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RESEARCH

The Role of Seed Bank and Germination Dynamics in the Restoration of a Tidal Freshwater Marsh in the Sacramento–San Joaquin Delta

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ABSTRACT

Liberty Island, California, is a historical freshwater tidal wetland that was converted to agricultural fields in the early 1900s. Liberty Island functioned as farmland until an accidental levee break flooded the area in 1997, inadvertently restoring tidal marsh hydrology. Since then, wetland vegetation has naturally recolonized part of the site. We conducted a seed bank assay at the site and found that despite a lack of germination or seedling recruitment at the site, the seed bank contained a diverse plant community, indicating that the site's continuous flooding was likely suppressing germination. Additionally, the frequency of germinating seeds in the seed bank did not represent the dominant adult plant community. We conducted a cold stratification study to determine if this observed disparity could be explained by seed germination dynamics, and whether germination could be enhanced using a pre-germination cold exposure, particularly for species of concern for wetland restoration. The cold stratification study showed that longer durations of pre-germination cold enhanced germination in *Schoenoplectus acutus*, but reduced germination in *Schoenoplectus californicus*, and had no effect on *Typha latifolia*. Overall, germination of *S. californicus* and *S. acutus* was much lower than *T. latifolia*. Our findings suggest that seeding may not be an effective restoration technique for *Schoenoplectus* spp., and, to improve restoration techniques, further study is needed to more comprehensively understand the reproduction ecology of important marsh species.

KEY WORDS

cold stratification, dormancy, restoration, *Schoenoplectus*, self-design, tidal freshwater, *Typha*

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INTRODUCTION

Worldwide, tidal freshwater wetlands have been in decline as a result of human alteration of natural hydrological regimes (Zonneveld 1960; Dahl 1990; Kotze et al. 1995; An et al. 2007; Barendregt et al. 2008; Davidson 2014). Efficient restoration of these degraded wetlands and creation of new wetlands habitats is desired globally to restore the important ecosystem functions these systems

provide. However, many candidate wetland restoration sites have undergone severe alteration to their physical and biological attributes, inhibiting their ability to achieve restoration goals. The need for successful restoration of tidal wetlands reflects a larger demand to rehabilitate and restore degraded ecosystems in general. The United Nations General Assembly announced earlier this year that 2021–2030 will be the Decade on Ecosystem Restoration (UN 2019). However, knowledge gaps still exist in basic plant ecology, which will be crucial to address, to ensure successful science-based ecosystem restoration, particularly in wetlands.

In tidal freshwater wetlands, three factors are generally understood to be the most influential in controlling ecosystem structure and function: hydrology, species dispersal, and biological dynamics of the species (i.e., ability to cope with abiotic conditions) (Grubb 1977; Harper 1977; van der Valk 1981). Site elevation and corresponding flooding characteristics are often the most influential physical parameters that control the establishment of the plant community (Barendregt et al. 2008; Mitsch and Gosselink 2015). Re-creating the proper hydrology and physical parameters is an essential first step to wetland restoration, but it is only part of a more complex combination of factors that must be addressed (Hilderbrand et al. 2005). Seed dispersal, germination, and seed abundance can further limit restoration outcomes after re-introduction of wetland hydrology (van Leeuwen et al. 2014). Meta-analyses compiled from a variety of ecosystems suggest that colonization of primary successional species depends on the interplay between the propagule and abiotic and biotic limitations on seedling establishment (Seabloom 2011; Titus and Bishop 2014). Additionally, abiotic conditions may differentially limit plant recruitment, depending on species and life-history stage (Shumway and Bertness 1992; Bunn and Arthington 2002; Hinkle and Mitsch 2005). To understand community structure and restoration dynamics, propagule limitations and abiotic constraints on plant recruitment must be understood (Moore and Elmendorf 2006).

Seed banks represent a composite of seeds of varying degrees of dormancy, and play an important role in the long-term and short-term preservation of species at a location (Baskin and Baskin 1978; Bigwood and Inouye 1988; van der Valk and Rosburg 1997; Peterson and Baldwin 2004). Because of limitations on seed dispersal and germination, the seed bank of a site may include a greater diversity of species than what is actually present in the standing adult plant community (Hopfensperger 2007). Understanding the species in the seed bank — and limitations to seed establishment — is crucial for wetland restoration or creation projects (van der Valk et al. 1992). Both self-design and designer restoration strategies would benefit from a better understanding of seed ecology and germination dynamics of key plant species as a means to improve seeding/planting approaches (Zedler 2000) or establish the proper abiotic conditions to facilitate natural recruitment (Palmer et al. 1997).

Seeding, or the intentional introduction of seeds of a target species, is a common restoration strategy in wetlands (Mitsch et al. 1998; Ruiz-Jaen and Aide 2005). Because of dormancy and germination dynamics in desired species, the use of pre-germination seed treatments — such as cold-stratification, dark conditioning, physical scarification, bleach scarification, or repeated cycles of imbibition — may be implemented to accelerate germination or increase total percent germination of seeds. These techniques have been used on a wide variety of species, including agriculturally important crops and target restoration species, throughout diverse biogeographical ranges (Heydecker et al. 1973; Schütz and Rave 1999; Kaye and Kuykendall 2001; Kulkarni et al. 2006). However, data gaps still remain regarding the seed ecology and germination dynamics of species important to freshwater tidal marshes.

