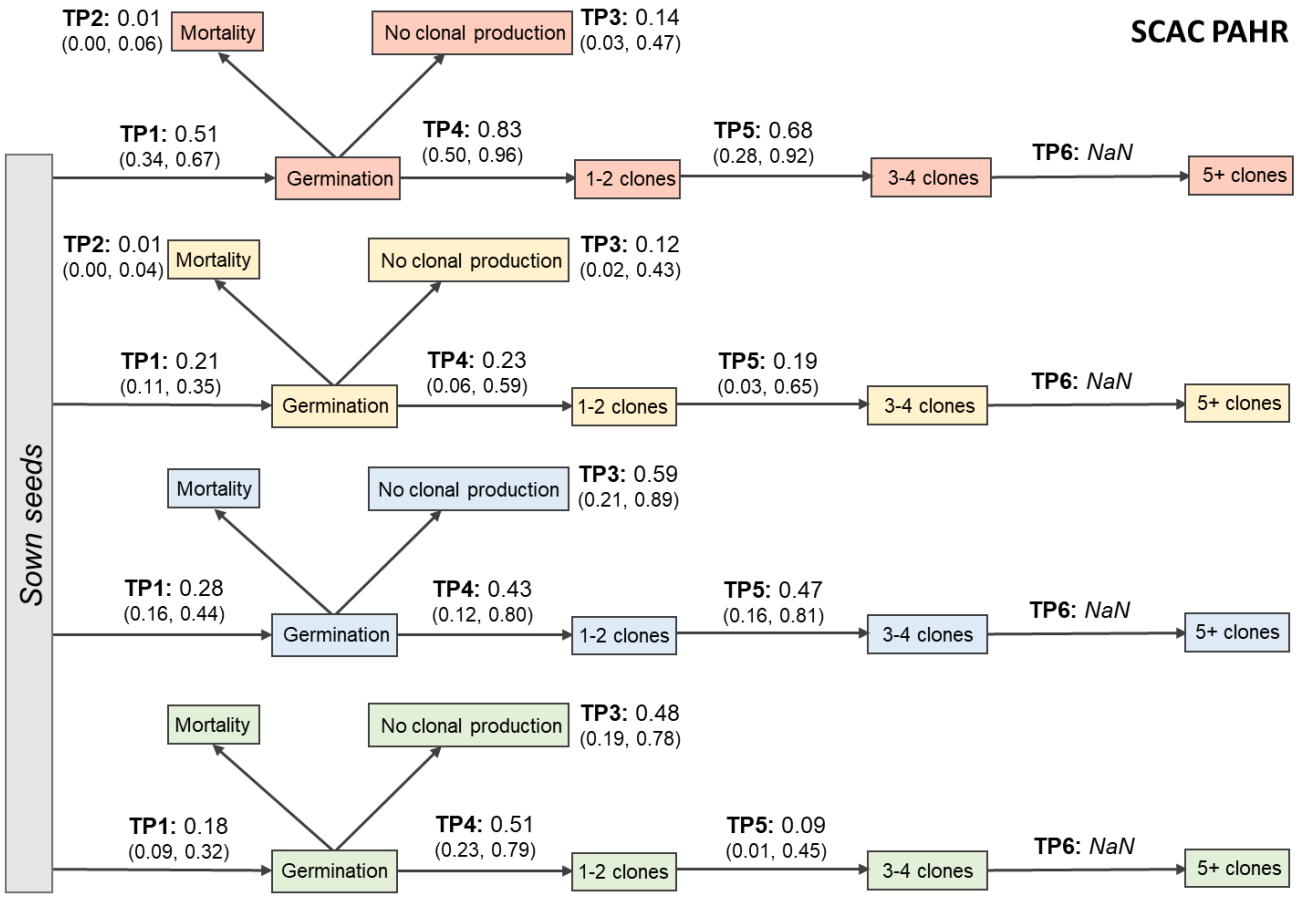

FIG. S.4.7. Life stage transition probabilities for *Schoenoplectus acutus* ('SCAC') sourced from Pahranagat National Wildlife Refuge ('PAHR'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

