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THE ECOLOGY AND GENETICS OF *SCHOENOPLECTUS MARITIMUS*, AN
IMPORTANT EMERGENT MACROPHYTE, ACROSS DIVERSE
HYDROLOGIC CONDITIONS—IMPLICATIONS FOR
RESTORATION

by

Amanda Sweetman

A thesis submitted for the fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2013

ABSTRACT

The Ecology and Genetics of *Schoenoplectus maritimus*, an
Important Emergent Macrophyte, Across Diverse
Hydrologic Conditions—Implications for
Restoration

by

Amanda Sweetman, Master of Science

Utah State University, 2013

Major Professor: Dr. Karin M. Kettenring
Program: Ecology

Revegetation projects in wetlands are challenging due to questions surrounding where to obtain plant materials and how hydrologic conditions, which are often unpredictable at restoration sites, may impact restoration success. We used a two-pronged approach to inform decisions on seed sourcing. Our study species, *Schoenoplectus maritimus* (alkali bulrush), is a widely distributed wetland plant. First, we investigated how genetic diversity was partitioned within and among populations of *S. maritimus*. We found five weakly differentiated populations and one distinct population. We found high levels of genetic diversity with the majority (92%) of diversity found within rather than among sites (8%). Also, the proportion of viable seed produced was surprisingly high within stands (mean = 0.64 ± 0.02) given the supposed prevalence of asexual reproduction in the species. Second, we conducted two studies to look at the

influence of hydrology, population of origin, and genetic diversity of seeds on the productivity of *S. maritimus*. In a field survey we measured environmental variables and productivity within established *S. maritimus* stands. In a greenhouse experiment we determined how source population identity and the genetic diversity of seeds impacted emergence and productivity under different hydrologic conditions. We found that stands of *S. maritimus* differed in proportion of time with water present, mean water level, and soil conditions. Productivity also differed, with 3-fold differences in stem density and biomass among sites. In the greenhouse experiment, we found that water treatment impacted all productivity measures; source population impacted seedling emergence and biomass allocation; and, number of source populations impacted sensitivity to drought. Advice for future restoration projects includes (1) limiting translocation of seeds among populations to conserve historic lineages, (2) when it is necessary to translocate seeds, collect seeds from many parent plants within populations that are in close geographic proximity to the restoration site, and (3) water level management is extremely important at all life stages of *S. maritimus* and should be an important consideration in wetland restoration and management in this water-limited region.

(88 pages)

PUBLIC ABSTRACT

Amanda Sweetman

Wetlands in the Intermountain West are typically dominated by large monotypic stands of emergent wetland plants, are highly productive, and support millions of migratory birds as important stops along the Pacific Flyway. In systems with low species diversity, such as these, diversity within a species (intraspecific diversity) can play an important role in population fitness and ecosystem functioning and can impact restoration success. Our research was designed to inform future restoration and management activities by studying the pattern of diversity within and among natural plant populations, and by studying how hydrology and plant materials used in restoration (source and diversity of seeds) influenced plant success (establishment and productivity). We focused our research on *Schoenoplectus maritimus* L Lye. (alkali bulrush), a wide-spread wetland plant that is widely used in restoration projects in our study area due to its' ecological importance.

In our second chapter we evaluate genetic diversity within and among stands of *S. maritimus* at six sites of southern Idaho and Utah (Bear Lake, Salt Creek, Bear River, Ogden Bay, Farmington Bay, and Fish Springs). We found that most genetic diversity was found within stands of *S. maritimus* and that all stands sampled are distinct populations. One population, Fish Springs, which was an isolated spring complex in the West desert of Utah, was very distinct from the other populations. We also found that the proportion of viable seeds produced was surprisingly high.

In our third chapter we discuss a field study and a greenhouse experiment that were conducted to look at the influence of hydrology, population of origin, and genetic diversity of seeds on *S. maritimus*. In the field study we measured environmental variables and productivity within established *S. maritimus* stands. In the greenhouse experiment we determined how source population identity and the genetic diversity of seeds impacted emergence and productivity under different hydrologic conditions. We found that stands of *S. maritimus* differed in proportion of time with water present, mean water level among sites, and soil conditions. Productivity also differed, with 3-fold differences in stem density and biomass among sites. In the greenhouse experiment, we found that productivity was reduced dramatically by drought and that seeds from some sources had greater seedling emergence and partitioned biomass to leaves or roots differently.

The results of the research presented here have important implications for the management and restoration of *S. maritimus*-dominated wetlands. First, populations of *S. maritimus* are sufficiently differentiated such that there should be limited translocation of plant materials between populations to conserve historic lineages. Second, if there are no remnant populations at a restoration site from which to obtain seeds, restoration practitioners should target source populations in close physical proximity to the proposed restoration area as no one seed source outperformed others in the greenhouse experiment. Third, genetic diversity is high within sites and genetic diversity may increase restoration success and reduce the risk of inbreeding, make sure to collect from many parent plants at any given site. Fourth, water level management is extremely important at all life stages of *S. maritimus* and should be an important consideration in wetland restoration and management in this water-limited region.

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Amanda C. Sweetman

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CHAPTER 1

INTRODUCTION TO WETLANDS OF THE INTERMOUNTAIN WEST REGION OF THE UNITED STATES, STUDY SPECIES, AND STUDY QUESTIONS

Restoration of wetlands in the arid Intermountain West region of the United States is becoming increasingly important as water resources become less predictable under continuing climate change. These wetlands are typically dominated by large monotypic stands of emergent wetland plants, are highly productive, and support millions of migratory birds as important stops along the Pacific Flyway (Olsen et al., 2004). In systems such as these, with low species diversity, research has shown that diversity within a species (intraspecific diversity) plays an important role in population fitness and ecosystem functioning, and can impact restoration success (Bangert et al., 2005; Reusch and Hughes, 2006). Therefore, research is needed to better understand the pattern of diversity in these natural plant populations and the importance of intraspecific diversity to ecosystem functioning to improve restoration practices such as seed sourcing.

Understanding the relationships between hydrology and productivity is also necessary to inform restoration success. To inform management and restoration practices, I evaluated the pattern and structure of genetic diversity in *Schoenoplectus maritimus* (alkali bulrush) to inform seed collection practices, and examined possible drivers of productivity and ecosystem functioning in these wetlands under diverse hydrologic conditions.

Deciding where to obtain plant materials for a restoration projects is challenging. Current best management practice is to use locally collected, genetically diverse seeds (Sackville Hamilton, 2001; Johnson et al., 2010). However, without direct information on the pattern and structure of genetic diversity within a species it is difficult to know where

and how to collect seeds. The translocation of seeds between populations not historically connected via gene flow can result in disrupting the genetic structure of the species and decrease landscape-scale diversity (Sackville Hamilton, 2001). The informed sourcing of seeds can avoid reductions in population fitness due to outbreeding depression (Montalvo and Ellstrand, 2001) and the displacement of local genotypes by more competitive alien genotypes (Saltonstall, 2002).

Genetic diversity within populations is important to restoration success for two reasons: genetic variation is the source of adaptive potential within species to react to new selective pressures such as climate change (Slatkin, 1987; Rice and Emery, 2003), and genetic diversity is correlated with population fitness and ecosystem functioning (Reed and Frankham, 2003; Bailey et al., 2009). Using seeds from low diversity seed sources can increase the risk of inbreeding depression, which can negatively impact establishment (Williams, 2001) and reproductive success (Charpentier et al., 2000). Low levels of genetic diversity in plant populations have also been associated with reduced annual productivity (Crutsinger et al., 2006), arthropod diversity (Bangert et al., 2005), resistance to disturbance (Hughes et al., 2004), recovery after disturbance (Reusch et al., 2005), and reproductive success (Reed and Frankham, 2003).

Genetic diversity within a species can also plant drive response to hydrologic extremes. (Ennos, 1985; Howard, 2010). However, there is relatively little research on the effect of intraspecific diversity on wetland plant response to hydrologic extremes (Loreti and Oesterheld, 1996; Lessmann et al., 1997; Chen et al., 2009), which is crucial information for wetland revegetation projects as flooding and drought can be detrimental to the productivity and establishment of wetland plants.

In Chapter 2, I investigate the pattern and structure of genetic diversity in *S. maritimus* to make recommendations to practitioners concerning where to collect seeds for restoration of *S. maritimus*. Patterns of genetic diversity are particularly interesting within this species because it is widely used for restoration projects in the region and because of the lack of information on population structuring and genetic diversity within the species. I specifically address the questions: (1) how is genetic variation partitioned among stands of *S. maritimus* (2) what are the levels of within-population genetic diversity, and (3) are pairwise geographic and genetic distances correlated? I collected genetic material from six stands of *S. maritimus* in Utah and Southern Idaho in the summer of 2009. The results of this study will indicate how similar populations of *S. maritimus* are to one another, and inform future seed sourcing.

In Chapter 3, I detail two studies exploring possible drivers of productivity and establishment of *S. maritimus* both in natural populations and in a controlled greenhouse study. In the descriptive field study, I measured productivity of four *S. maritimus* seed source populations, and quantified how water level and other abiotic factors might influence productivity in the summer of 2009. In the greenhouse trial, I focused on how hydrologic extremes, source population identity, and the number of source populations used for revegetation impacted emergence and productivity of *S. maritimus*. These findings will provide useful information for future management of limited water resources, and for the sourcing of seeds for restoration.

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CHAPTER 2
THE PATTERN AND STRUCTURE OF GENETIC DIVERSITY OF
SCHOENOPLECTUS MARITIMUS: IMPLICATIONS FOR
WETLAND REVEGETATION^{1,2}

Abstract

When collecting seed for wetland restoration projects, it is important to understand the genetic diversity within and among source populations to balance the risks of inbreeding and outbreeding depression while maintaining genetic diversity to maximize adaptive potential. To inform future restoration projects, we investigated the patterns and structure of genetic diversity of *Schoenoplectus maritimus* L. Lye. stands within six wetlands in Utah and Idaho, U.S.A. *S. maritimus*, a perennial wetland plant, reproduces via seed and clonal spread and is an obligate outcrosser. Our results indicate the presence of five weakly differentiated populations and one distinct population (Fish Springs). We found high levels of genetic diversity with the majority (92%) of diversity found within rather than among sites (8%). We also found that the proportion of viable seed produced was surprisingly high within stands (mean = 0.64 ± 0.02) given that *S. maritimus* is a clonally spreading plant. Taken together, these findings indicate that (1) all populations sampled were genetically distinct and (2) that the high levels of genetic diversity, and therefore increased availability of outcross pollen, may contribute to the

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high proportion of viable seeds produced. We suggest that each population be treated as an independent management unit to preserve population structure and that seeds be collected broadly within one or a few populations in close geographic proximity to a proposed restoration site to minimize the risk of inbreeding or outbreeding depression and increase the adaptive potential of restored plant populations.

1. Introduction

There is growing evidence that genetic diversity within and among plant populations is a form of biological insurance critical to the short- and long-term success of natural and restored populations (Hughes et al., 2004; Naeem, 2006; Bischoff et al., 2008). Genetic diversity *within* populations (*i.e.*, allelic diversity) is positively related with population fitness (Reed and Frankham, 2003) and ecosystem function (Hersch-Green et al., 2011), and it is a source of raw genetic material for species to adapt to novel selective pressures (Slatkin, 1987; Rice and Emery, 2003). It follows that using low-diversity plant materials in restorations can cause genetic bottlenecks that lead to reduced population fitness (Williams, 2001). Genetic diversity *among* populations represents the species' evolutionary history (unique combinations of genetic drift and selection) and potential adaptation to local conditions. Disrupting population structure via the translocation of seeds for restoration may increase the risk of outbreeding depression (the reduced fitness in hybrids between local and non-local plants) (Montalvo and Ellstrand, 2001). Balancing the risks of inbreeding and outbreeding depression while maintaining diversity to maximize adaptive potential are common challenges in restoration (Edmands, 2007).

Making appropriate decisions about seed source populations for restoration requires an understanding of genetic structuring in native populations of target species (Fenster and Dudash, 1994; Fant et al., 2008; Vander Mijnsbrugge et al., 2010). Genetic structure within and among these populations is a function of the degree of sexual vs. asexual reproduction; the dispersal dynamics of rhizomes, pollen, and seed; and landscape features influencing seed germination and recruitment (Watkinson and Powell, 1993; Silvertown and Charlesworth, 2001; Santamaria, 2002). However, direct measurement of genetic structure is cost prohibitive for most restoration projects. Therefore, there is a need for studies that investigate genetic structure of plant species or groups of species, which are broadly utilized in restoration and underrepresented in the scientific literature, such as emergent wetland plants. Emergent wetland plants, many of which spread via seed and clonal expansion, form large stands that provide important functions in wetlands (Zedler and Kercher, 2005; Mitsch and Gosselink, 2007). The patterns of genetic diversity within and among populations of emergent wetland plants on the landscape are of particular interest because genetic structure within these species can be complex due to the addition of asexual reproduction. Research that does exist on emergent wetland plants gives divergent predictions on genetic structuring (and therefore inconclusive recommendations for wetland revegetation projects) (Charpentier et al., 2000; Santamaria, 2002; Bussell et al., 2006).