In this study, we implemented a seed bank assay at Liberty Island, a post-levee breach wetland restoration site in the Sacramento San-Joaquin Delta in California. To complement our seed bank assay, we also conducted a cold stratification study to understand germination dynamics and determine whether germination in three tidal

marsh plant species could be artificially improved with this technique. Additionally, to understand how hydrology may limit seed germination, we conducted an inundation study in which we exposed seeds (that had already been exposed to various pre-germination cold stratification treatments) to varying depths of flooding.

Our controlled germination studies used seeds from three emergent tidal marsh macrophyte plant species that are native to California and commonly implemented in restoration plantings: California bulrush (*Schoenoplectus californicus*, family: Cyperaceae), hardstem bulrush (*Schoenoplectus acutus*, family: Cyperaceae) and broadleaf cattail (*Typha latifolia*, family: Typhaceae). All three of these species are classified as obligate wetland plant species (USDA 2019) and tolerate being inundated >60% of the day (Sloey et al. 2016). However, much less is known about the hydrologic conditions needed for germination and seedling recruitment in these species. Studies in other regions have reported high seed germination rates in *Typha latifolia* (Sifton 1959; Keddy and Ellis 1985), whereas few studies have examined *Schoenoplectus* spp. germination dynamics. Kellogg et al. (2003) found that *S. acutus* seeds did not germinate when flooded, and showed very low percent germination (1%) even when not inundated. *Schoenoplectus californicus* is documented in literature as producing viable seed, but appears to spread locally mainly via asexual fragmentation (de Lange et al. 1998). Tur and Rossi (1976) found that germination of *S. californicus* varied from year to year, but remained relatively low, and Heiser (1978) reported that seeds collected from *S. californicus* failed to germinate. Other *Schoenoplectus/Scirpus* species have been reported to have low germination rates (Giroux and Bedard 1995), but few studies have specifically focused on *S. californicus* or *S. acutus* within the Sacramento-San Joaquin Delta.

Several studies have investigated techniques to increase germination in a variety of species within the *Schoenoplectus* genus (formerly *Scirpus*), including cold stratification and bleach scarification (Clevering 1995). Although long durations of cold temperatures are not characteristic of California's Mediterranean climate, the intention of our study was to determine if pre-germination treatments could be used to artificially improve species germination; restoration practitioners want this to improve the practices of restoration by seeding. Furthermore, understanding how cold periods affect the way species respond to seed germination may inform understanding of species regeneration and colonization dynamics at broader regional scales. The objective of our study was to (1) determine if viable wetland seeds existed in the seed bank of the Liberty Island mudflats, (2) determine if cold treatment could enhance germination for three dominant wetland plant species, and (3) understand how hydrology affects germination in those three wetland plant species. The overarching goal of these combined studies was to increase understanding of seed-germination requirements and colonization dynamics in tidally-influenced wetlands to maximize restoration efficiency in similar systems in the future.

MATERIALS AND METHODS

Seed Bank Assay

Site Description

Liberty Island is a freshwater (salinity <0.2 ppt) tidal marsh restoration site in the Sacramento-San Joaquin Bay Delta, California (N 38°17' W 121°41'). Regularly flooded areas in the Delta are typically covered by dense stands of emergent plants such as tule (*Schoenoplectus/Scirpus* spp.), cattail (*Typha* spp.), and rushes (*Phragmites* spp.) (Herbold and Moyle 1989). All these emergent wetland plant species tolerate flooded conditions and can reproduce via seed production and asexual clonal expansion. In the early 20th century, levee construction hydrologically altered this wetland, along with 95% of those in the Delta, with extensive parcels of land converted for agricultural use. Liberty Island was drained and farmed for various crops (Malcolm 1981), until the surrounding levee failed in 1997 (Hart 2010). The levee was not repaired, and now the site is regularly flooded by a semi-diurnal tide, and influenced by water exchange between the adjacent rivers, thus restoring tidal marsh hydrology. During the time of this study (June

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to September 2011), water levels at Liberty Island fluctuated between 0.79 m at Mean Lower Low Water (MLLW) to 2.04 m at Mean Higher High Water (MHHW) with a Mean Tide Level (MTL) of 1.43 m (NAVD 88).

Since the levee breach, three emergent wetland plant species have naturally re-colonized Liberty Island: California Bulrush (*Schoenoplectus californicus*), Hardstem Bulrush (*Schoenoplectus acutus*), and Cattail (*Typha latifolia* and *T. angustifolia*), as well as floating and submerged aquatic vegetation (e.g., *Ludwigia* spp. and *Egeria densa*). From bi-annual trips to the site for 3years (2010 to 2012) to investigate the rate of vegetative colonization, Hester et al. (2016) indicated that asexual clonal spread of *S. californicus* dominated vegetation colonization, because they had not observed germination or seedling recruitment at flooded portions of the site. The content of the seed bank before the breach of the levee had not been studied, but since the site had functioned as farmland for nearly a century prior, the seed bank might be expected to contain a mixture of crop species and upland weeds, in addition to some wetland species. Though now a desirable wetland restoration site, the rate of colonization of desired plant species after this levee breach was unknown and unpredictable. Recent concerns about the health of the Delta and the quality of the water supply have given impetus to intentional breaching of levees and re-introduction of tidal marsh hydrology to restore wetlands (Simenstad and Thom 1996; EcoRestore 2018). Given Liberty Island's unique history as an accidental levee breach wetland restoration site, this site is ideal to observe the potential for similar wetland restoration strategies in other parts of the Sacramento-San Joaquin Delta.