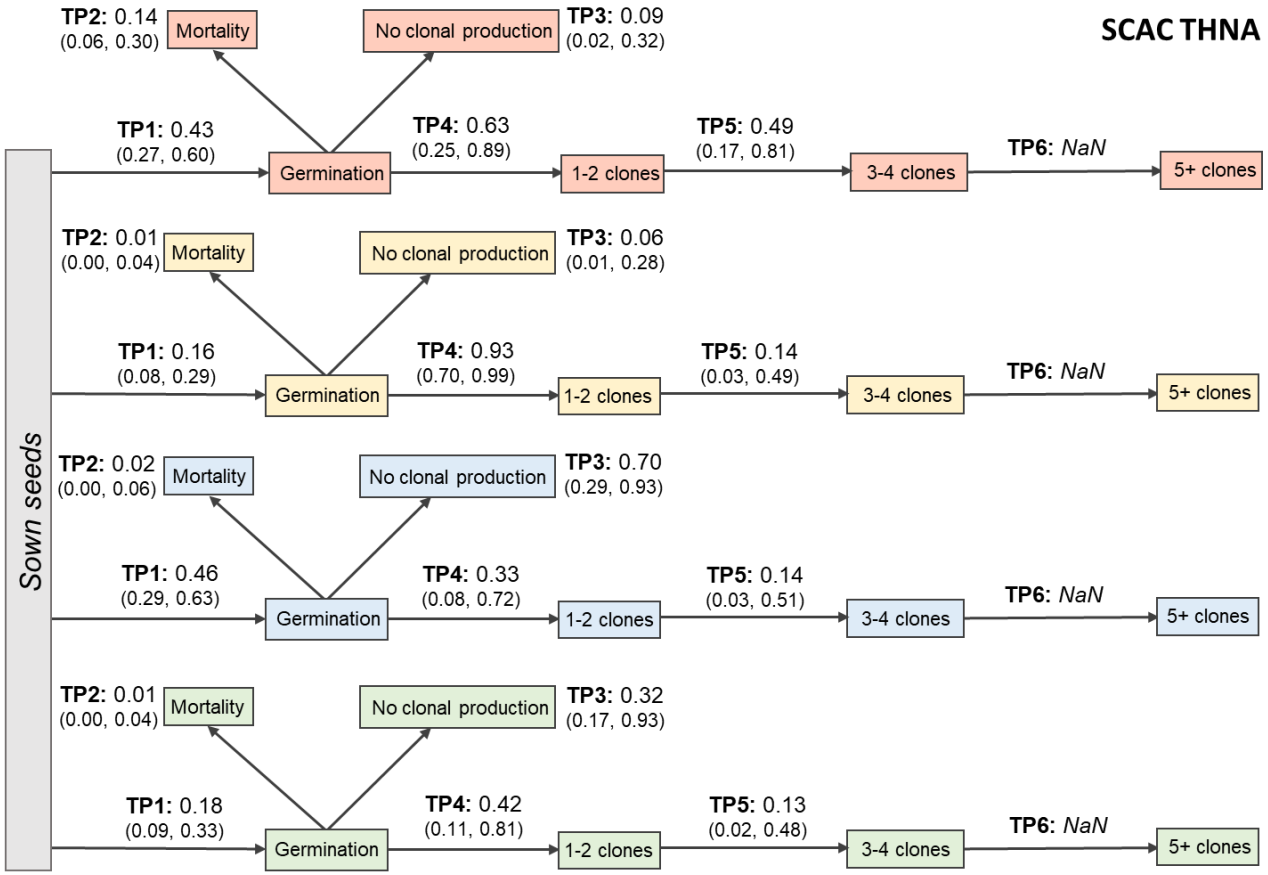

FIG. S.4.8. Life stage transition probabilities for *Schoenoplectus acutus* ('SCAC') sourced from The Nature Conservancy Shorelands Preserve ('THNA'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