For example, when rates of sexual reproduction are low in these species, particularly in obligate outcrossers, clones may become large and clonal richness (within population genetic diversity) may be quite low (Silvertown, 2008; Kettenring and Mock, 2012) providing source populations of limited genetic material for restoration

(Charpentier et al., 2000). Low levels of within-population genetic diversity would suggest that restoration practitioners should collect from multiple stands to capture high enough levels of diversity to avoid inbreeding and decreases in ecosystem function.

In contrast, a combination of wind pollination and broad seed dispersal by migratory birds could result in a very low degree of population structuring (among population diversity) (Wongsriphuek et al., 2008), suggesting the use of broader seed collection zones within areas of natural gene flow to maximize allelic diversity in restored populations (Broadhurst et al., 2008). Alternatively, populations of many aquatic species have high among-population genetic variation due to historic isolation via biological or geographical barriers to dispersal (Santamaria, 2002), resulting in pronounced population-level structure. This structure suggests the use of small, localized seed collection zones in restoration to minimize interbreeding of divergent populations.

In this study, we focus on the patterns of genetic diversity and how genetic diversity is related to one measure of fitness, viable seed production, in *Schoenoplectus maritimus* L. Lye (alkali bulrush) stands within six sites in Utah and Idaho, U.S.A. We specifically address the questions: (1) how is genetic variation partitioned among populations of *S. maritimus* (*i.e.*, number of populations and how different they are from one another), (2) what are the levels of within-population genetic diversity, and (3) how is genetic diversity related to reproduction? *S. maritimus* was selected, in particular, because it is globally distributed and is one of the dominant species in wetlands of the study region (Great Salt Lake watershed). It also has global importance as a source of food and nesting habitat for migratory birds that use the wetlands along the Great Salt Lake (GSL)—a critical stop for birds on the Pacific and Central Flyways (Olsen et al.,

2004; Dugger et al., 2007). Wetlands in the GSL watershed, as with many other wetland systems, have been highly impacted by land use conversion, water limitations due to upstream diversions for agriculture, and invasive species (Olsen et al., 2004; Denton, 2007). Improving our understanding of the pattern and structure of genetic diversity within *S. maritimus* will not only advance restoration with this important species, but can also suggest important avenues of inquiry for future work with other emergent wetland plants in disturbed systems.

2. Methods

2.1. Study species

S. maritimus grows in large monospecific stands in fresh and brackish wetlands worldwide. *S. maritimus* reproduces vegetatively through rhizomes and tubers. Rhizomes and aboveground shoots can live for one growing season while tubers can persist for several years (Lieffers and Shay, 1982). Sexual reproduction via wind pollination produces achenes, which are buoyant, ripen in late summer, and are primarily dispersed by water and waterfowl (Charpentier et al., 2000). The species is self-incompatible, and stands with few genetic individuals can have reduced fecundity due to pollen limitation (Charpentier and Stuefer, 1999; Charpentier et al., 2000). In our region of study, *S. maritimus* has been observed growing in widely different environments, and exhibits a broad range of phenotypes within and among different stands, suggesting possible genetic differentiation (Chapter 3).

2.2. Site selection and sampling

We studied *S. maritimus* at six sites located on public lands in Utah and southern Idaho (Figure 2.1). Here we describe the sites. Sites are listed in geographical order, with the most northerly site being first and the most southerly site being last. The Bear Lake National Wildlife Refuge (Bear Lake), located at 42°12'20.83" N 111°19'30.55" W, was the furthest north, at the highest elevation (1809 m), and separated from the other sites by the Bear River mountain range. The Salt Creek Waterfowl Management Area (Salt Creek), located at 41°40'19.76" N 112°13'30.94" W elevation 1302 m, was north of the GSL and primarily influenced by stream and spring discharge. The Bear River Migratory Bird Refuge (Bear River), located at 41°28'45.43" N 112°16'00.81" W elevation 1284 m, was located at the northern end of the GSL. The Ogden Bay Waterfowl Management Area (Ogden Bay), located at 41°10'37.40" N 112°09'49.40" W elevation 1286 m, was located along the eastern shore of the GSL. The Farmington Bay Waterfowl Management Area (Farmington Bay), located at 40°55'43.00" N 111°55'48.04" W elevation 1283 m, was located along the southeastern shore of the GSL. The Fish Springs National Wildlife Refuge (Fish Springs), located at 39°53'50.80" N 113°23'04.77" W elevation 1308 m, was an isolated spring-fed wetland complex, separated from the other sites and the GSL by the West Desert. Distances between sites ranged from 24 km to 172 km. Within each site we found three monotypic stands (>90% cover by *S. maritimus*) that were at least 150 m apart. Within each of these stands we haphazardly established three 1 m² plots that were 5-20 m apart. We recorded GPS coordinates for each plot to calculate geographic distances between each plot, stand, and site. To look at patterns of *S. maritimus* genetic diversity within and among populations, we collected a single *S. maritimus* leaf in three

of the corners (haphazardly chosen) of each plot at five of the sites in fall 2009. Leaves were immediately placed in a granular silica desiccant, where they were stored until DNA extraction. The majority of plants had already senesced at Fish Springs in the fall of 2009—which necessitated the collection of samples in August 2010 to obtain fresh tissue. We looked at stand-level data to assess the relationship between genetic diversity and viable seed production. We haphazardly chose one *S. maritimus* seed head per plot for an assessment of viable seed production (n=3 seed heads per stand). Note that Fish Springs was not included in this analysis as seeds could not be collected at all sites due to logistical constraints. We assessed seed viability using an illuminated desk magnifier with a 1.75× magnification. Achenes were considered viable if they were firm and brown in color and full of endosperm. Shriveled or shrunken achenes with little to no endosperm were considered non-viable. Previous investigations found that these classifications reflected germination ability of non-dormant seeds (Kettenring, *unpubl. data*). We averaged the total number of viable and non-viable seeds for the three seed heads to obtain the mean stand-level proportion of viable seeds.

2.3. Genotypic analyses

2.3.1. Methods for AFLPs and extraction

Genomic DNA was extracted from genetic samples using a QIAGEN DNEasy 96 Plant Kit, following the manufacturer's protocol. Amplified Fragment Length Polymorphisms (AFLPs) analysis was performed following Vos et al. (1995), with modifications described in Mock et al. (2004). A set of 8 selective primer combinations were used in the AFLP analysis, all with a 6-FAM fluorescent label on the Eco primer:

(Eco-AGG/Mse-ACT; Eco-ACG/Mse-ACA; Eco-ACC/Mse-ACT; Eco-AGG/Mse-ACA; Eco-ACG/Mse-AGT; Eco-ATC/Mse-AAG; Eco-ATC/Mse-ACA; Eco-ACG/Mse-ATC).

An ABI 3730 automated sequencer was used with a LIZ 500 (Applied Biosystems) size standard to separate the amplicons, which were scored using Genographer 2.1 software (Benham, 2001). Ten percent of the samples were replicated from the extraction step as a quality control measure. Individual loci were scored if they were polymorphic (maximum of 95% either present or absent) and if there was a clearly dichotomous pattern (present vs. absent) across the sample set.

2.4. Data analysis

2.4.1. Genet identification

Due to the clonal nature of this species, we needed to determine how many of the individual samples (ramets) were the same genetic individual (a genet). However, the presence of low-level polymorphism from somatic mutations and scoring errors prevented us from using the simple criterion of any mismatches to identify distinct genets. Therefore, we used the strongly bimodal nature of the distribution of the number of mismatches present across all loci and individuals to distinguish distinct genets (Meirmans and Van Tienderen, 2004). Multilocus AFLP genotypes differing by 0–7 mismatches (mean 1.7, mode 0) were pooled into single genets (with the most common genotype considered representative), and genotypes differing by between 8 and 52 mismatches (mean 29.1, mode 27) were considered as distinct genets.

2.4.2. Genetic variation among populations

To determine the number of populations we analyzed population structuring at both the individual and site-level. To assess the probability that an individual sampled at a site actually originated at that site (based on site allele frequencies), we used the population assignment test in AFLPop 1.1 (Duchesne and Bernatchez, 2002). The number of populations (K) and the probability that individual samples assigned to those populations was found using the software program STRUCTURE (Pritchard et al., 2000). As per Falush et al. (2007), we used the admixture model and assumed correlated allele frequencies among populations. We also used the default settings in STRUCTURE: alpha was inferred from the data and lambda was set to one. Our burn-in length was 10,000 iterations and we used 20,000 Markov chain Monte Carlo (MCMC) iterations. We tested K=1–8 with 20 iterations per K without using prior site identities. We determined the best possible K by determining the maximum probability [lnP(D)] of the data and with the ΔK method described by Evanno et al. (2005).

For our site-based analysis of population structuring we used linearized genetic distances (Smouse and Peakall, 1999) to perform an analysis of molecular variance (AMOVA; Excoffier et al., 1992) with GenAlEx software (Peakall and Smouse, 2006). The significance of the calculated Φ_{pt} was ascertained by permuting the data 1000 \times . We also used the software program Tools for Population Genetic Analysis (Miller, 1997) to create a population-based UPGMA dendrogram with Nei's (1972) genetic distance matrix. We assessed nodal support by bootstrapping 1000x over the loci.

The significance of genetic differentiation between sites was tested using permutational MANOVA (perMANOVA; Anderson, 2001) using the software program

R. This test has no formal assumptions and can be used with any measure of dissimilarity between groups. We used Nei's genetic distance (1972) to characterize the level of genetic dissimilarity between pairs of sites. Significance was assessed with 9999 permutations and Bray Curtis dissimilarity. We tested for homogeneity of multivariate dispersion with 1000 unstratified, free permutations to assure that differences in variability among groups were not overly influencing results, a common problem when using MANOVA. Non-metric multidimensional scaling (NMDS) was used to create a visual representation of the perMANOVA results (McCune et al., 2002).

To assess the pattern of genetic diversity on the landscape we used PC-ORD (v.6) to calculate the pairwise genetic [$\Phi_{pt}/(1 - \Phi_{pt})$] (Rousset, 1997) and geographic (km) Euclidean distances between sites. We averaged the plot and stand-level data by site for this analysis. To create a visual representation of the relative genetic similarity of the sites, we ran a principle coordinates analysis (PCoA) in GenAlEx using a Nei's (1972) genetic distance matrix. A Mantel test (Mantel, 1967) was then used to assess the relationship between geographic and genetic distance matrices, and the probability of the observed correlation was assessed with 1000 permutations. We also ran a Mantel test without the samples from Fish Springs, the most isolated of the populations, to assess the correlation between genetic distance and geographic distance at a finer scale.

2.4.3. Genetic diversity within populations

Once the number of populations was determined, population-level genetic diversity was estimated using two approaches. The proportion of polymorphic bands out of the 104 bands scored, a measure of allelic diversity within individuals, was calculated

for each stand and across all stands within each population. We also calculated genet richness for each stand across all stands within each population as the proportion of genets found out of the total number of samples that ran successfully.

2.4.4. Viable seed production and genetic diversity

To look at the relationship between diversity and viable seed production, the average proportion of viable seeds produced per seed head per stand was compared to the stand-level genetic diversity metrics (genet richness and proportion polymorphic bands) using simple linear regression in SigmaPlot (Systat Software Inc., 2004).

3. Results

3.1. Genet identification

We determined that individuals (ramets) with between 1 and 7 mismatches represented one genet (genetic individual) with minor variants due to somatic mutations or scoring error. This was a conservative estimate given the distribution of mismatches. This result led us to determine that out of the 152 samples that ran successfully, there were 85 unique genets represented by 1–6 ramets (Table 2.1).