Experimental Design

In June (peak growing season) and September 2011 (post seed dispersal), we collected seed bank samples from non-vegetated mudflats at Liberty Island. Sampling sites were located on the west and east sides of Liberty Island in both protected and exposed mudflats (Figure 1). Protected areas were delineated as such because they were located on the bank-side of standing *S. californicus* marsh, whereas exposed areas were located on the open water-side of vegetation. Models of bed shear stress for this area have also indicated that the exposed areas experienced higher wind energy and friction of water moving against the channel bed (Sloey and Hester 2016). In 2011, western protected sites were flooded 93% to 97% of the time, and exposed sites were flooded 82% to 92% of the time; the eastern sites were generally flooded 100% of the time (Sloey et al. 2015; Hester et al. 2016). At each site (hereafter: West Protected, West Exposed, East Protected, and East Exposed), we collected 16 soil samples from the top 5 cm of sediment using an aluminum soil corer (5-cm-diameter). We extracted cores from four replicate sites at each area. Each replicate consisted of four soil cores collected from the top 5 cm of sediment, which were combined and homogenized for a total of 1,570 cm^3 of sediment, or 315 cm^2 surface area, from each site. Hutchings (1986) previously determined that this volume of soil is adequate to determine the seed bank's species composition.

We stored soil cores in the dark at 4 + 1° C for transport from field site to greenhouse. Following common seed bank assessment methods (Ter Heerdt et al. 1996), we homogenized and rinsed each sample on a 0.5-cm metal sieve to remove coarse organic material without removing seeds. We then spread oil samples no thicker than 1.5 cm on top of sterilized (rinsed and heated) sand in plastic containers. We perforated each container at the bottom and placed it in an individual reservoir of water to keep seed bank soils moist but not flooded. We placed samples in a randomized fashion in a greenhouse at the Ecology Center at the University of Louisiana at Lafayette. Temperatures in the greenhouse ranged from 15° C to 36° C during this time. Using the emergence method (van der Valk and Davis 1978; Kirkman and Shartiz 1994; Leck and Simpson 1995; Baldwin et al. 1996; Baldwin and Derico 1999; Peterson and Baldwin 2004), we enumerated germinating seeds and allowed them to grow until we could identify them to species (up to 4 months). To prevent competitive exclusion of other species, we removed seedlings once identified. From each seed bank core collected, we determined the species richness and seed density (number of each germinating species) per sample.

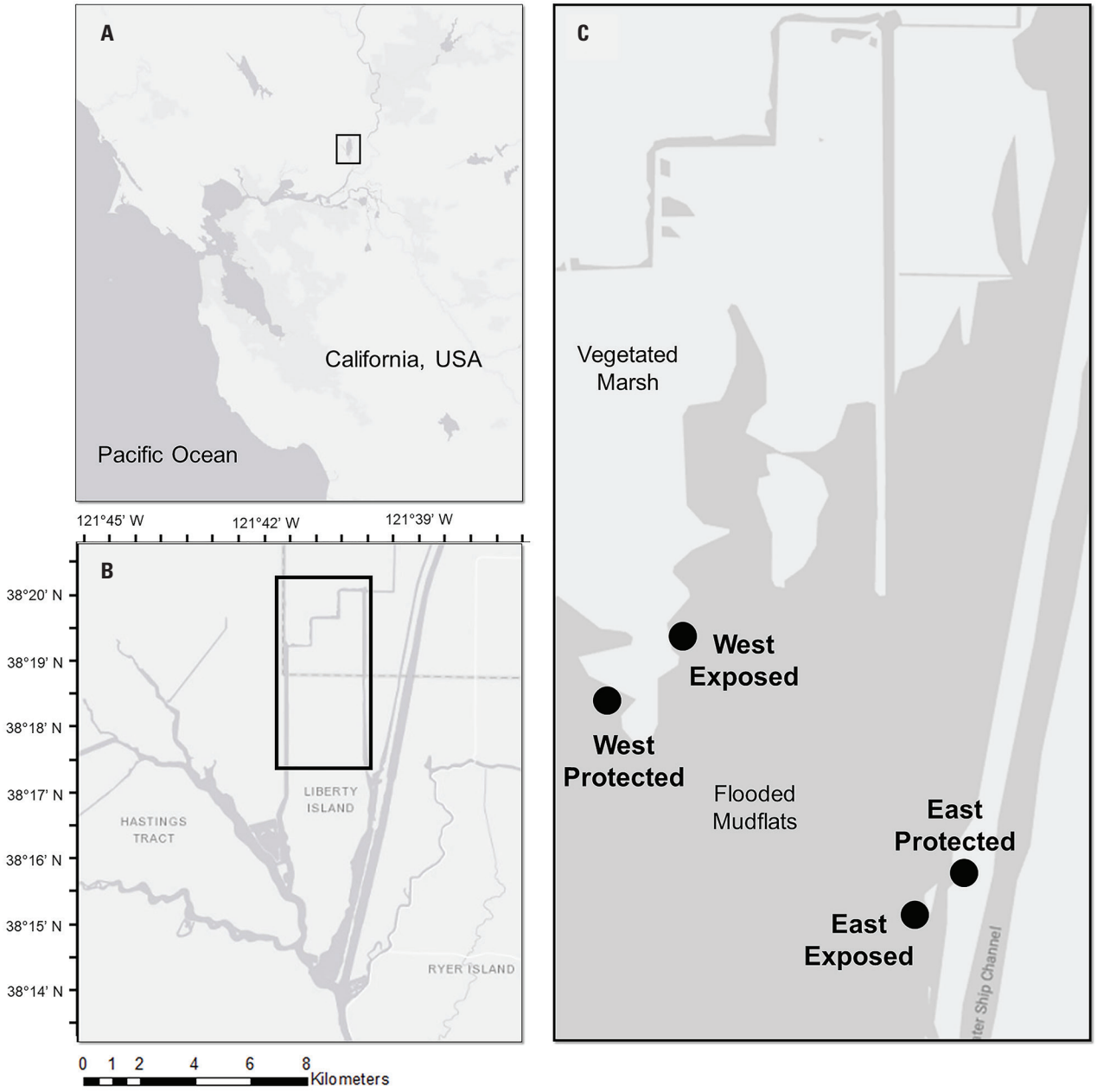

Figure 1 (**A**) Location of Liberty Island within the greater Sacramento-San Joaquin Delta; (**B**) Liberty Island restoration site (N 38°17′ W 121°41′); (**C**) Seed bank sampling locations at Liberty Island