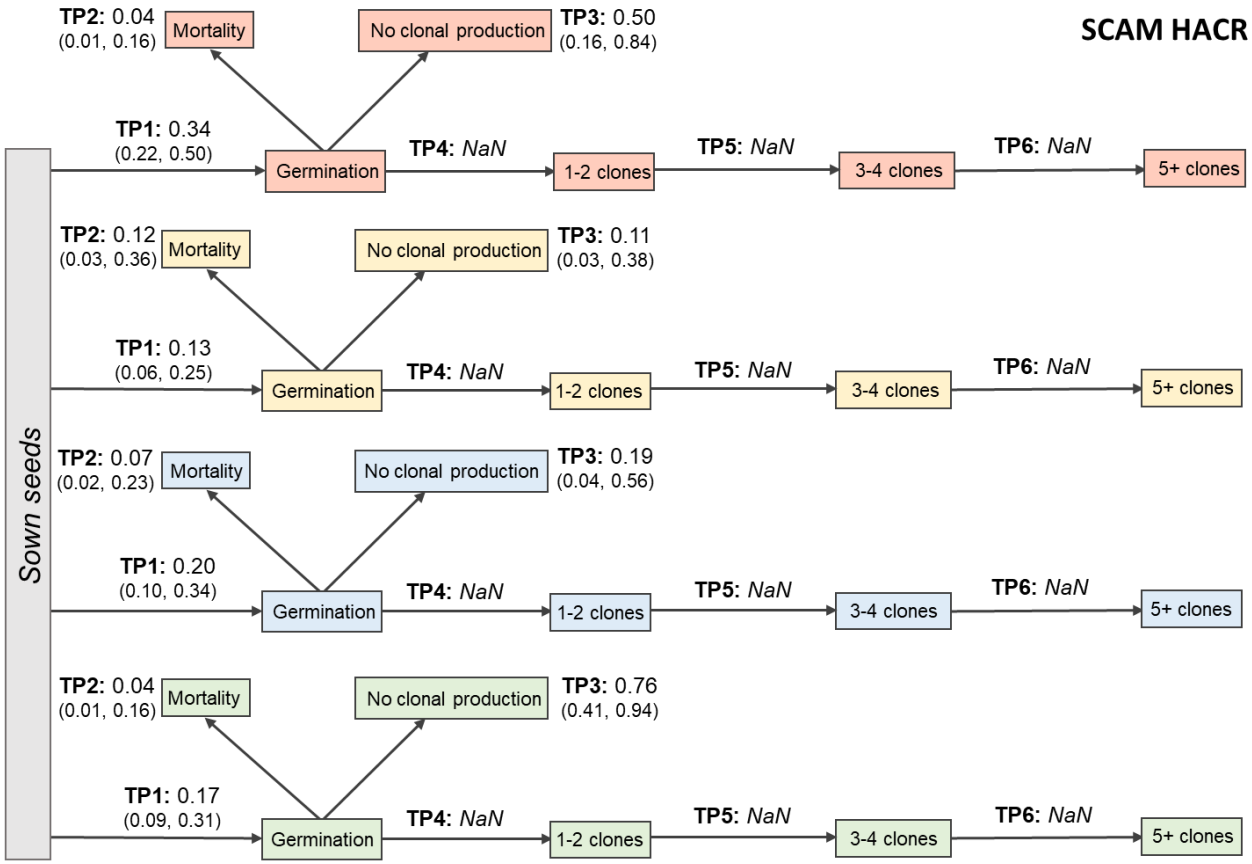

FIG. S.4.9. Life stage transition probabilities for *Schoenoplectus americanus* ('SCAM') sourced from Harold Crane Waterfowl Management Area ('HACR'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

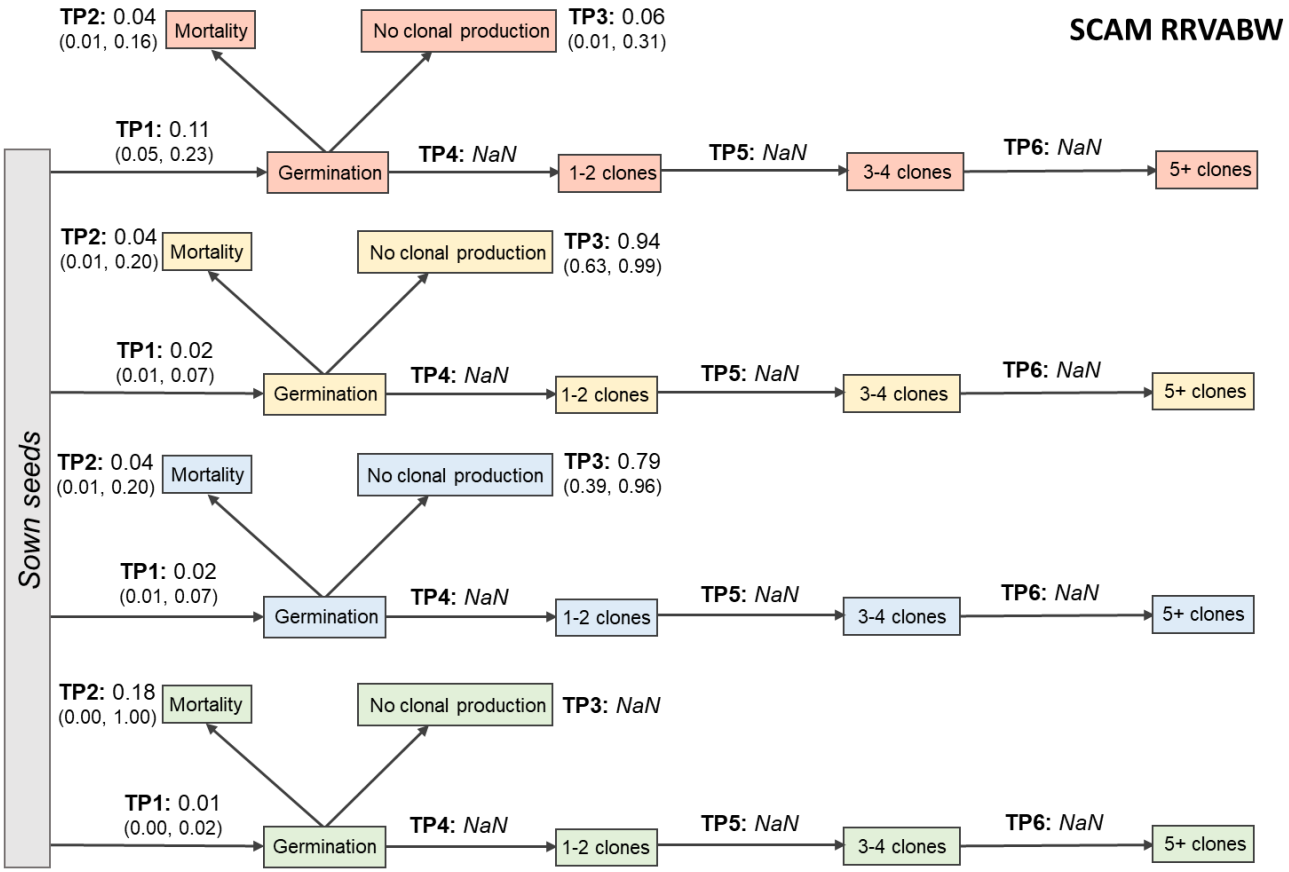

FIG. S.4.10. Life stage transition probabilities for *Schoenoplectus americanus* ('SCAM') sourced from Railroad Valley Waterfowl Management Area at Big Wells ('RRVABW'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