3.2. Genetic variation among populations

Our individual assignment test showed that the probability of a sample being assigned to its' population of origin ranged from 86–100% (Figure 2.2). There were two noticeable patterns when an individual did not assign to its population of origin: (1) individuals sampled from northern populations tended to assign to more southern populations (Bear Lake to Salt Creek and Ogden Bay; Bear River to Ogden and

Farmington Bays; Ogden Bay to Farmington Bay), and (2) the three populations along the GSL (Bear River, Ogden Bay, Farmington Bay) had the highest level of mixing. The high level of mixing is supported by the individual-based Bayesian assignment analysis where we found that the optimal number of populations (K) was five or six depending on the metric used (highest $\ln P(D)$ optimal $K=6$, with greatest ΔK optimal $K=5$). The STRUCTURE graph of $K=6$ shows high levels of admixture, especially among the populations along the GSL (Figure 2.3). Fish Springs is the only population to show notable differentiation from the other populations.

The AMOVA results showed that the majority of the genetic variation was found within (92%) vs. between (8%) populations. The overall Φ_{pt} value was 0.085 ($p < 0.001$), which indicated weak population structuring as suggested by the STRUCTURE results. Despite the weak structuring, the perMANOVA results indicated that genetic differentiation was significant between all pairs of sites (Table 2.1). The permutation test for homogeneity of multivariate dispersion was non-significant ($p > 0.678$) indicating that results were not overly influenced by differences in variability among groups. The NMDS figure (not shown here) highlighted that individuals from Fish Springs were distinct from the individuals of other populations, which were closely grouped, which supports our finding of weak, but significant genetic structure. Similarly, the UPGMA dendrogram showed that sites with direct connections to the GSL were more genetically similar while the other three sites were less genetically similar (Figure 2.4).

PCoA results (data not shown) for genetic similarity among sites showed a very similar pattern to that in the UPGMA tree, with the sites located along the GSL being most genetically similar. Interestingly, the UPGMA dendrogram showed Bear Lake as

the most distinct population while the NMDS and perMANOVA showed that Fish Springs was the most distinct population. One possible explanation for this discrepancy is that the nodal support value was very low (0.61) at the branching of Bear Lake and Fish Springs in the UPGMA tree, indicating that the placement of Fish Springs and Bear Lake on the tree was weakly supported. The Mantel test showed that genetic distance and geographic distance were strongly correlated (slope= 7.49, R=0.68, p=0.012; Figure 2.5). The Mantel test run without the Fish Springs samples showed a much weaker relationship between genetic and geographic distance (slope = 0.0005, R=0.19, p=0.237).

Taken together these results suggest that each site represented a distinct population; however, this structuring was weak with the exception of Fish Springs, which was clearly separate from all other populations.

3.3. Genetic diversity within populations

Within populations, the proportion of polymorphic bands ranged from 0.67 to 0.81 (Table 2.1). Genet richness ranged from 0.40 at Bear Lake to 0.77 at Ogden Bay (Table 2.1). There were no genets found at multiple sites or stands, indicating that clone size was relatively small and/or that rhizome dispersal was limited. There was only one genet detected in multiple plots; these samples were separated by 9 m and occurred at Salt Creek. Within plots, we found 1–3 genets (of three possible; Table 2.3). At one extreme was Bear Lake, with most plots consisting of identical genets indicating fewer, larger clones. On the other extreme, plots at Ogden Bay usually consisted of three unique genets, an indication of more, smaller clones.

3.4. Viable seed production and genetic diversity

The average proportion of viable seeds produced per stand ranged from 0.28 to 0.82 (mean = 0.64 ± 0.02) (Table 2.4). We found no relationship between stand-level proportion of viable seeds and genet richness ($r^2 = 0.021$) or between proportion of viable seeds and the proportion of polymorphic bands ($r^2 = 0.021$).

4. Discussion

Our results reveal a pattern of genetic diversity and population structuring that contradicts past research and will be important for restoration projects in the future. There was weak, yet significant differentiation among all sampled sites, indicating that each stand was a discrete population. Also, clones were small, sites had generally high levels of genetic diversity (genet richness and proportion of polymorphic bands), and a high proportion of viable seed was produced. Here we suggest reasons for why our findings may have differed from past research, and discuss important implications of these findings for the restoration of *S. maritimus*-dominated wetlands.

4.1.1. Genetic variation among populations

We found shallow, yet significant, levels of genetic divergence among populations despite pronounced physical barriers to dispersal (i.e., Bear River Mountain Range and the West Desert), expansive physical distances between sites, habitat fragmentation, and evidence of genetic exchange between populations of *S. maritimus*. These results are in contrast to another native emergent wetland species, *Phragmites australis* subsp. *americanus*, occurring in the same geographic range, which is also a wind-pollinated outcrossing species (Kettenring and Mock, 2012). We suggest that bird

dispersal may be at least partially responsible for this difference. *S. maritimus* is an important food source for many migratory bird species (Olsen et al., 2004), especially during the southern migration when seeds are ripe (Sweetman, *personal observation*); whereas, *P. australis* subsp. *americanus* is not a significant food source for migratory birds. Past research has shown that waterfowl are potentially capable of dispersing *S. maritimus* up to 2,520 km (Wongsriphuek et al., 2008). Use as an avian food source would promote the movement of seeds from northern populations such as Bear Lake to more southern populations such as Salt Creek and Ogden Bay as birds migrate south. We also found evidence of seed dispersal among sites located along the GSL. We believe this result may be due to the prolonged residence time of the birds on the GSL, a major staging area during the winter migration (Evans and Martinson, 2008), which would promote migration of seeds between these sites either via mud on feet or gut passage.

We note that the genetic distances among pairs of populations along the GSL were more genetically similar than expected based on the overall isolation by distance pattern (Figure 2.5). The differentiation of Fish Springs from all other sites is likely due to geographic isolation. There was no evidence of seed dispersal to this site from other study sites even though Wongsriphuek et al. (2008) suggested that birds could disperse seeds of *S. maritimus* much further than the 172 km separating this site from the next closest study site. However, the number of seeds Wongsriphuek et al. (2008) found that could be dispersed at this distance was very low. We also know that fewer birds utilize Fish Springs during the fall migration in comparison with GSL wetlands, which could lead to effective isolation of this site (Amezaga et al., 2002).

4.2. Genetic diversity within populations

The relatively high genet richness (number of genetically distinct individuals) is an unexpected finding because seedling recruitment is rarely observed for emergent wetland plants (Clevering, 1995), and work done by Charpentier et al. (2000) in southern France suggested that stands of this species in small ponds (ranging from 10m² to 400m²) were often composed of one or a few large clones. Surprisingly high levels of genet richness were also found in other populations of clonal wetland species such as *Phragmites australis* (in North America), *Mesomelaena pseudostygia*, and *Alexgeorgea nitens* (Bussell et al., 2006; Kettenring et al., 2010; Sinclair et al., 2010), and were attributed to high rates of pollen transfer and successful seeding.

Clonal richness is also often correlated with the age of populations and how frequently populations are disturbed (Silvertown, 2008). The sites with the highest levels of genet richness, *i.e.*, the populations with many smaller clones (Bear River and Ogden Bay), are located along the GSL. These sites, while protected by a system of dikes, do experience disturbance due to flooding. However, Farmington Bay, which is also located along the GSL and is highly disturbed by upstream water usage and pollution, had intermediate levels of genet richness, suggesting either that flood-disturbance may not be uniform or that other factors are working to drive genet richness at sites. Small-scale disturbances, such as variability in water level during the growing season could also impact genetic diversity. A study by Baldwin et al. (2010) suggests that frequent, small-scale disturbance could increase opportunities for successful seedling establishment in an area and thus increase genetic diversity within stands of emergent wetland plants. Drivers of these patterns within stands of *S. maritimus* require further investigation.

4.3. Viable seed production

Past research has shown that *S. maritimus* had limited fecundity when self-pollinated, and in stands with limited numbers of genetic individuals there was limited production of viable seed (Charpentier et al., 2000). However, we found no stands with extremely low genetic diversity. We believe the presence of multiple genets in GSL *S. maritimus* populations contributed to the high viable seed production we observed i.e., there was an adequate number genetic individuals within the stand to provide sufficient outcross pollen. A similar finding was found for invasive *P. australis*, another emergent wetland perennial, where most patches (roughly spatially equivalent to our “stands”) evaluated in the Chesapeake Bay had >1 genotype present and when that occurred, seed viability was significantly greater (Kettenring et al., 2011). A controlled pollination experiment confirmed that increased seed viability was due to the availability of outcross pollen.

4.4. Implications for restoration

Our results indicate the presence of five weakly differentiated populations and one distinct population (Fish Springs), and that substantial viable seed production may be due to high levels of genetic diversity within stands. Other work on intraspecific variation within this species has shown that the population of origin did impact the number and timing of seedling emergence and root: shoot ratios in greenhouse experiments (this document, chapter 3). While this variation may or may not correspond with selective pressures or adaptive variance at these sites, it does suggest genetic divergence that might be lost as a result of the introduction of other lineages as part of the

translocation of plant materials for restoration (Moritz, 2002). Thus, the most conservative approach to the conservation of genetic variation within these sites would be to designate each as its own management unit (Moritz, 1999). Management units have been defined as demographically independent populations that are shallowly, yet significantly different populations and are useful designations for maximizing conservation efforts (Markwith and Parker, 2007). This approach may seem unnecessary due to natural translocation that likely occurs via bird dispersal. However, due to the large amount of plant materials that humans introduce to new sites during restoration, these restoration practices could easily disrupt pre-existing genetic structuring if source populations are too distant from the restoration site.

Management and restoration of this species, including decisions about the sourcing of seeds, should consider the number of individual plants sampled (*i.e.* the allelic diversity), and the biological connectivity and geographic distances between these wetlands. For example, since the populations directly along the GSL show high levels of migration among them, one approach to revegetating a site along the GSL would be to gather a large proportion of the seeds from many individuals in one geographically proximal neighboring wetland and gather a small proportion of seeds from other sites along the lake or from more northern populations. This practice would preserve population structure while increasing genetic diversity, which might increase seed production. We believe it would be inappropriate to transfer seeds in or out of the Fish Springs population or other similarly isolated populations due to potential genetic isolation and potential adaptive divergence from other populations. This approach is consistent with recommendations by other researchers to collect broadly from local

sources in order to capture high levels of genetic variation without disrupting population structuring (Montalvo et al., 1997; Lesica and Allendorf, 1999; Gustafson et al., 2002).

Our findings suggest that that maintaining genetic diversity is important to the production of viable seeds, potentially impacting the long-term success of restoration projects and the persistence of populations (Falk et al., 2006; Bischoff et al., 2008).

Genetic diversity within and among populations, natural or restored, can also be thought of as biological insurance against future environmental fluctuations, which will be of growing importance as the effects of climate change become more prevalent (Bischoff et al., 2008). Thus, it is important to create guidelines such as these to preserve and maintain the historic patterns and structure of genetic diversity within a species.

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Table 2.1 Genet richness and genetic diversity in *S. maritimus* populations in Utah and southern Idaho. The proportion of polymorphic bands (P) represents the diversity among genets. Note that the number of samples varies among sites because some samples failed to give AFLP data.

Site	No. samples	No. of genets	Genet richness	P
Bear Lake	25	10	0.4	0.73
Salt Creek	24	10	0.41	0.69
Bear River	21	15	0.71	0.78
Ogden Bay	27	21	0.77	0.81
Farmington Bay	27	15	0.55	0.68
Fish Springs	26	14	0.54	0.69

Table 2.2 perMANOVA p-values for pairwise comparisons of genetic distance by site. F-values are below and R² values are above the dash.

	Bear Lake	Salt Creek	Bear River	Ogden Bay	Farmington Bay	Fish Springs
Bear Lake	--	0.174	0.102	0.092	0.181	0.214
Salt Creek	3.798**	--	0.218	0.094	0.206	0.274
Bear River	2.620*	6.416***	--	0.065	0.110	0.169
Ogden Bay	2.937*	2.995*	2.345*	--	0.069	0.183
Farmington Bay	5.081**	5.967***	3.463**	2.506*	--	0.292
Fish Springs	5.974***	8.288***	5.473***	7.390***	11.119***	--

Significance: *p<0.05, **p<0.01, ***p<0.001

Table 2.3 The relative diversity among and within 1 m² plots of *S. maritimus*. Three leaf samples were taken per plot.

Site	Among plot diversity	Within plot diversity		
	Proportion of plots where genets are shared	Proportion of plots with 1 genet	Proportion of plots with 2 genets	Proportion of plots with 3 genets
Bear Lake	0	0.89	0.11	0.00
Salt Creek	0.1	0.63	0.38	0.00
Bear River	0	0.14	0.57	0.29
Ogden Bay	0	0.22	0.22	0.56
Farmington Bay	0	0.56	0.22	0.22
Fish Springs	0	0.44	0.56	0.00
Total	0.02	0.49	0.33	0.18

Table 2.4 Proportion of viable seed produced per seed head at each stand (mean \pm 1 s.e.).