We analyzed all data using an Analysis of Variance (ANOVA) (SAS 2010). We used a Tukey post hoc test to analyze all pairwise comparisons. We extrapolated values for the area surveyed to obtain the average seed density per m^2 (Table 1). The ANOVA revealed no significant effect of sampling month (June vs. September), so we removed sampling month as an effect, and combined samples for further analysis. We used an ANOVA to test the effect of site (West vs. East) and exposure (Exposed vs. Protected) on species richness and seed density. We tested all data for normal distribution and used a Tukey post hoc test to analyze all pairwise comparisons.

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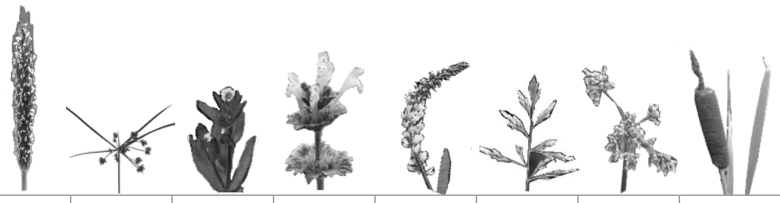
Table 1 Relative abundance of species in the seed bank (expressed as a percentage of the total number of seeds germinating from the sediment collected from each site). Actual N = total number of germinating seeds observed from each site collection (315 cm^3); N/m^2 = extrapolated number of seeds per square meter.



	Actual N	N m^{-2}	*Alopecurus carolinianus* Native | FACW	*Cyperus eragrostis* Native | FACW	*Gratiola ebracteata* Native | OBL	*Lamium amplexicaule* Non-Native | UPL	*Melilotus alba* Non-Native** | FACU	*Poa annua* Non-Native | FAC	*Schoenoplectus californicus* Native | OBL	*Typha* sp. Native | OBL	Unknown dicot tree
			Percentage of seeds per species								
West Exposed	245	8167	0	20.4	0	0.4	0	0	0.8	78.4	0
West Protected	26	867	0	15.4	3.8	0	3.8	3.8	3.8	69.4	0
East Exposed	20	667	10	20	0	0	0	0	5	60	5
East Protected	64	2133	1.6	7.8	0	0	0	0	7.8	82.8	0

Cold Stratification Study

Experimental Design

We tested the effect of cold stratification on germination of three wetland plant species (*Schoenoplectus acutus*, *S. californicus*, and *Typha latifolia*) using eight pre-germination cold duration treatments (untreated [0 weeks], 1 week, 2 weeks, 3 weeks, 4 weeks, 8 weeks, 12 weeks and 16 weeks), with four replicates of each treatment combination. We obtained untreated seeds from Stover Seed Company (Los Angeles, California, USA). We rinsed seeds with deionized water and placed 25 seeds of a single species on Whatman #3 filter paper in clear plastic Petri dishes (10-cm diameter) to which we added 20 ml of de-ionized water to moisten the filter paper. We sealed Petri dishes with transparent lids to prevent desiccation and remoistened them every 5 days, as needed. We assigned each experimental unit, or Petri dish, a cold stratification duration, and kept it in dark conditions at 4 °C + 1 °C for the assigned time. After cold stratification, we exposed seeds to alternating photo-thermo periods of 14 hours at 25 °C in light and 10 hours at 10 °C in darkness, in randomly assigned positions in the growth chamber. Stratification methodology and light regimes were based on previous germination studies (Thullen and Eberts 1995; Baskin et al. 2000; Gucker 2008). Temperatures were based on a 30-year average of daily summer temperatures in Sacramento, California (~30 km from Liberty Island), which averaged 22-24 °C (NOAA 2008). We enumerated and removed seeds as they germinated. We then measured each unit for total percent germination (number of seeds that germinated after 100 days) and germination rate (speed of seed germination). We analyzed data in SAS (SAS 2010), and used an ANOVA to determine the effect of species and duration of cold stratification on total percent germination.

Flooding Study

Experimental Design

We investigated the effect of flooding on seed germination in three species (*S. acutus*, *S. californicus*, and *Typha latifolia*), using four pre-germination cold stratification duration treatments (untreated [0 weeks], 2 weeks, 4 weeks, and 12 weeks); two flooding depths (10 cm and 30 cm); and four replicates of each. We placed all seeds into the bottom of their containers. After cold stratification, we placed 25 seeds of a single species (also obtained from Stover Seed Company)

in clear plastic containers (30-cm tall and 5-cm diameter) and filled them with tap water to the depth of their respective treatment. We placed these containers in the same alternating photo-thermo periods as the cold stratification study (14 h at 25 °C in light and 10 h at 10 °C in darkness). For 100 d, we observed the units every 2 d for seed germination.