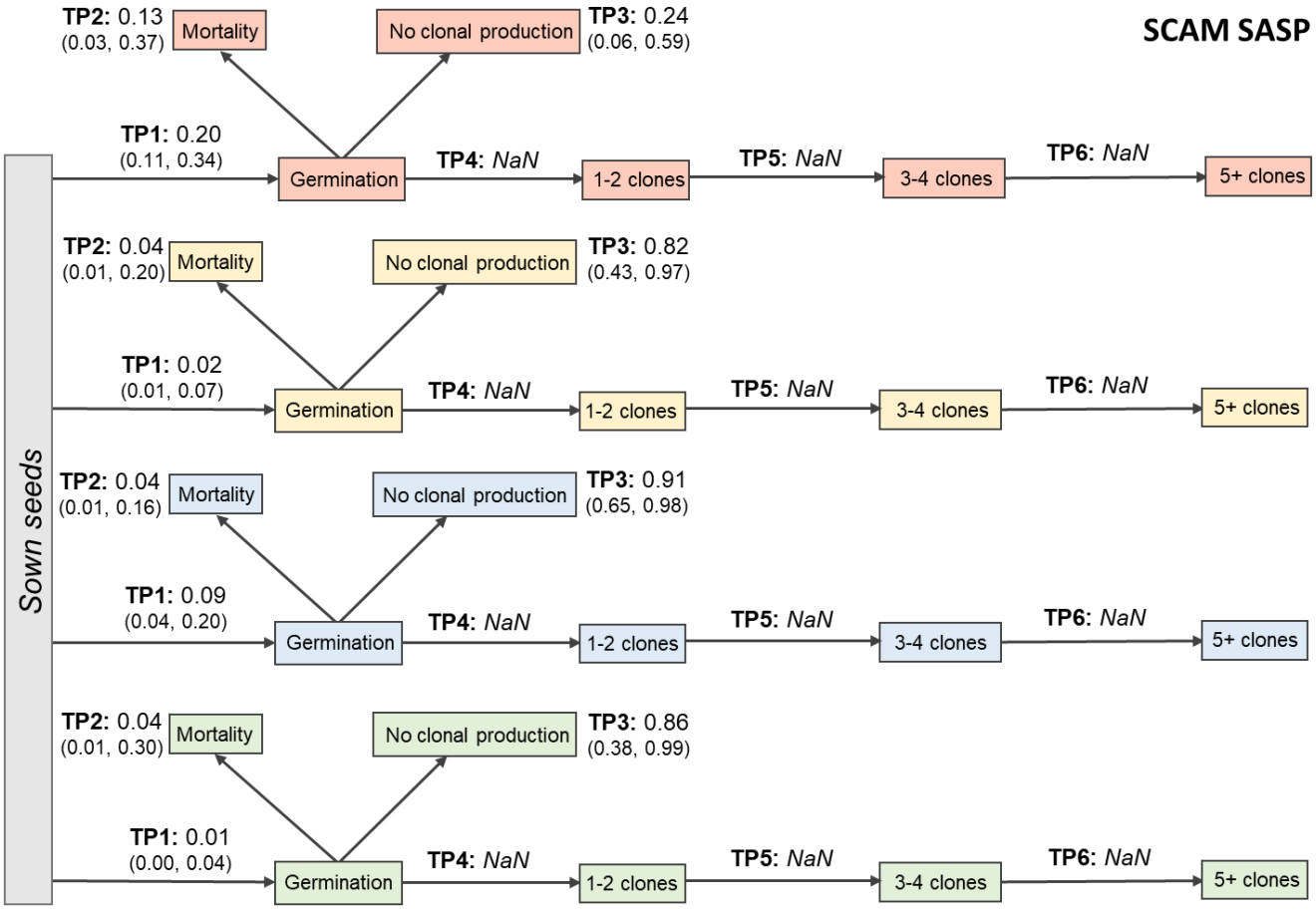

FIG. S.4.11. Life stage transition probabilities for *Schoenoplectus americanus* ('SCAM') sourced from Salt Springs Waterfowl Management Area ('SASP'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