Site	Stand	Proportion viable
Bear Lake	1	0.47 \pm 0.17
Bear Lake	2	0.82 \pm 0.04
Bear Lake	3	0.73 \pm 0.04
Salt Creek	1	0.56 \pm 0.16
Salt Creek	2	0.80 \pm 0.06
Salt Creek	3	0.79 \pm 0.04
Bear River	1	0.43 \pm 0.06
Bear River	2	0.59 \pm 0.19
Bear River	3	0.67 \pm 0.02
Ogden Bay	1	0.60 \pm 0.28
Ogden Bay	2	0.78 \pm 0.05
Ogden Bay	3	0.73 \pm 0.04
Farmington Bay	1	0.28 \pm 0.20
Farmington Bay	2	0.62 \pm 0.12
Farmington Bay	3	0.68 \pm 0.12
Overall mean		0.64\pm0.02

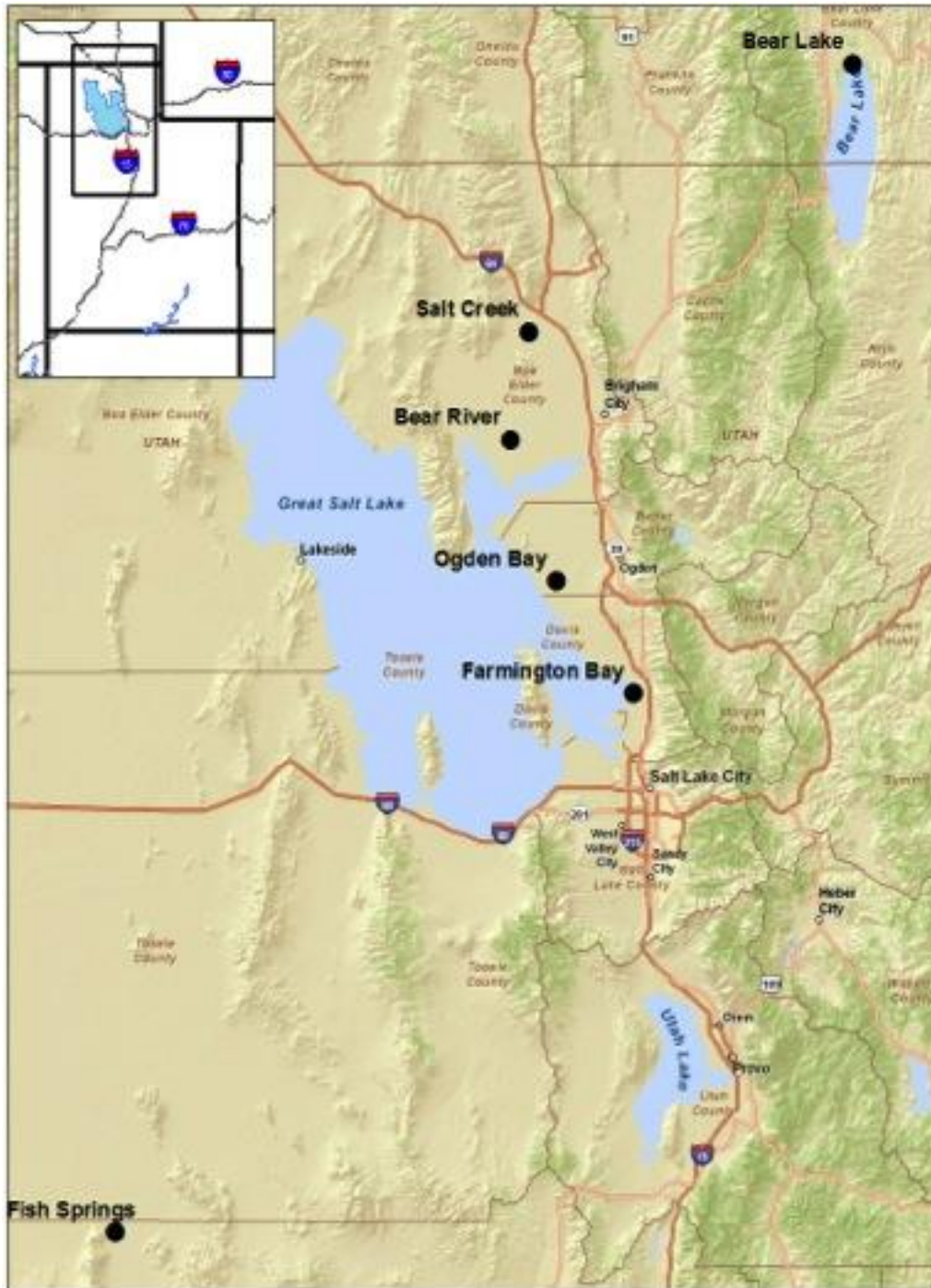


Figure 2.1 Sample site locations in Utah and southern Idaho. Genetic samples were taken at all six sites. Phenotypic and environmental data were collected at all sites except Fish Springs.

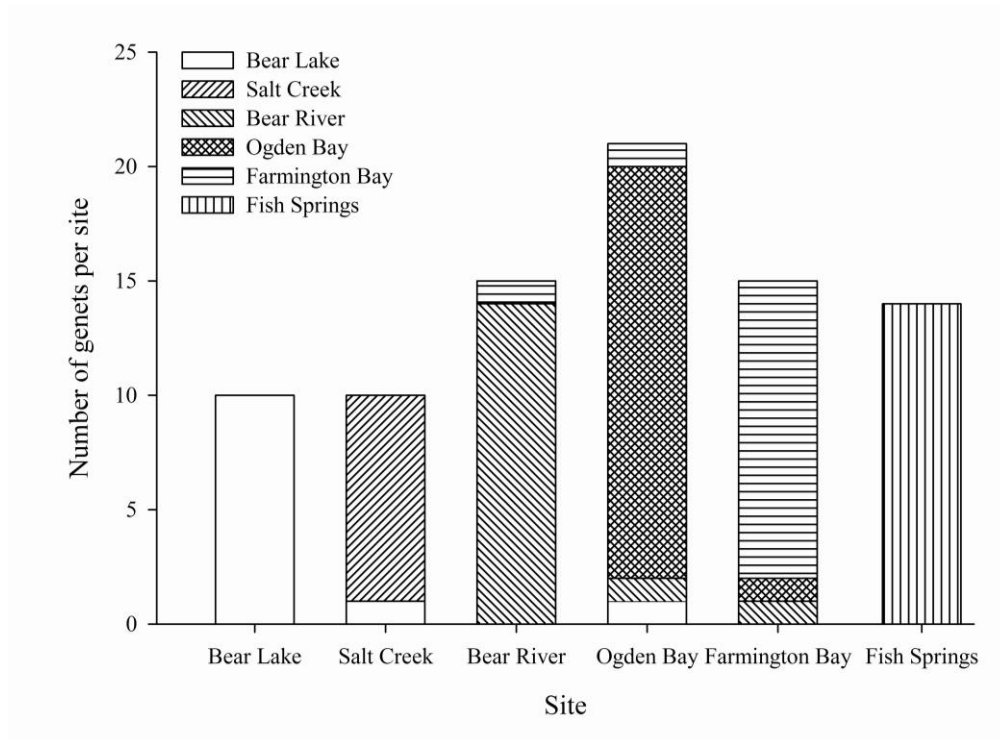


Figure 2.2 Results of the assignment test for genetically unique samples of *S. maritimus*. Each unique sample is represented within each bar; the color of the individual indicates its most likely population of origin as listed in the legend. Note that populations are arranged based on geographic location with the most northern population at the left and the most southern population on the right.

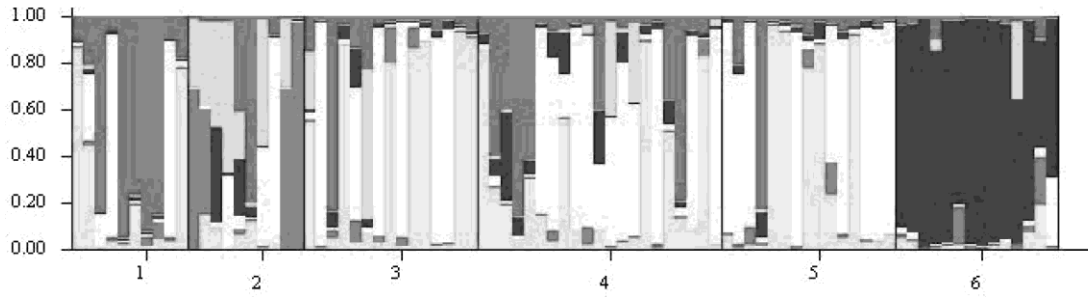


Figure 2.3 STRUCTURE results showing the probability that individual samples assigned to one of the populations ($K=6$). Black lines within the figure delineate populations. Numbers below the figure indicate source population (1=Bear Lake, 2= Salt Creek, 3= Bear River, 4= Ogden Bay, 5= Farmington, 6= Fish Springs).

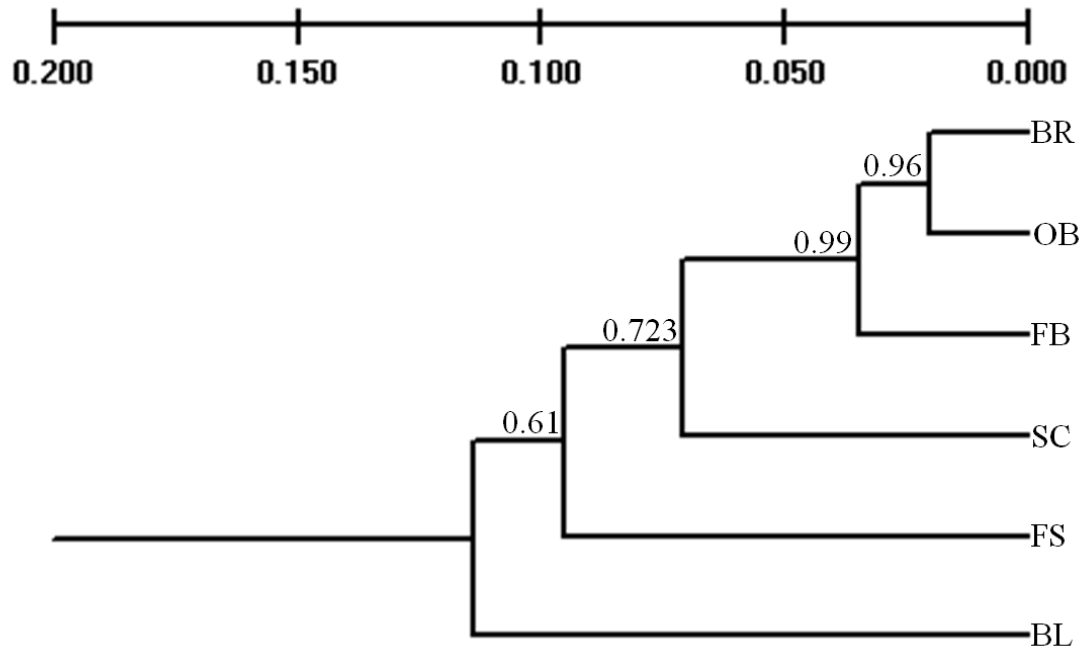


Figure 2.4 A population-based UPGMA dendrogram organized by sampling site, created with the AFLP data from *S. maritimus* and Nei's (1972) distance matrix. Nodal support based on proportion of 1000x replicates is shown at each node.