RESULTS

Seed Bank Assay

A total of nine species emerged from the seed bank: *Alopecurus carolinianus*, *Cyperus eragrostis*, *Gratiola ebracteata*, *Lamium amplexicaule*, *Melilotus alba*, *Poa annua*, *Schoenoplectus californicus*, *Typha* sp., and an unidentifiable dicot, which died before we could identify it. We enumerated relative abundance of each germinating species for each of the four sampling sites (Table 1). *Typha* sp. and *C. eragrostis* were the most common germinating species, occurring in almost all sites, with *Typha* sp. accounting for more than 60% of the germinating seeds in the seed bank, and *C. eragrostis* accounting for 8% to 20% of the germinating seeds. *Schoenoplectus californicus*, the most prominent plant species in the extant plant community, had a low abundance in the germinating seed bank. Most species we observed were native to California, though several non-native species emerged (Table 1). Seed density per sample was significantly greater at the West Exposed site compared to all other sites, as revealed by a significant interaction between site and exposure ($F_{1,\ 229}\ 15 = 22.5$, $p = 0.0015$). Seed bank samples collected from the West Exposed areas showed an order-of- magnitude greater seed density than West Protected or East Exposed sites, and four times greater seed densities than those collected in East Protected sites.

Cold Stratification Study

The cold stratification study showed significant disparities between germination of species and the effect of cold stratification duration. The ANOVA revealed a significant interaction between species and cold stratification treatment on total percent germination ($F_{14,72} = 14.06$, $p < 0.0001$), so we analyzed the effect of cold stratification on germination at the individual species level. *Schoenoplectus acutus* seeds exposed to 0 to 2 weeks of cold showed no germination, whereas seeds exposed to 3 to 8 weeks of cold showed up to 20% germination — and seeds exposed to 12 weeks to 16 weeks of pre-germination cold stratification showed significantly greater germination than those exposed to shorter durations ($F_{7,24} = 13.75$, $p < 0.001$) (Figure 2). In contrast, *S. californicus* seeds exposed to 8 weeks or longer of cold treatment showed significantly lower germination rates than those exposed to no cold treatment ($F_{7,24} = 2.51$, $p = 0.043$) (Figure 2). Pre-germination cold treatment duration had no effect on *T. latifolia* germination (Figure 2). In general, *T. latifolia* reached peak germination more rapidly than the other species, reaching maximum germination percentages in fewer than 10 days, whereas *Schoenoplectus* spp. seeds took much longer to reach peak germination (30 to 70 days) (Figure 3).

Flooding Study

At the completion of this 100-day study, germination did not occur for any seed of the three species (*S. californicus*, *S. acutus*, or *T. latifolia*) in either flooding treatment (10-cm or 30-cm depths).

DISCUSSION

Wetland restoration outcomes partially depend on the interplay of three controlling factors: (1) hydrology; (2) plant species source (natural recruitment from seed bank, asexual clonal expansion, or planting); and (3) plant biological dynamics (e.g., phenology, physiological tolerance to abiotic conditions, etc). Our studies used a combination of field observations and controlled greenhouse experiments to better understand how hydrology, the existing seed bank dynamics, and improved pre-planting seed treatments can affect freshwater tidal wetland restoration outcomes in the Sacramento-San Joaquin Bay Delta, California.

Hydrology may influence restoration and species establishment through two main pathways: by influencing propagule dispersal and by suppressing germination. The increased density of germinating seeds observed at the West

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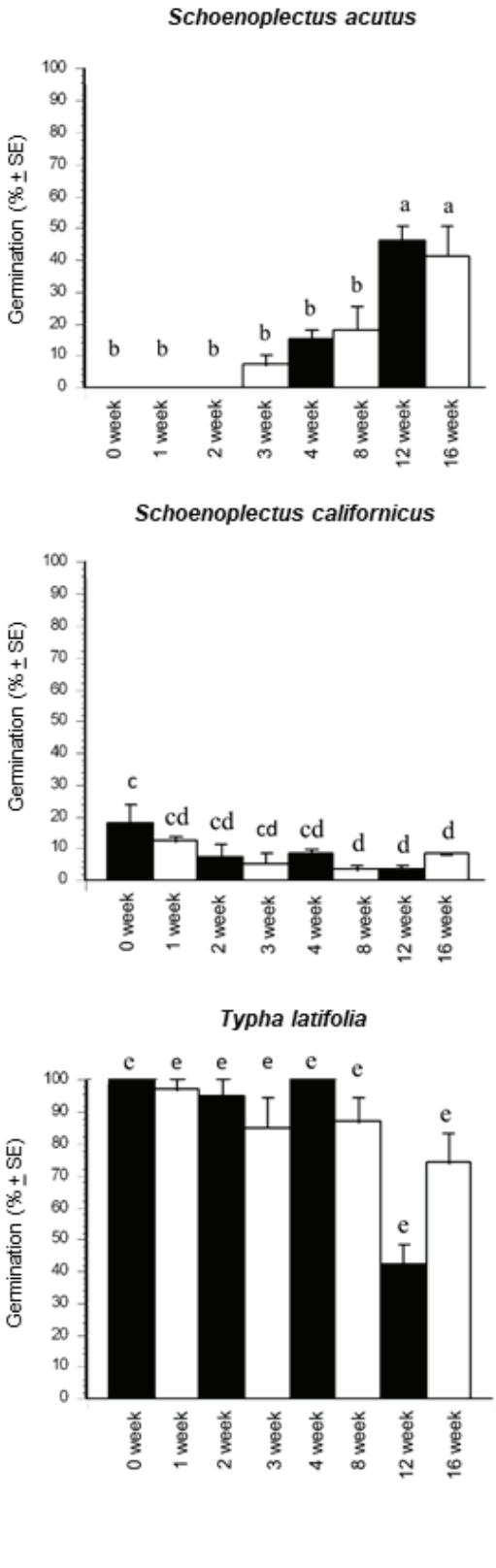