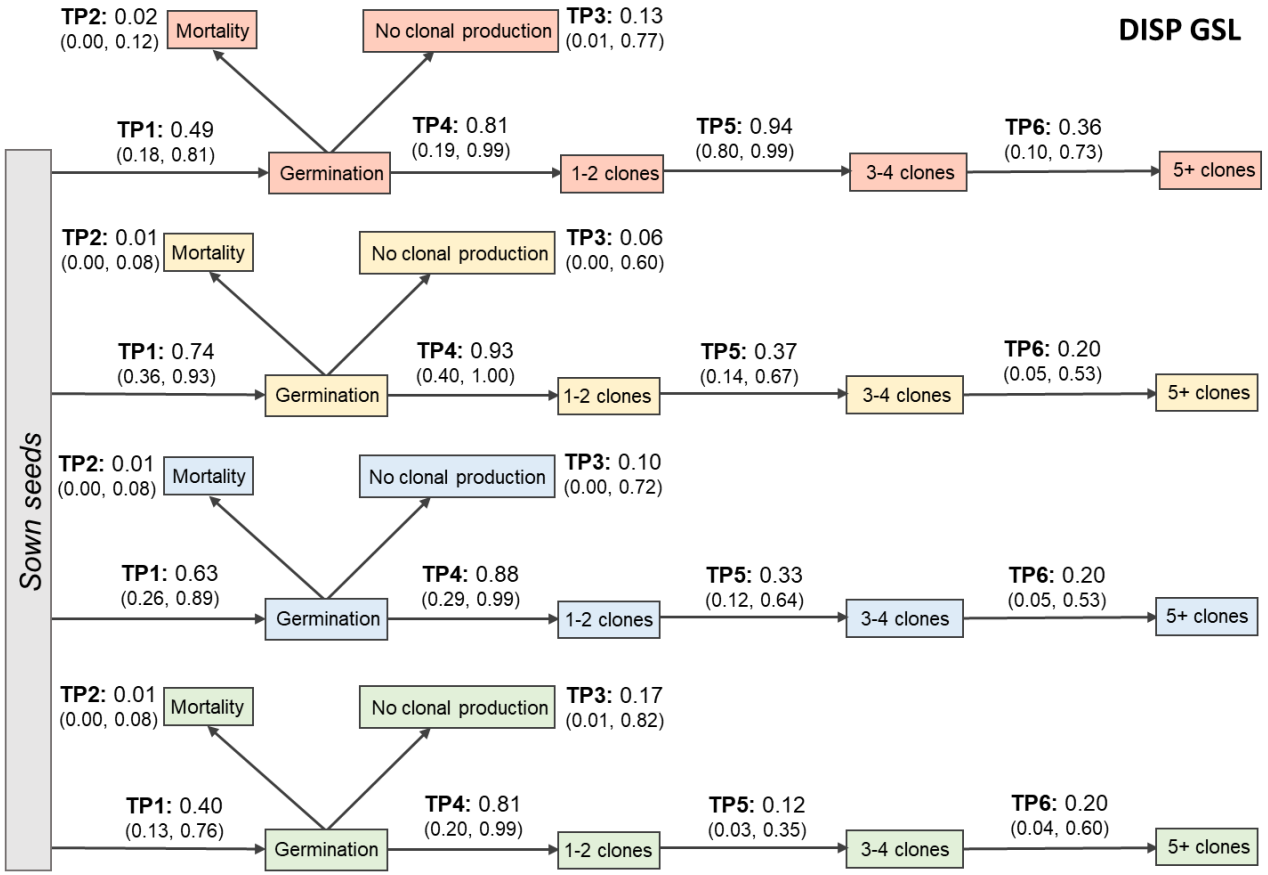

FIG. S.4.12. Life stage transition probabilities for *Distichlis spicata* ('DISP') sourced from Great Salt Lake wetlands ('GSL'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

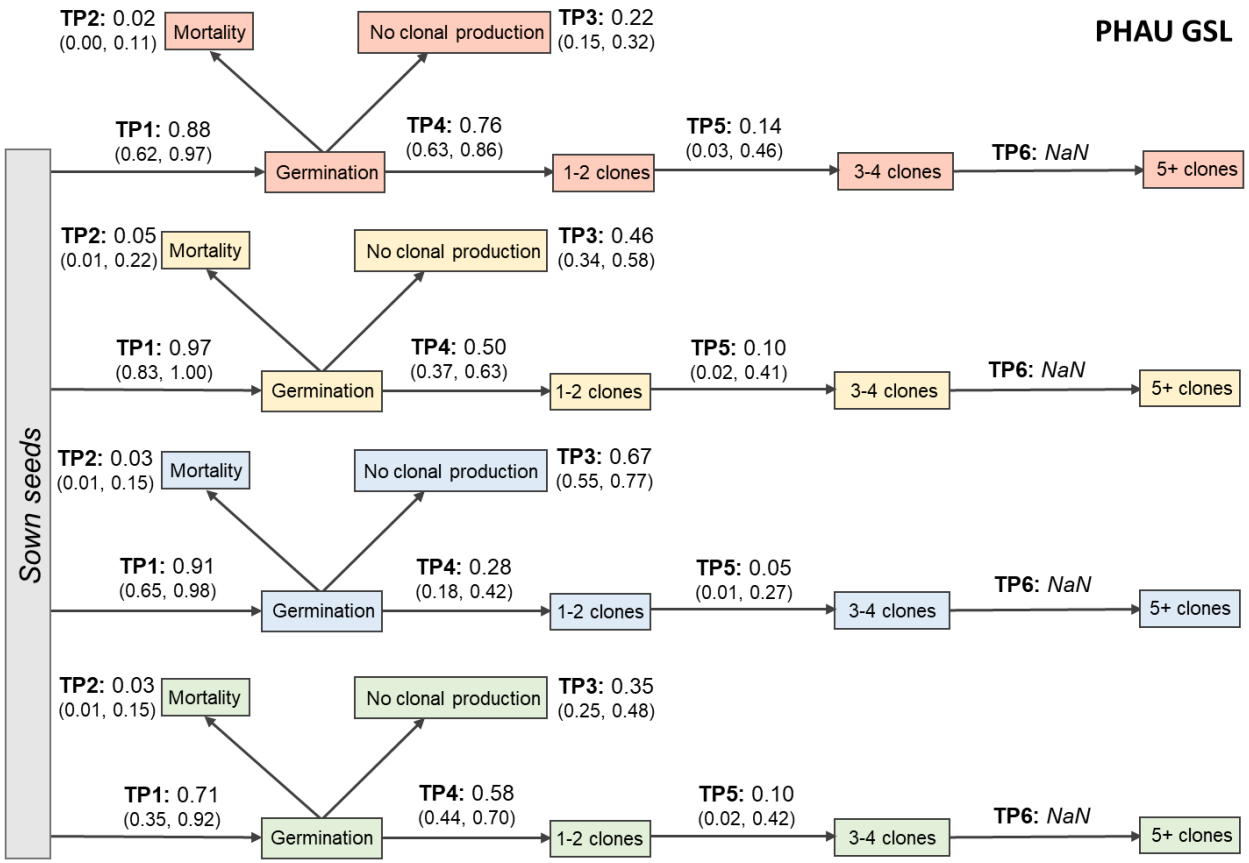

FIG. S.4.13. Life stage transition probabilities for *Phragmites australis* ('PHAU') sourced from Great Salt Lake wetlands ('GSL'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling].*