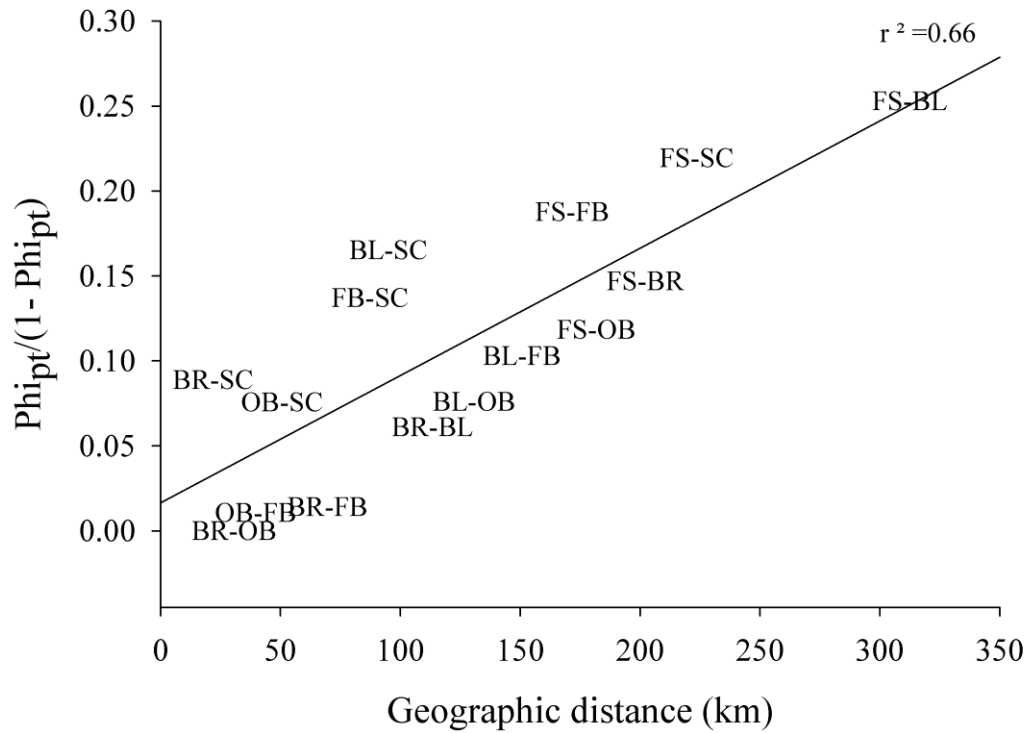


Figure 2.5 The relationship between genetic distance and geographic distance (km) in pairs of populations. A Mantel test was used to test for a significant relationship between these two metrics.

CHAPTER 3

DRIVERS OF EMERGENCE AND PRODUCTIVITY OF A WIDESPREAD
WETLAND PLANT: THE ROLES OF SEED SOURCE IDENTITY,
SEED SOURCE DIVERSITY AND HYDROLOGY**Abstract**

We conducted two studies to look at the influence of hydrology, population of origin, and genetic diversity of seeds on the productivity of a widely distributed wetland plant, *Schoenoplectus maritimus*. In a field survey we measured environmental variables and productivity within established *S. maritimus* stands. In a greenhouse experiment we determined how source population identity and the genetic diversity of seeds impacted emergence and productivity under different hydrologic conditions. We found that stands of *S. maritimus* differed in proportion of time with water present, mean water level among sites, and soil conditions. Productivity also differed, with 3-fold differences in stem density and biomass among sites. In the greenhouse experiment, we found that water treatment impacted all productivity measures; source population impacted seedling emergence and biomass allocation; and number of source populations impacted sensitivity to drought. Our results indicate that (1) water level management is important for productivity within established stands and for the establishment of seedlings; (2) water level during the establishment of seedlings may impact biomass allocation and, potentially, long-term fitness; and (3) seed sources differed in terms of establishment and biomass allocation, suggesting that seeds should be collected from multiple individual plants within one site.

Introduction

The goal of most wetland restoration projects is to establish productive systems, which provide habitat and wetland functions such as erosion control, water quality improvement, and floodwater retention (Zedler 2000). To achieve these goals in wetland restoration, active revegetation with seeds is usually necessary to overcome dispersal limitations (Neff and Baldwin 2005; Fraser and Madson 2008; Kettenring and Galatowitsch 2011). Seeding is a common practice due to the additional costs associated with the use of rhizomes and seedlings (Galatowitsch et al. 1999). Therefore, the success of many of these projects is dependent on seedling establishment and the productivity of the species of interest. The rate at which seeds establish is important for short- and long-term restoration success. Faster establishment rates are essential because wetlands are dynamic systems in which the window of opportunity for germination and establishment may be short. Also, rapid establishment of a desired species can reduce the number of invasive species at a site by decreasing available light and nutrients for competitors (Iannone III and Galatowitsch 2008). Plant productivity (defined here as stem density, stem height, and aboveground biomass) of desired species can also impact restoration because increasing productivity leads to increases in ecosystem functions (Zedler 2000).

Hydrologic regime (depth, duration, and frequency of flooding at a site) plays an important role in determining seedling establishment and productivity of wetland plants (Casanova and Brock 2000; Güsewell et al. 2003). The presence of too much water at the onset of a reseeded project can lead to the drowning of seedlings and the formation of aerenchyma, and shallow root systems (*i.e.*, low root:shoot ratios) (Rea and Ganf 1994a; Clevering and Hundscheid 1998; Lenssen et al. 2004) which can cause plants to be

poorly suited to lower water levels in the future. On the other hand, the presence of too little water at the onset of a project can lead to seedling mortality and slow development of aboveground biomass (*i.e.*, high root:shoot ratios) which can cause plants to be less productive and poorly suited to higher water levels in the future (Touchette et al. 2010). Therefore, it is important for wetland restoration practitioners to understand the response of a species of interest to water levels to increase seedling survival and biomass production.

Controlling water levels can be particularly challenging in restored wetlands where water levels are known to be more variable within and among years than in their natural counterparts (Bohnen and Galatowitsch 2005). However, selecting seed materials with high genetic diversity and from appropriate sources can promote seedling establishment and productivity and mitigate the effects of extreme hydrologic conditions. The rate at which seeds establish can be different among source populations (Bischoff et al. 2006). Therefore, it is important to understand the rate and timing of seedling establishment of plants from all potential source populations to determine the source population(s) most suited to the conditions at the restoration site. Increasing genetic diversity (number of genotypes) in a population can also lead to greater productivity and resistance to disturbance (Hughes et al. 2004; Crutsinger et al. 2006; Reusch and Hughes 2006). In some instances, the effects of genetic diversity are only measurable under stress, such as flooding or drought. For example, when two white clover (*Trifolium repens*) genotypes, one with short roots and the other with longer roots, were planted together, the population had greater biomass production than populations of either genotype when planted alone only in drought conditions (Ennos 1985). Most research on

how hydrology, seed source, and genetic diversity impacts on restoration has simply assessed genetic effects by manipulating the number of clones present at a site. But, due to the pervasive use of seeds for restoration work (Vander Mijnsbrugge et al. 2010), research that manipulates genetic diversity in seed mixes is also important.

To investigate how hydrology and genetic factors impact restoration success of populations grown from seed, we conducted a descriptive study of natural populations and a controlled greenhouse experiment with *Schoenoplectus maritimus* (alkali bulrush). In the present research we focus on three factors—hydrology, population of origin of the seeds, and the number of donor plants (*i.e.*, genetic diversity)—that may impact seedling establishment and productivity. Not only is restoration success dependent on these factors, but it is also often possible to control water level, seed source, and genetic diversity during the restoration process. *S. maritimus* is one of the dominant species in wetlands in the Intermountain West region of the United States, which are typified by large monotypic stands of emergent wetland plants and where hydrologic extremes are part of the annual hydrologic cycle (Wise 2012). We selected *S. maritimus* for our study because it has been observed growing in widely divergent environments (*e.g.* different water levels and soil types) where noticeable phenotypic differences among individuals and populations have been observed (Sweetman *pers. obs.*). *S. maritimus* populations in the region are known to have high levels of neutral genetic diversity and low, yet significant, levels of population differentiation (Sweetman et al. 2013) all of which is suggestive of neutral or adaptive genetic variation among populations. Our research objective for the descriptive study was to establish baseline data on the environmental conditions and productivity within established stands of *S. maritimus*. The objectives for

our greenhouse experiment were to quantify how (1) population origin of seeds, and (2) genetic diversity impacts seedling establishment and productivity of *S. maritimus* plants under experimentally manipulated hydrologic conditions.

Methods

Study species

S. maritimus grows in large monospecific stands in fresh and brackish wetlands worldwide (Charpentier and Stuefer 1999). Vegetative reproduction via rhizomes and tubers is common; rhizomes and aboveground shoots live for one growing season while tubers can persist for several (Liefers and Shay 1982). *S. maritimus* is wind pollinated and has achenes that ripen in the late summer, which are primarily dispersed by water and waterfowl (Charpentier et al. 2000). The species is self-incompatible and populations with few genetic individuals can have reduced fecundity due to pollen limitation (Charpentier et al. 2000); however, previous work on populations of *S. maritimus* in our study region revealed high levels of genetic diversity and sexual reproduction within populations (Sweetman et al. 2013).

Descriptive study

To address our first objective, we studied stands of *S. maritimus* under natural conditions to evaluate differences in plant productivity and water level variation in four sites located in Utah (Figure 3.1) during the summer of 2009. Two of the sites, Ogden Bay Waterfowl Management Area (Ogden) and Farmington Bay Waterfowl Management Area (Farmington), were located on the shores of the GSL. The Bear River Migratory Bird Refuge (Bear River) site was located on the historic delta of the Bear River at the

northeast arm of the GSL and was influenced hydrologically by both the Bear River and the GSL. The Salt Creek Waterfowl Management Area (Salt Creek) was northeast of the GSL, was not influenced by lacustrine inputs, and received the majority of its water from Salt Creek and springs in the region (Christiansen and Low 1970). Within each site we located three monotypic stands (< 10% cover by species other than *S. maritimus*) that were at least 150 m apart. Within each of these stands, we haphazardly established three 1m² plots that were between 5 and 20 m apart. To measure productivity we measured the height of five marked plants once a month, and, after 5 months, we measured stem density and collected aboveground biomass at each plot. For biomass sampling all *S. maritimus* stems in a plot were harvested, dried at 60° C to a constant weight (at least 24 hours), and weighed to 0.1 g. As the three plots were subsamples, we used the mean value of the three plots to obtain stand-level data, which was used for comparisons within and among sites.

We also measured abiotic factors (water level and soil properties) that might have influenced *S. maritimus* productivity. Water level was measured at each plot at two-week intervals for a total of five months. If there was no standing water, visual and tactile assessments were used to determine if soils were saturated, damp, or dry. If the soil was saturated we recorded the water level as 0cm; if the soil was damp we recorded the water level as -1cm; and, if the soil was completely dry we recorded the water level as -5cm. We created hydrographs to better visualize the differences among and within sites. One soil sample was taken at each plot (n=36) and analyzed by the Utah State University Analytical Lab for pH, electrical conductivity (EC; dS/m), phosphorus (mg/kg), potassium (mg/kg), nitrate (mg/kg), and ammonium (mg/kg). Again, the mean value of

the three plots within each stand was calculated to obtain stand-level data, which was used for comparisons within and among sites.

Greenhouse experiment

Experimental design: To evaluate the effects of seed source population, the genetic diversity of seed sources, and water levels on *S. maritimus* establishment and productivity, we conducted a complete factorial experiment in a greenhouse on the Utah State University campus (41°45'28.71"N, 111°48'47.17"W). Our main factors were seed treatment and water level (3 levels: flood, control, and drought). Seed treatment is an overarching term for source population (n=5) and the diversity of seed sources in a mix (n=6; seeds from the five populations planted singly—referred to by collection site name—and seeds from all source populations mixed together in equal proportions—referred to as “mixed” seed treatment).

Seed collection: Seeds were collected by hand from each site described in the descriptive study (see above); we also used seeds collected from a fifth site, Timpie Springs (Figure 3.1). Timpie Springs was not included in the descriptive study due to logistical constraints. We included seeds from this site due to availability and to increase the number of seed sources evaluated. At each site, seeds were collected from haphazardly selected plants $\geq 3\text{m}$ apart over a 150 m^2 area to obtain a genetically diverse sample representative of the population (as per Bischoff et al. 2008). Seeds were cleaned and stored at room temperature until sowing. Seeds were collected in fall 2008 from Bear River, Ogden, Farmington, and Salt Creek, and in fall 2009 from Timpie.

Water levels: The water treatments were designed to approximate the hydrologic extremes that this plant was known to experience in the field (see descriptive study). Field surveys in our region demonstrated *S. maritimus* growing in water levels of 0 to 39.5 cm (Figure 3.2). Water level was controlled by the height of a pot within a pool. Flood treated pots were submerged to a depth of 5 cm. Control pots, which had five small holes drilled into the bottom, were kept moist by resting in 5 cm of water. This treatment was designed to minimize stress from either flooding or drought. The drought pots were raised above the water entirely and were kept just above the permanent wilting point (~8% water content for our soil type—sandy loam soils). We used simulations run on the software package, HYDRUS, to determine the amount of water to add to achieve our drought treatment (Šimůnek et al. 2008). Based on the results of this simulation, we developed a watering scheme where all pots were brought up to saturation at the onset of the water manipulation experiment, the drought pots received a 0.5 cm precipitation event 5 days after water manipulations began, and after that drought pots received a 1 cm precipitation event every 7 days. To track the actual water content drought pots received, they were weighed pre- and post-watering. For the duration of the water manipulation, the drought pots ranged from 18-22% water capacity just post-watering and 5-10% water content pre-watering. Water level within the ponds was adjusted by hand every few days.