Figure 2 Total percent germination (mean + SE) of *S. acutus*, *S. californicus*, and *T. latifolia* seeds exposed to varying durations of cold stratification

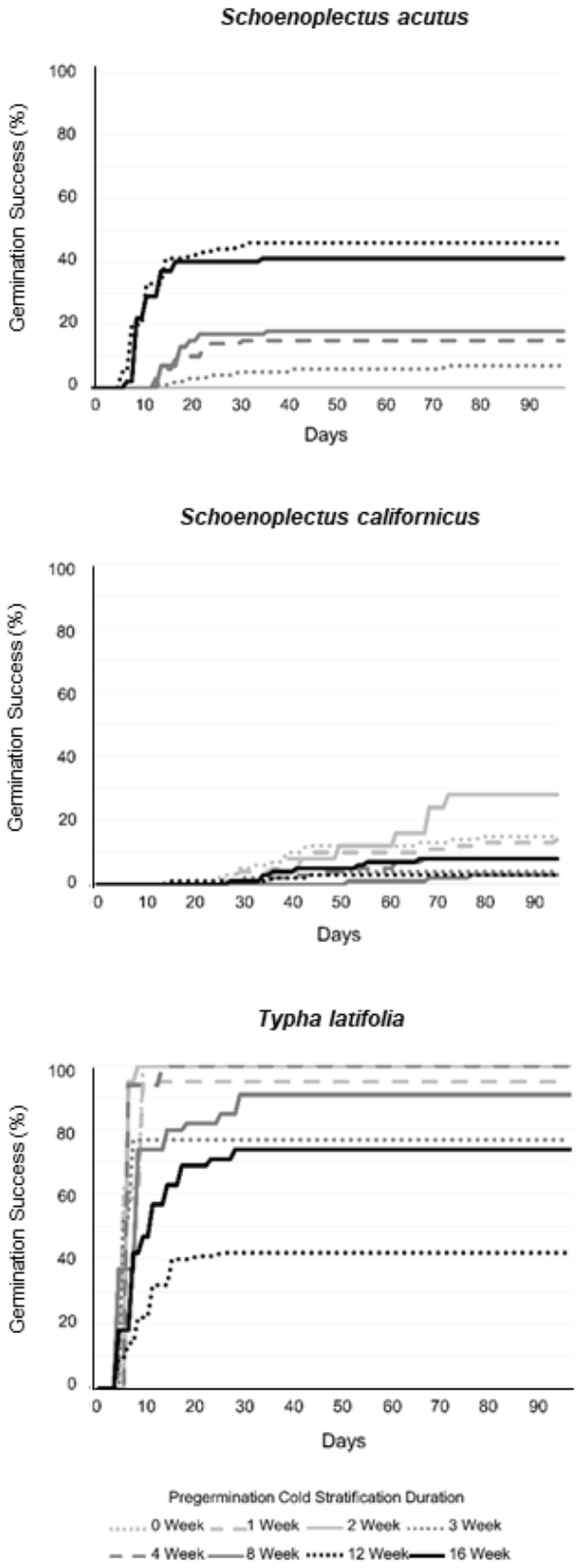

Figure 3 Germination rate for *S. acutus*, *S. californicus*, and *T. latifolia* seeds exposed to varying durations of cold stratification

Exposed sites compared to other sampled sites suggest that prevailing winds and hydrologic flow both control seed dispersal at this site. In Rio Vista, California — the nearest weather station to Liberty Island — the dominant wind direction is from southwest to northeast (Windfinder 2018). Additionally, semi-diurnal tidal movement runs from north to south. With these combined influences, it makes sense that congregation of anemochorous seeds may occur on the west side of an existing stand of seed-producing vegetation, whereas seeds produced in the West Protected or East Protected sites may be translocated out of the immediate area (Figure 1).

Furthermore, the hydrology at Liberty Island appears to prohibit seed germination. Our field observations and seed bank assay demonstrated that even if viable seeds are present in the seed bank, the site's hydrology may suppress germination of those species. Our controlled inundation experiment further supports this observation, because none of the seeds germinated when flooded.

Although hydrologic regime plays a pivotal role in wetland restoration, the ability for restored wetlands to meet desired ecosystem goals and trajectories depends on more than the re-establishment of wetland hydrology (Zedler 2000). Nature management practices that involve re-wetting or re-introduction of wetland hydrology after severe drainage rely on the seed bank or seed dispersal as a sources of species (Oomes 1992; Grootjans and Van Diggelen 1995; Bakker et al. 1996). The seed bank assay at Liberty Island showed a greater proportion of *Typha latifolia* and *Cyperus eragrostis* seeds, whereas *S. californicus* dominated the adult community. van den Broek et al. (2005) conducted a comprehensive study that compared the seed buoyancy of a variety of wetland plant species with the flooding regimes at which those species reside. Although their study did not directly address *Schoenoplectus* spp., *Typha latifolia*, or *Cyperus eragrostis*, their findings suggest that species that tolerate longer durations of flooding also have seeds with longer buoyancy times. Thus, we might conclude that flood-tolerant *Schoenoplectus* spp. seeds may have floated out of the system, whereas *Cyperus* and *Typha* seeds may sink faster and have a shorter dispersal range. However, given the sheer volume of *Schoenoplectus* spp. seed sources compared to other species at the site, factors other than buoyancy are likely to influence our observations. Thus, biological qualities such as physiological tolerance to flooding and germination dynamics play an important role in controlling species composition at this site.