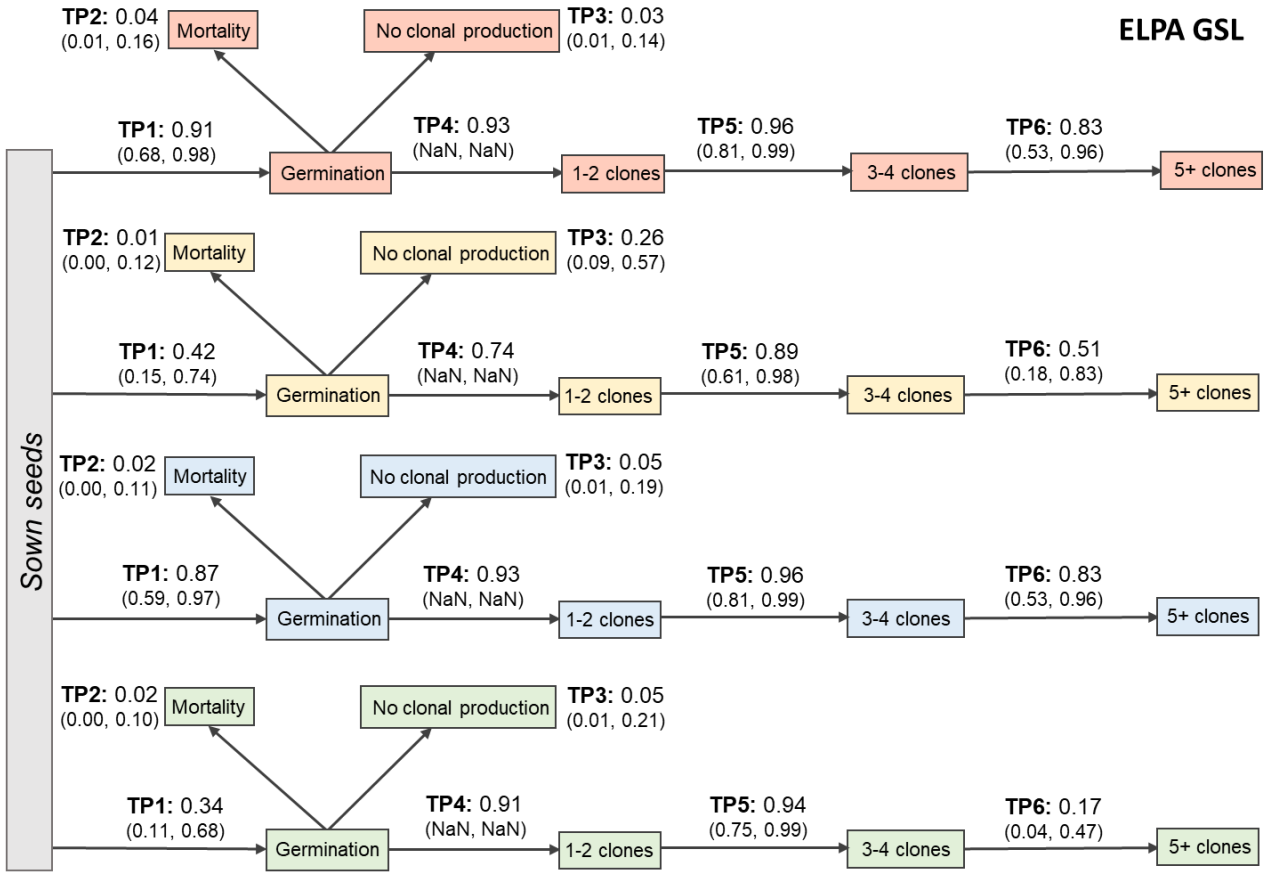

FIG. S.4.14. Life stage transition probabilities for *Eleocharis palustris* ('ELPA') sourced from Great Salt Lake wetlands ('GSL'). Model predicted probabilities are displayed with 95% upper and lower confidence intervals in parentheses. *Transition probabilities: TP1 [sown seed → germinated seed]; TP2 [germinated seed → mortality]; TP3 [germinated seed → no clonal production]; TP4 [germinated seed → 1–2 clones per seedling]; TP5 [1–2 clones per seedling → 3–4 clones per seedling]; TP6 [3–4 clones per seedling → 5+ clones per seedling.*

APPENDIX E

PERMISSION TO REPRINT CHAPTER 2 IN *ECOLOGICAL APPLICATIONS*

October 01, 2022

Dear Bailey Holdaway,

I am in the process of preparing my dissertation in the Department of Watershed Sciences at Utah State University.