Experiment implementation: Fifty-four viable seeds were sown onto the surface of each pot (volume = 2.66 liters; surface area 0.3 m²)—a realistic approximation of field-observed stem densities (see descriptive study). To promote germination, seeds were treated with a 3% bleach solution for 12 hours (Kettenring *unpublished data*), thoroughly rinsed with tap water, and planted immediately post treatment on April 3, 2010. Each pot

was filled with a sandy loam mixture and received 35 g of Osmocote 15-9-12 at the beginning of the experiment.

Pots were randomly assigned to one of three artificial ponds (1.2 m by 3.65 m) and randomly placed within that pond. There was space for 32 pots per pond (=block). So each water level x seed treatment (n=18) was represented at least once in each pond and the remaining spaces in the pools were assigned treatments randomly. When two pots of the same treatment were present within the same pond they were considered subsamples; response variables associated with those pots were averaged to avoid pseudoreplication. Temperatures within the greenhouse ranged from 25° C during the day to 18° C at night. A 16-hour photoperiod was maintained with 1000 W high-pressure sodium lamps. After planting, to elevate humidity and surface temperature to improve germination, pots were covered with cellophane until germination began. Pots were kept saturated for four weeks prior to the onset of the water manipulation experiment (i.e., the establishment period). The experiment ran for nine weeks (i.e., the experimental period) after the four-week establishment period.

Plant response measurements: The total number of emerged seedlings was measured weekly during the establishment period. During the experimental period, we measured mean maximum stem height and the number of stems per pot every two weeks. At the conclusion of the study, aboveground biomass was collected by clipping stems at the soil surface. Belowground biomass was collected by rinsing roots over a fiberglass screen with 0.025cm diameter mesh. Biomass samples were processed as described above.

Tests for possible maternal effects: Using seed directly sourced from natural populations could have lead to non-genetic effects impacting our results. For example, environmental conditions experienced by maternal plants can affect seed mass and thus potentially germination. To look for effects of provisioning by maternal plants we used t-tests to compare the mean seed mass of each site (Richards et al. 2010). Simple linear regression was also used to assess the impact of mean seed mass on percent germination at the conclusion of the four-week establishment period.

Outliers: Three pots in which no plants successfully established prior to the beginning of the water-level manipulation were excluded from data analysis. Two other pots in which no germination had occurred until the seventh and ninth weeks of the experiment were also excluded due to their late germination.

Analysis: We ran analyses for total biomass and root: shoot ratios using a two-way ANOVA in a randomized block design. The fixed effects were water level (3 levels: flood, control, and drought) and seedling mix (5 levels). We ran analyses for the proportion of seedlings emerging, mean maximum height, and stem count using a two-way ANOVA in a randomized block design with repeated measures in time using the most parsimonious covariance structure for each response to account for autocorrelation in time, based on the lowest corrected Akaike information criteria (AICc) (with smaller values being better) (Table 3.1). The fixed effects were water level (3 levels: flood, control, and drought), seedling mix (5 levels), and time (number of levels). Block was included as a random effect in all models. Degrees of freedom were calculated using the Satterthwaite (1946) approximation. Some variables were transformed prior to analysis to better meet the model assumptions of normality and homogeneity of variance (Table

3.1). We used an alpha of (0.05) as our critical significance level. However, when multiple comparisons were made within a treatment to test for the effect of individual seed treatments, on repeated or non-repeated measures, we used the Tukey-Kramer method and we assessed results at $\alpha= 0.11$ to increase power (Day and Quinn 1989). Data analyses were obtained using the GLIMMIX procedure in SAS/STAT software version 9.2 in the SAS system for Windows (SAS Institute Inc. 2009).

Sensitivity to flooding and drought: As per Kercher and Zedler (2004), the sensitivity of each seed treatment to flooding and drought was calculated as $(1 - [\text{mean}(\text{response}) \text{ flood or drought} / \text{mean}(\text{response}) \text{ control}])$. Response variables evaluated were total biomass, final mean maximum height, and final mean stem count. Sensitivity values could have ranged from -1 to 1. Higher positive values indicated a sensitive seed treatment (i.e., a seed treatment that was affected more by the water level treatment). Lower, positive numbers indicated a tolerant seed treatment. Negative numbers indicated a responsive seed treatment (i.e., a seed treatment that benefitted from the water level treatment).

Results

Descriptive study

We found dramatic differences in stem density, biomass, proportion of time wet, mean water level, and soil conditions (Figure 3.2, Figure 3.3, Table 3.2) among sites and between stands within sites. There were 3-fold differences in average stem density and biomass production among sites; Salt Creek plots had the highest stem densities and

biomass production while Bear River had the lowest stem density and Ogden had the lowest biomass production.

The hydrographs revealed highly divergent patterns of timing, duration, and depth of flooding among the sites (Figure 3.2). The proportion of time a site had water present ranged from 20-100%. Bear River was the driest site, with peaks early and late in the season. Farmington had the highest mean water level and the greatest variation among stands. Ogden also had high among-stand variation, and at the site-level Ogden had water present more often than any other site. Salt Creek had low water levels, and the least among stand variation. Salt Creek was the most moderate site—plants experienced neither excessive flooding nor drought.

We also found highly variable soil conditions among the sites (Table 3.2). Ammonium was 2.6 times higher at Farmington than at Salt Creek. Nitrate was 3.5 times higher at Bear River than at Ogden. EC and Potassium were respectfully 3.8- and 1.2-times higher at Bear River than at Salt Creek. Phosphorus was 3.8-times higher at Farmington than at Bear River.

Greenhouse experiment

Tests for possible maternal effects: Seed mass did have a very weak positive linear relationship with percent germination ($p=0.017$, adjusted $r^2= 0.0902$). However, it is doubtful that there was a significant maternal effect as Timpie, the seed treatment with the lowest mean seed mass, had the highest total seedling emergence, the opposite pattern from what you would expect with a maternal effect.

Seedling emergence: Seedling emergence was affected by seed treatment, time, and seed treatment*time (Table 3.1, Figure 3.4). Within seed treatment, Timpie seedling emergence was greater than emergence of seeds collected from Bear River, Farmington, Ogden, and Salt Creek. Within time, seedling emergences at times one and two were different from each other and from emergences at times three and four, which were statistically the same.

Productivity: Stem count and mean maximum height were affected by water level, time, and water*time (Table 3.1). Stem count was significantly lower in drought pots than at other water levels. The mean maximum stem height was significantly different at all water levels. Stem count and mean maximum height increased significantly at every 2-week interval.

Total biomass was significantly lower in drought pots than at other water levels, whereas root:shoot ratios were different at all water levels. Root:shoot ratios were also impacted by the water*seed treatment interaction (Table 3.1, Figure 3.5). Within the drought treatment, the root: shoot ratios of Timpie plants were lower than those of Bear River, Farmington, and Ogden, and the root:shoot ratios of Ogden plants were higher than those of the Mixed treatment. Within the control water treatment, root:shoot ratios of Bear River plants were significantly lower than those of Salt Creek and Mixed plants. The flood treatment did not yield significantly different root:shoot ratios between any seed treatment. Within seed treatments, the root:shoot ratios of all seed treatments except Salt Creek were much higher in the drought treatments than in the flooding and control treatments. The Salt Creek root:shoot ratios responded differently to all three water level treatments.

Sensitivity to flooding and drought: Ogden was the most drought-sensitive with the highest sensitivity value for all responses; the mixed seed treatment had the least reduction in stem count in the drought treatment (Figure 3.6). Interestingly, there was greater variation in seed treatment sensitivity to flooding than to drought conditions.

Discussion

Seed source populations of *S. maritimus* experienced highly divergent abiotic conditions in the field and levels of productivity were highly variable among sites and among stands within sites. Under controlled greenhouse conditions, hydrology—not seed source population or diversity—had an overall significant effect on productivity. However, the location from which seeds originated impacted biomass partitioning and establishment success, whereas seed source diversity impacted sensitivity to drought. Here we discuss possible drivers of the patterns seen in the four natural populations of *S. maritimus* and the response of the plants under greenhouse settings. We particularly focus on restoration implications of how seed source population, diversity, and hydrologic extremes can affect the establishment and productivity of *S. maritimus*.

Our results highlight the differences in hydrologic patterns among and within sites that reflect the intersection of water availability with management practices. In the past, the wetlands in the region experienced high water levels in early spring due to montane-derived snowmelt runoff and then gradual lowering due to low precipitation and high evapotranspiration in the summer months. Thus, the depth and duration of flooding in the spring was influenced by large-scale climate cycles that drove annual winter snowpack, all of which led to large seasonal and inter-annual variation in water level at

these wetlands. Now, due to agricultural diversions and the creation of reservoirs upstream, water resources are limited and seasonal and inter-annual hydrologic patterns have been altered (Christiansen and Low 1970). In order to maintain suitable habitat for migratory birds, private and governmental organizations have purchased important wildlife habitat and impounded the majority of remaining wetlands. Impoundment allows land managers to manipulate water levels to maximize waterfowl production (Olsen et al. 2004). Interestingly, the hydrographs of these heavily manipulated wetland impoundments rarely mimic what would have occurred naturally. The interaction of upstream water use and management practice is especially apparent in the severe decrease in water level during the growing season in the Bear River wetlands. Because the Refuge has a lower priority water right to upstream agricultural uses, most growing seasons including during our study year, many wetland impoundments can go dry (Downard 2010). The large-scale alterations of hydrologic conditions in these wetlands may have long-term effects on wetland plant populations, including their productivity, and is an interesting area of future research in controlled experiments such as our greenhouse trial and in longer-term field-based experiments.

Hydrologic conditions affected productivity of the observed populations as well as those grown in the greenhouse. Biomass production at Salt Creek, which had low but relatively constant water levels, was more than double that of any other site. These findings are similar to results in an experimental study on effect of water level stabilization on *Typha X glauca* (invasive, hybrid cattail) that showed plants grown at a constant 5-10 cm water level had 56% higher biomass accumulation than plants grown in fluctuating conditions (Boers and Zedler 2008). Other studies have shown that water

levels greater than 20 cm, which were commonly recorded at some of the least productive sites (Farmington and Ogden), can severely retard growth of *S. maritimus* and other members of the genus (Clevering and Hundscheid 1998; Blanch et al. 1999). Field sites, such as Bear River, that experienced dewatered conditions had surprisingly high productivity given the extreme negative response drought conditions had on the plants grown in the greenhouse. This discrepancy could be due to the presence of well-developed belowground resources in field populations that buffered them from the dewatered conditions, or the difference in the severity of drought conditions between the field and greenhouse. Also, it is possible that the majority of growth in the field had occurred prior to the dewatering of units, as other studies have shown that the presence of water early in the season is most important for productivity of other emergent graminoids (Yetka and Galatowitsch 1999).

Other factors such as nutrient levels, salinity, temperature, population dynamics, and genetic variation could also impact plant productivity. Increasing nutrient levels in wetlands, particularly nitrate as it is often limiting in these systems, can increase wetland plant productivity (Venterink et al. 2002). Also, increasing salinity and clone age decreases productivity of *S. maritimus* stands (Lieffers and Shay 1982; Jelinski et al. 2001; Lillebø et al. 2003). Neutral or adaptive genetic variation among sites could also result in differences in productivity among sites. A study on the patterns of neutral genetic variation within populations of *S. maritimus* in the region showed low, but significant, levels of population differentiation (Sweetman et al. 2013). The results of the greenhouse experiment are a first step in linking neutral genetic variation between plants

from different sites to quantitative trait variation, and in quantifying how these differences might impact productivity and response to hydrologic extremes.

Our results show that different seed sources partitioned biomass differently in response to hydrologic conditions in the greenhouse—which may be an adaptive response to past hydrologic conditions at sites because water regime is a strong selective pressure on wetland plants (Silvertown et al. 2001). Herbaceous plants alter root:shoot ratios in response to changing water levels (Rea and Ganf 1994c; Kennedy et al. 2003; Touchette et al. 2008). Similar to past research, root:shoot ratios of plants in our greenhouse study increased in drought conditions as compared to the control or flood conditions (Sala and Nowak 1997). Higher root:shoot ratios in the drought treatment can potentially increase foraging for water resources, making some seed sources better suited to low water conditions. Past research on a suite of emergent wetland species, including *S. maritimus*, showed that root:shoot ratios of flood treated plants decreased in response to flood as shoots elongated to emerge from the water (Rea and Ganf 1994c; Clevering and Hundscheid 1998). In our study, only Salt Creek communities had significantly lower root:shoot ratios in response to flood conditions. There was an overall non-significant trend for flood treated communities to have lower root:shoot ratios, and it is possible that our flood treatment water level was too shallow to have elicited elongation of shoots at the expense of belowground structures as had been documented in past studies.