The low abundance of *S. californicus* in the seed bank assay was likely a result of the seeds' poor germination success. While it is understood that the emergence method may not comprehensively assess seed flora (Major and Pyott 1966; Galinato and van der Valk 1986), many studies have reported high germination rates in *Typha latifolia* (Sifton 1959; Keddy and Ellis 1985), whereas germination rates reported for *Schoenoplectus* spp. are generally very low. Maximum documented germination for *S. acutus* (85.6%) was reached artificially through in vitro embryo cultures (Lauzer 2003). Studies that investigated germination of other *Schoenoplectus/Scirpus* species reported similarly low germination success, and concluded that seeding is an ineffective restoration strategy for this genus (Giroux and Bedard 1995). Our cold stratification study showed that *T. latifolia* seeds do not require pre-germination treatments to exhibit maximum germination success, whereas longer durations of pre-germination cold exposure increased germination rates in *S. acutus*. The treatment was unsuccessful for improving germination in *S. californicus*. It is possible that *S. californicus* seeds exist in a state of "natural dormancy" and have low germination (Brenchley and Warington 1930; Fenner 1985). Numerous wetland restoration projects use seeding and seed mixes (Reinartz 1993; Mitsch et al. 1998; Ruiz-Jaen and Aide 2005; MBWSR 2017), and many restoration projects worldwide incorporate *Schoenoplectus* spp. because this cosmopolitan and ethnobotanically significant genus is ideal for providing habitat, nesting, and food to species of waterfowl desirable for hunting and recreation (USFWS 1985; DiTomaso and Healy 2003). Our study, like many before it, suggests that *S. californicus* is not suitable for seeding,

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and predominantly spreads via asexual clonal expansion (de Lange et al. 1998).

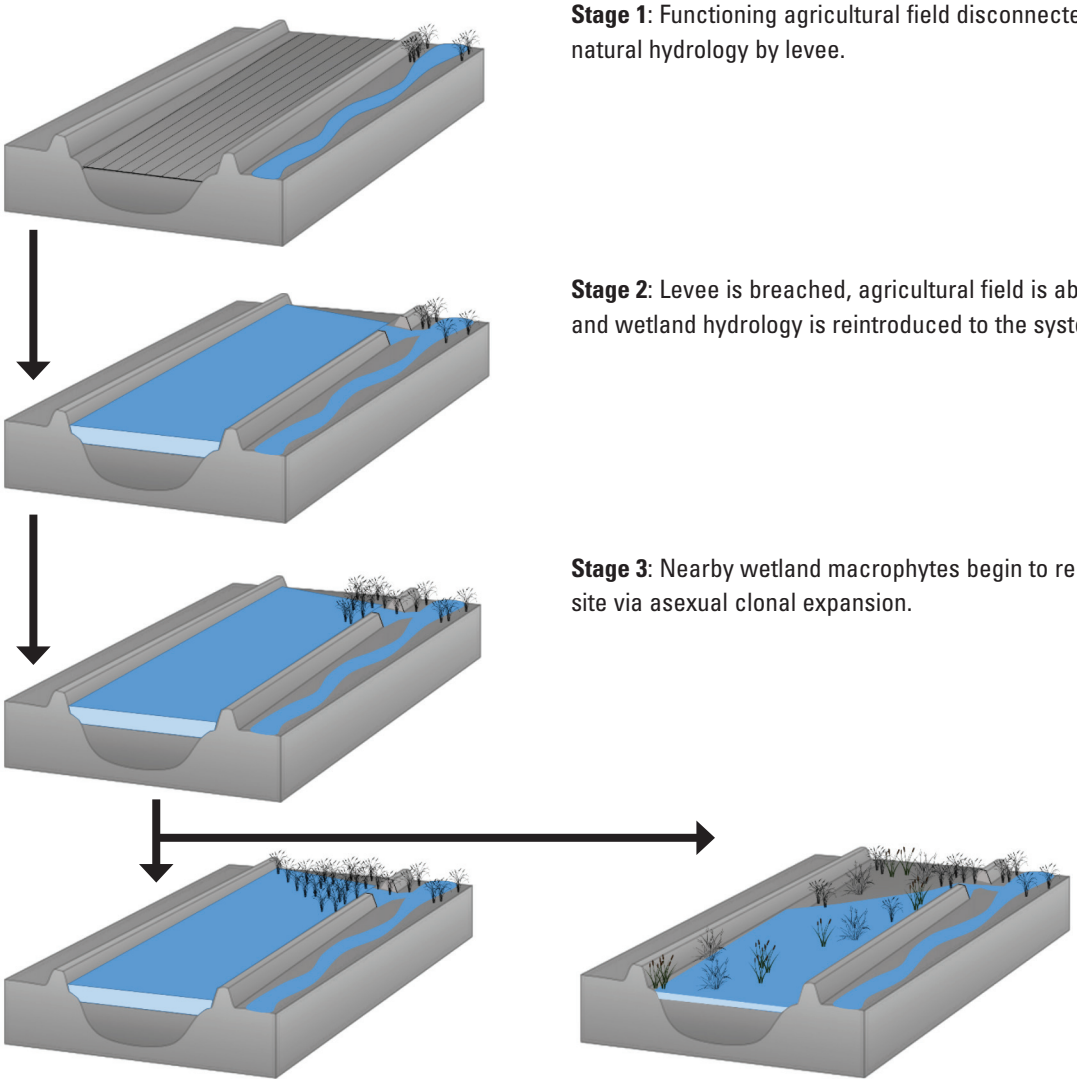
RECOMMENDATIONS FOR RESTORATION

Vast areas of historically converted agricultural fields have been abandoned worldwide (Benayas et al. 2007), and knowing how to effectively restore these sites is increasingly important (Haynes and Moore 1988; Galatowitsch and van der Valk 1995; Middleton 1999). The efficacy of converting these farmlands back to wetlands — with ecosystem structure and function equivalent to a natural wetland — depends on the physical setting of the site (hydrology, elevation, hydrologic exchange, etc.), as well as the species source, and the availability and recruitment of seeds and propagules under these physical settings (Middleton 1999). Below, based on these combined studies, we offer some suggestions and insights for tidal freshwater wetland restoration in the Sacramento-San Joaquin Bay Delta.