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Tarsa, E. E., Holdaway, B. M., & Kettenring, K. M. (2022). Tipping the balance: The role of seed density, abiotic filters, and priority effects in seed-based wetland restoration. *Ecological Applications*, e2706.

Signed: 

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EDUCATION

Ph.D., Ecology, Utah State University ***Present***
Dissertation: "Seed ecology and regeneration processes to inform seed-based wetland restoration"
Dissertation Advisor: Dr. Karin Kettenring

B.S., Environmental Science, SUNY – Environmental Science and Forestry **2013**
Graduated Magna Cum Laude

PROFESSIONAL EXPERIENCE

Utah State University **2017 – *Present***
Ph.D. Candidate and Graduate Research Assistant; Wetland Ecology and Restoration Lab

- Design and execute greenhouse, laboratory, and field experiments to investigate seed-based restoration following *Phragmites australis* control in Great Salt Lake wetlands
- Collaborate and coordinate with land managers, state agencies, and faculty
- Present research findings and recommendations to stakeholders
- Direct and supervise undergraduate students and lab technicians
- Collaborate on report writing and journal publications

Ogden Nature Center **2014 – 2017**
Volunteer Coordinator | *full time position*

- Performed all aspects of volunteer management including recruiting, interviewing, communicating, scheduling, and supervising thousands of volunteers
- Developed, maintained, and nurtured contacts with community partners
- Trained and supervised UCC AmeriCorps habitat restoration interns
- Oversaw budgets and project implementation for wetland restoration and invasive species management grants

Habitat Restoration and Environmental Education | *internship*

- Performed habitat restoration field work and noxious weed management
- Prepared grant and secured $80,000 in funding to restore wetland habitats on the preserve
- Independently developed, organized, and delivered education programs and led thousands of volunteers in habitat restoration projects throughout the property
- Developed curriculum and taught over 3,000 K-5 students attending field trips at the nature center

New York State Department of Environmental Conservation **2013**

Forest Pest Outreach Educator | *internship*

- Assisted in trapping and surveying Emerald Ash Borer throughout New York State
- Provided education and outreach to the public regarding state firewood regulations and forest pests
- Composed engaging lesson plans and delivered educational programs to youth throughout the state

New York State Parks **2012 – 2013**

Natural Resource Steward Biologist Assistant | *work study*

- Promoted the Friends of Recreation, Conservation and Environmental Stewardship (FORCES), a volunteer program aimed at recruiting students to participate in service-learning projects in state parks
- Involved in invasive species surveying and removal projects
- Recruited and supervised volunteers partaking in service-learning projects
- Organized and managed FORCES volunteer and promotional events

Adirondack Watershed Institute **2012**

Environmental Educator & Watershed Steward | *internship*

- Created and presented lesson plans, educational programs, and interpretive displays
- Designed and led invasive species interpretive nature walks
- Collected, analyzed, and interpreted boat launch usage data

PEER REVIEWED PUBLICATIONS

* Undergraduate student mentored

In review/revision

Byun, C., K.M. Kettenring, **E.E. Tarsa**, and S. de Blois. (*In review*). Applying ecological principles to maximize resistance to invasion in restored plant communities. Ecological Monographs.

Journal articles

Tarsa, E.E., B.M. Holdaway*, and K.M. Kettenring. (2022). Tipping the balance: manipulating native sowing density, abiotic conditions, and priority effects to favor native-dominated plant communities in wetland restoration. Ecological Applications.

Kettenring, K.M. and **E.E. Tarsa. 2020**. Need to seed? Ecological and evolutionary keys to seed-based wetland restoration. Frontiers in Environmental Science, 8 (109): 1-30.

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Tarsa, E.E.; R. Robinson; C. Hebert; D. England; K. Hambrecht; C. Cranney; and K.M. Kettenring. **2022**. "Seeding the Way: A Guide to Restoring Native Plants in Great Salt Lake Wetlands" Paper 2246. https://digitalcommons.usu.edu/extension_curall/2246.

Science communications

Robinson, R., **E.E. Tarsa**, and K.M. Kettenring. **2021**. Seeds not weeds: Research informs best practices for the revegetation of native plant species in wetlands. Society for Ecological Restoration Great Basin Chapter Newsletter. May 2021.

Book chapters

Kettenring, K.M., C. Cranney, R. Downard, K. Hambrecht, **E.E. Tarsa,** D. Menuz, and C.B. Rohal. **2020**. Invasive plants of Great Salt Lake wetlands: what, where, how, and why? in B. Baxter and J. Butler (eds.) Great Salt Lake: biology of a terminal lake in the age of change. Springer.