Similar to past research, we found that seed source population affected seedling establishment of *S. maritimus* (Keller and Kollmann 1999; Bischoff et al. 2006). Rapid establishment can have lasting impacts on the competitive ability of a plant species

(Keller and Kollmann 1999), and is particularly important in dynamic systems such as wetlands because the duration of favorable conditions for germination and establishment is often limited (Rea and Ganf 1994b). We used field-collected seeds in our experiment to maximize the relevance of our findings to restoration. One limitation of this approach is that we cannot definitively say that differences among seed sources are due to genetic effects rather than non-genetic effects such as abiotic impacts on maternal plants during seed production (Baskin and Baskin 1998). However, our results suggest that maternal effects, as measured by seed mass, did not appear to affect establishment or productivity. Further research is needed to confirm that the origin of any differences among seed sources in establishment (or productivity) is genetic rather than environmental.

The amount of genetic variation present within a species and within populations has been shown to positively affect individual- and population-level fitness (Charpentier et al. 2000; Reed and Frankham 2003) and ecological processes such as annual productivity and resistance to disturbance (for review see Crutsinger et al. 2006; Hughes et al. 2008). While the mixed seed treatment did not impact productivity or establishment in our statistical tests, it was the least sensitive to drought (*i.e.*, it had the least reduction in stem count in drought conditions as compared to the control). This result is similar to those from a study on genotypic diversity of sea grass beds (*Zostera mariana*), in which clonal diversity only had a measurable effect after a major disturbance (Hughes et al. 2004), rather than under non-stress conditions. Similarly, only when exposed to drought conditions did stands of white clover (*Trifolium repens*) with multiple genotypes planted together have significantly higher biomass production than stands planted with one genotype (Ennos 1985). One possible explanation for the lack of a diversity effect for

other response factors is that genetic diversity was already high within each seed source population (Sweetman et al. 2013), and there was no additional benefit to adding seeds from multiple sources.

Implications for Management and Restoration

Our results indicate that hydrology, seed source identity, and seed source diversity impact establishment and productivity of *S. maritimus* populations. These findings have important implications for the management and restoration of *S. maritimus* populations. First, the management of water level is important for the establishment of seedlings and may impact the productivity of established stands. Second, the water level during the initial growth of seedlings can impact root:shoot ratios. Therefore it is important to consider the prevailing conditions at a potential restoration site to maximize seedling survival (*e.g.*, if a site is prone to drought but seedlings are grown in flooded conditions then those plants may have lower root:shoot ratios and thus be vulnerable to drought in the future) (Elcan and Pezeshki 2002). Third, when sourcing seeds for revegetation projects, the most conservative choice is to collect widely within one proximal and ecologically similar site as no one seed source appears to have a clear advantage over other sources, and there is broad variation within seed sources. This practice will capture a large amount of genetic variation, which may decrease sensitivity to drought, while preserving the population structuring found in past research (Sweetman et al. 2013). We hope that the information here will land managers and aid in successful restoration of wetlands.

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Table 3.1: ANOVA table – Summary of test statistics for greenhouse experiment.

Response (transformation, covariance structure)	Effect	df	F Value	Pr > F
Root-to-shoot (log, none)	W	2 , 33	129.81	<0.0001
	ST	5 , 33	0.92	0.48
	W*ST	10 , 33	4.27	0.0007
Total biomass ¹ (sqrt, none)	W	2 , 15.71	319.71	<0.0001
	ST	5 , 23.36	0.65	0.66
	W*ST	10 , 17.01	0.23	0.99
Seedling emergence (sqrt, arh(1))	W	2 , 33.65	1.64	0.21
	ST	5 , 33.65	2.12	0.09
	W*ST	10 , 33.65	1.26	0.29
	T	3 , 60.66	60.67	<0.0001
	W*T	6 , 71.74	0.94	0.47
	ST*T	15 , 82.79	1.58	0.09
	W*ST*T	30 , 83.13	1.01	0.46
Stem count (sqrt, arh(1)+re)	W	2 , 32.07	10.51	0.0003
	ST	5 , 32.07	1.93	0.12
	W*ST	10 , 32.06	0.66	0.75
	T	3 , 49.56	435.07	<0.0001
	W*T	6 , 59.78	33.99	<0.0001
	ST*T	15 , 70.54	0.34	0.99
	W*ST*T	30 , 71.1	0.49	0.98
Mean max height (sqrt, toep)	W	2 , 37.41	114.59	<0.0001
	ST	5 , 37.41	1.61	0.18
	W*ST	10 , 37.41	0.67	0.75
	T	3 , 62.98	384.89	<0.0001
	W*T	6 , 72.12	50.27	<0.0001
	ST*T	15 , 79.82	0.58	0.89
	W*ST*T	30 , 78.07	0.68	0.88

df= degrees of freedom, W=water, ST=seed treatment T=time; sqrt=squareroot

transformed, ¹analyzed with heterogeneous variance for water, arh (1) + re=

heterogeneous autoregressive with random statement, toep= Toeplitz.

Table 3.2: Soil characteristics at stands of *S. maritimus* within sites.

Site, stand	pH	EC	Phosphorus	Potassium	Nitrate	Ammonium
Salt Creek S1	7.55	4.32	18.50	579.00	7.78	13.40
Salt Creek S2	7.79	6.51	15.77	655.00	4.83	9.95
Salt Creek S3	8.17	10.94	22.20	678.00	7.30	5.69
Bear River S1	7.21	21.82	12.37	842.00	8.90	6.87
Bear River S2	7.44	29.13	8.70	890.67	8.50	8.13
Bear River S3	7.23	34.13	11.63	696.33	13.65	6.82
Ogden S1	8.06	9.86	43.33	619.67	2.76	12.45
Ogden S2	7.98	9.93	39.33	853.67	3.56	10.00
Ogden S3	7.59	13.56	42.00	900.00	2.42	20.77
Farmington S1	8.01	11.86	20.75	846.50	2.94	22.70
Farmington S2	7.62	22.33	74.00	900.00	10.63	7.73
Farmington S3	7.46	4.60	33.50	434.00	3.30	26.40

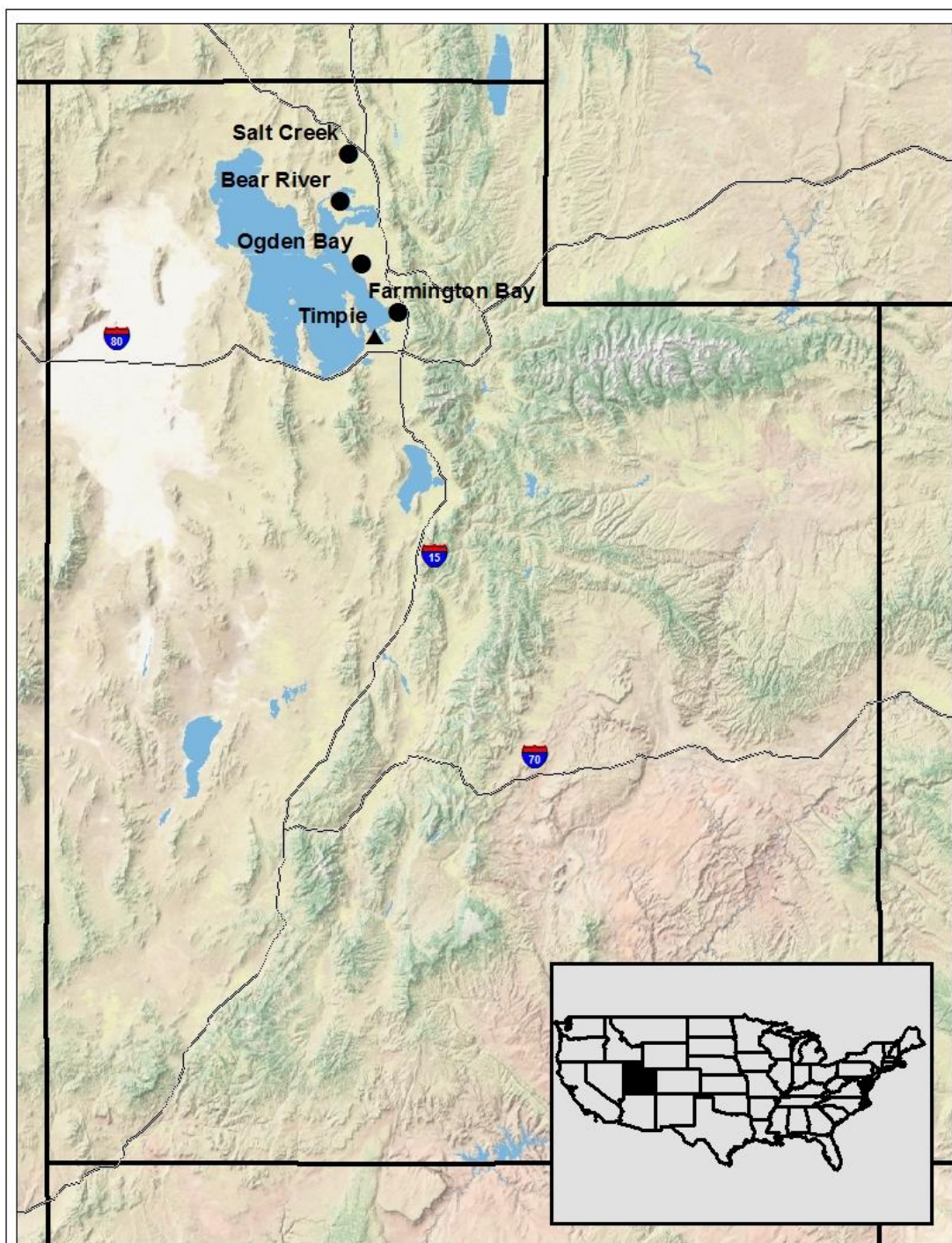


Figure 3.1: Sample site locations in Utah. Sites marked with circles were studied for the field study. Seeds were collected at all sites.

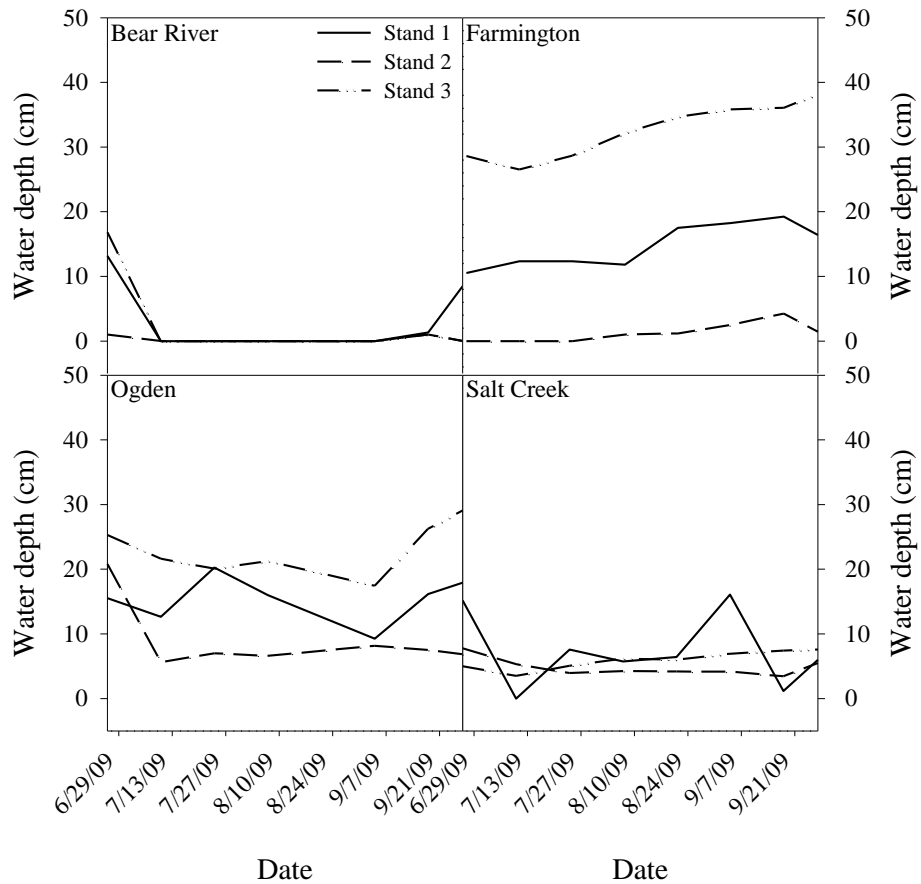


Figure 3.2: Mean water level by stand and site for the duration of the field study.