First, to achieve restoration goals, seed dispersal is not recommended for *Schoenoplectus* spp. Transplanting *S. acutus* and *S. californicus* adults at their respective appropriate elevation/hydrologic regimes can be successful, but using seeds is not recommended. Additional research is warranted to determine a pre-germination treatment to significantly improve germination of these species. Second, since reproduction of desired tidal marsh plant species in this region may be largely limited to asexual lateral expansion, we recommend that restoration practitioners plan for a slower rate of ecosystem revegetation in their ecosystem trajectory. The maximum rate of *S. californicus* marsh edge expansion at Liberty Island is approximately 1.0 m year^{-1} (Hester et al. 2016), with slower expansion rates occurring at lower elevations with more compacted soils (Sloey et al. 2015; Hester et al. 2016). Although the site's hydrology may slow the revegetation rate by suppressing the germination of desired species and slowing the rate of clonal expansion, the hydrology also suppresses the germination and establishment of invasive and undesirable species present in the seed bank.

Finally, the interplay among hydrology, species source, and species' ecological dynamics should inform understanding of the long-term evolution of a restored wetland. The hydraulics of a post-levee-breach restored wetland may change over time. The role of the seed bank may become increasingly important after the hydrologic regime continues to evolve, as tidal creeks and breaches change shape, and adjacent plots become reconnected to the larger landscape. For example, during draw-down events or drought, germination and colonization of species once excluded by the site's hydrology may be possible in moist soil versus submerged soil (Smith and Kadlec 1983). Drought, a systemic problem in California and many other regions of the world, has also caused the die-off of bank-stabilizing riparian vegetation (Kondolf and Curry 1984), thus depleting plant communities that were dominant before disturbance. Such change may result in a shift of the dominant plant species community, or allow for establishment of non-desirable or invasive species (Figure 4).

Our results suggest that achieving target hydrology is crucial for attaining a desired species composition and re-vegetation rate. For example, the mudflats of a recently constructed wetland restoration site, at which source populations of *Schoenoplectus* spp. and *Typha* spp. are both present, may slowly become dominated by asexual spread of flood-tolerant *Schoenoplectus* spp. if the hydrology impedes seed germination. However, if the site's hydrology allows for seed germination and seedling recruitment, the mudflat is likely to be rapidly colonized by another species with high germination rates, for example, *Typha* spp. Species with rapid germination rates, such as *Typha* spp., are competitive for colonizing mudflats even if the draw-down period is relatively short. In this circumstance, previously established dominant species like *S. californicus* and *S. acutus* may still persist, but will likely expand at a slower rate because their seed fecundity is low, resulting in a *Typha* spp.-dominated plant community. If water levels fluctuate at the restoration site, longer durations of flooding (>90% of the day) may cause mortality in *T. latifolia* seedlings and adults, whereas adult *Schoenoplectus* spp. will



Stage 1: Functioning agricultural field disconnected from natural hydrology by levee.

Stage 2: Levee is breached, agricultural field is abandoned, and wetland hydrology is reintroduced to the system.

Stage 3: Nearby wetland macrophytes begin to recolonize the site via asexual clonal expansion.

Stage 4A: Hydrology prevents seed germination and the site is gradually recolonized through clonal expansion of flood tolerant monocultures (e.g., *Schoenoplectus californicus*).

Stage 4B: In a drawdown event, or after sedimentation and accretion, reduced flooding allows for seed germination, more rapid plant colonization of the site, and recruitment of other species, including both native species with high rates of germination, and undesirable non-native species.

Figure 4 Conceptual diagram showing evolution of an abandoned agricultural field following re-introduction of wetland hydrology

survive (Sloey et al. 2015). Ecological theories differ as to whether one particular species is critical for restoration, however a dominant species does influence ecosystem development and function (Junk et al. 1989; Smock and Gilinsky 1992; Middleton 2003). It is important to recognize that the relationship between seed bank composition and hydrology may influence the system well beyond the initial phase of a restoration effort.

Self-design restoration approaches have long been criticized for failing to account for a lacking seed bank (Middleton 2003), but even when viable seeds are present, restoration success (defined as meeting pre-determined target species goals and ecosystem trajectories) is not guaranteed. Seedling germination and seedling establishment are essential for wetland succession (van den Broek and Beltman 2006); however, germination and/or establishment may be unachievable given

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differences in species seed dormancy, tolerance to hydrology, and presence of undesirable species. To best position the site for successful recruitment of desired species, it is important that (1) source species (via seed and asexual expansion) be proximal to the site (Reinartz 1993), (2) proper hydrology is maintained, and (3) the site is monitored regularly to ensure that the development of desired plant communities and conditions is on track. Finally, a commitment to incorporating empirical science and monitoring in restoration practice will continue to advance our knowledge base of species ecology while helping restoration efforts achieve their goals.

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