PROFESSIONAL PRESENTATIONS

Tarsa, E. and K.M. Kettenring. **2020**. Modeling restoration outcomes to optimize native plant establishment, Utah Geological Survey Working Wetlands Group meeting.
Martin, E. and K.M. Kettenring. **2019**. The role of native seed sowing density and Phragmites competition in Great Salt Lake wetland restoration, Society of Wetland Scientists, Baltimore, MD.
Martin, E. and K.M. Kettenring. **2018**. Seed-based restoration of native plant communities following Phragmites control in Great Salt Lake wetlands, Society of Wetland Scientists, Denver, CO.
Martin, E. and K.M. Kettenring. **2018**. Seed-based restoration of native plant communities following Phragmites control in Great Salt Lake wetlands, Great Salt Lake Issues Forum, Salt Lake City, UT.
Martin, E. and K.M. Kettenring. **2017**. *Seed-based Restoration of Native Plant Communities Following Phragmites Control in Great Salt Lake Wetlands.* March 2017. Department of Watershed Sciences Graduate Research Symposium. Utah State University, Logan, UT.
Invited presentations
Tarsa, E. and K.M. Kettenring. **2022**. Modeling restoration outcomes to optimize native plant establishment, Ducks Unlimited Canada Research Roundup.
Tarsa, E. and K.M. Kettenring. **2021**. Seed-based wetland restoration following *Phragmites australis* removal: harnessing seed traits and systems modeling to promote native plant establishment, Great Lakes Phragmites Collaborative.
Tarsa, E. and K.M. Kettenring. **2020**. Restoring Great Salt Lake wetlands following Phragmites control using native seeds: challenges and opportunities ahead, Utah Division of Wildlife Resources and USGS Cooperative Fish & Wildlife Research Unit Brown Bag Luncheon Series.
Tarsa, E. and K.M. Kettenring. **2019**. The role of seeding density, species composition, and abiotic constrains to competitively exclude Phragmites reinvasion in Great Salt Lake wetland restoration, Society of Ecological Restoration, Cape Town, South Africa.
Martin, E. and K.M. Kettenring. **2018**. Seed-based restoration of native plant communities following *Phragmites* control in Great Salt Lake wetlands, Great Lakes Phragmites Collaborative, online webinar.

REPORTS

Kettenring, K.M., **E.E. Tarsa**, R. Robinson, and J. Braun. **2020**. Revegetation strategies to mitigate the impacts of invasive *Phragmites australis* in northern Utah wetlands: Final report to Utah Department of Agriculture and Food. 28 pp.
Kettenring, K.M., **E.E. Tarsa**, and R. Robinson. **2020**. Restoration of native plants through hydroseeding: Final report to Utah Division of Wildlife Resources. 15 pp.
Kettenring, K.M., **E.E. Tarsa**, R. Robinson, C.L. Hebert, and E. Leonard. **2020**. Reestablishing native plant communities in Great Salt Lake wetlands to prevent *Phragmites* reinvasion and restore avian habitat: Final report to Utah Division of Forestry, Fire & State Lands. 30 pp.

Kettenring, K.M. and **E.E. Martin. 2018**. Restoration of native, habitat-forming plants following *Phragmites* control in Utah wetlands: Final report to Utah Division of Wildlife Resources. 16 pp.
Kettenring, K.M. and **E.E. Martin**. **2018**. Techniques for successful revegetation of native plants in Great Salt Lake wetlands to prevent *Phragmites* reinvasion and restore avian habitat: Final report to Utah Division of Forestry, Fire & State Lands. 18 pp.

TEACHING EXPERIENCE

Wetland Ecology, Management, and Conservation | *Guest Lecturer* **Spring 2022**
Autonomous University of Queretaro (Mexico)

Ecology & Restoration of Wetland Plants | *Guest Lecturer* **Spring 2019**
Utah State University

Principles of Watershed Management | *Guest Lecturer* **Spring 2018**
Brigham Young University

Dendrology | *Teaching Assistant & Field Lab Lead* **Fall 2012**
SUNY-Environmental Science and Forestry

UNDERGRADUATE STUDENTS MENTORED

Chatterton, Sage; Light requirements for germination of native Intermountain West wetland species in competition with *Phragmites australis*. **2021**

Holdaway, Bailey; Native seed density and priority effects drive invasion resistance against *Phragmites australis* in wetland restoration. **2019**

Hart, Anders; Effect of seed coating and water level on alkali bulrush biomass and germination. **2017**

Judd, Gabriela; Intraspecific variation in regenerations traits: improving predictability in *Bolboschoenus maritimus* reestablishment. **2017**

GRANTS & FELLOWSHIPS

- Garden Club of America Fellowship in Ecological Restoration; $8,000 **2020**
- Ducks Unlimited Canada Spencer T. and Ann W. Olin Foundation Wetlands and Waterfowl Research Fellowship; $23,500 **2019**
- Research funding – Utah State University Ecology Center; $2,450 **2019**
- Research funding – Utah State University Ecology Center; $5,000 **2018**
- Invasive species mitigation grant – Utah Department of Agriculture; $18,331 **2016**
- Invasive species mitigation grant – Utah Department of Agriculture; $16,056 **2015**
- Wetland restoration and education grant – Utah Division of Water Quality; $80,000 **2014**

AWARDS & HONORS

- Doctoral Student Researcher of the Year **2022**
  Utah State University College of Natural Resources

- SUNY-ESF Robin Hood Oak Award **2013**
  in recognition of efforts to improve the quality of campus life
- Who's Who Among Students in American Universities and Colleges Award **2013**
  in recognition of scholastic and community achievements
- SUNY-ESF Maple Leaf Award **2013**
  in recognition of significant volunteer service to the college
- SUNY-ESF President's Award for Community Service **2013**

CERTIFICATIONS & MEMBERSHIPS

- Society for Ecological Restoration | *member* ***Present***
- Society for Wetland Scientists | *member* ***Present***
- Utah Environmental Educator | *professional certificate* **2014**