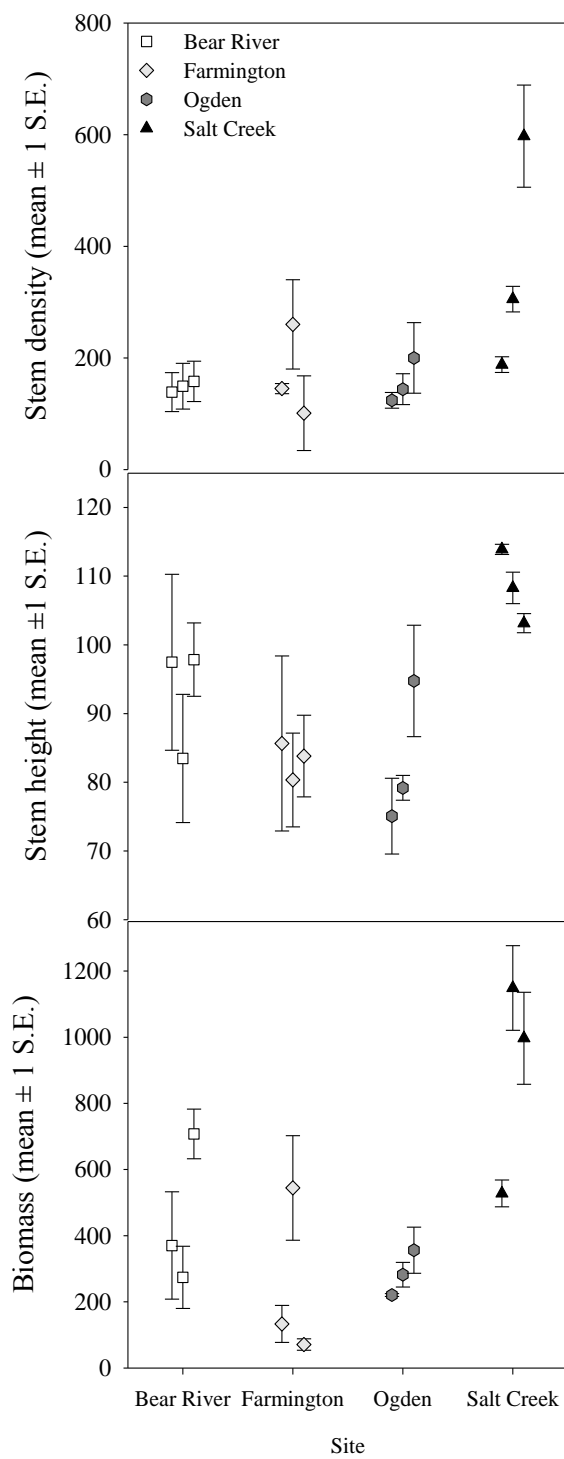


Figure 3.3: Stand-level phenotypic characteristics of four populations of *S. maritimus* growing in the field.

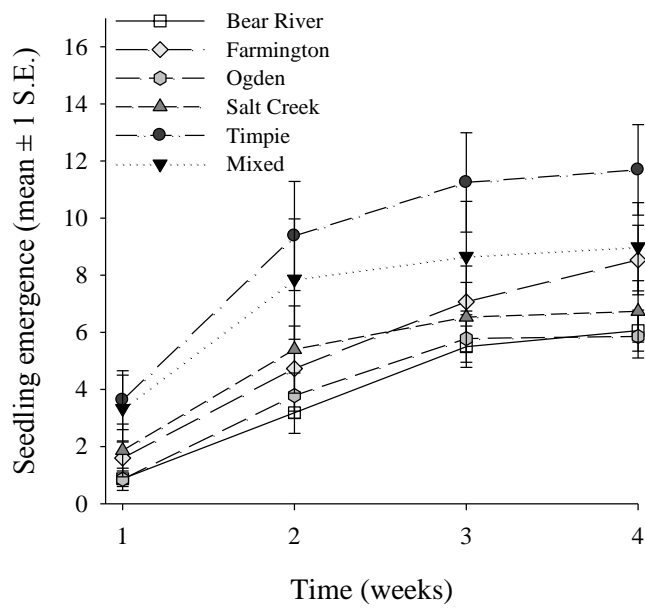


Figure 3.4: Effect of seed treatment on the number of seedlings emerging through time.

Measurements were taken weekly for four weeks.

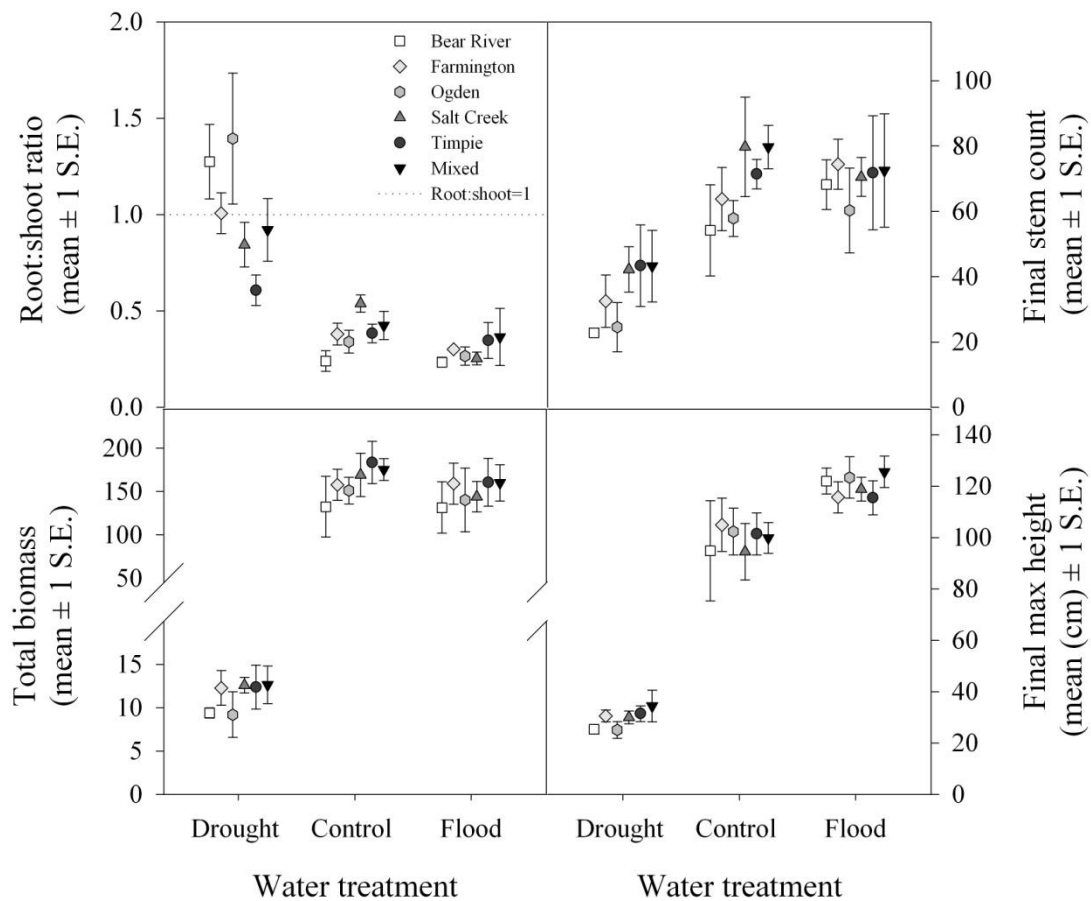


Figure 3.5: The effect of seed treatment and water treatment on plant productivity in the greenhouse experiment.

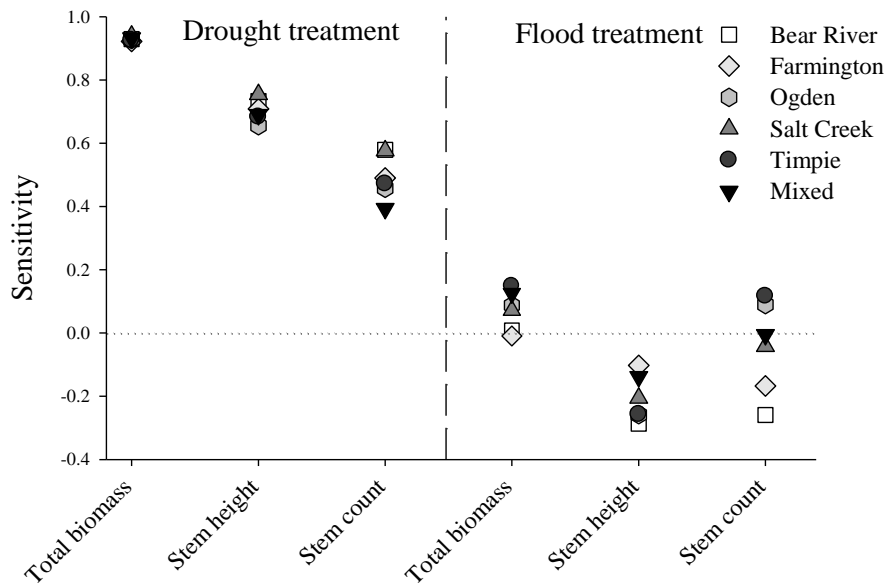


Figure 3.6: Sensitivity of *S. maritimus* total biomass, stem height, and stem count to flooding and drought. Higher values show greater sensitivity to the treatment; lower values show tolerance to treatment (negative values indicate better overall response to the treatment relative to the control).

CHAPTER 4

SUMMARY AND CONCLUSIONS

Revegetation projects in wetlands are challenging due to competing interests for limited water resources and the unpredictable conditions often found at restoration sites (Bohnen and Galatowitsch, 2005). Using seeds from local, genetically diverse sources has been shown to improve revegetation efforts (Vander Mijnsbrugge et al., 2010). However, little information existed on how seed source or diversity might impact restoration success under the extreme hydrologic conditions known to exist in many restoration projects. This thesis was designed to provide information on the ecology and genetics of *Schoenoplectus maritimus* so that future restoration and management actions may be more appropriately executed. Specifically, I examined patterns of population structuring and genetic diversity of *S. maritimus* (Ch 2); and how seed source population, the number source populations, and hydrologic extremes impacted establishment and productivity of seedlings (Ch 3).

My studies described in Chapter 2 on the patterns of population structuring and genetic diversity revealed shallow population structuring, high levels of within-population diversity, and that seed viability was surprisingly high. These results were unexpected given the low level of sexual reproduction thought to occur in established stands of *S. maritimus* (Charpentier et al., 2000) and the geographic barriers to gene flow among the studied populations which could have led to much higher levels of population structuring and lower levels of genetic diversity. I hypothesized that the observed patterns were the result of seed dispersal by birds and disturbance patterns. Past research has

shown that this species can be widely dispersed by waterfowl (Wongsriphuek et al., 2008). And the strong isolation by distance gradient and the patterns of apparent gene flow seen in the individual assignment tests are both indicative of bird dispersal, which would be high among geographically proximal sites and follow migration routes.

In Chapter 3, I discuss possible drivers of the differences in productivity among natural stands of *S. maritimus*, and how seed source population, the number of source populations, and hydrologic extremes impacted establishment and productivity of seedlings. Natural stands of *S. maritimus* experienced drastically different hydrologic conditions and other abiotic conditions and productivity varied greatly among stands. In the greenhouse experiment, we found that drought strongly negatively influenced productivity, seed source population identity impacted seedling establishment, while the number of seed sources had a slight impact on sensitivity to drought.

The results of the research presented here have important implications for the management and restoration of *S. maritimus*-dominated wetlands. First, populations of *S. maritimus* are sufficiently differentiated such that there should be limited translocation of plant materials between populations to conserve historic lineages. Second, restoration practitioners should target source populations in close physical proximity to the proposed restoration area because geographic distance was strongly correlated with genetic distance and no one seed source outperformed others in the greenhouse experiment. Third, water level management is extremely important at all life stages of *S. maritimus* and should be an important consideration in wetland restoration and management in this water-limited region.

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APPENDIX

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